

UNIVERSIDADE FEDERAL DO PARANÁ

CAMILA CRISTINA FERREIRA DA COSTA

EFEITO DOS MICROAMBIENTES SOBRE A ESTRUTURA DA GUILDA DE
ABELHAS E VESPAS QUE NIDIFICAM EM NINHOS-ARMADILHA E SOBRE
SEUS INIMIGOS NATURAIS EM ÁREA DE FLORESTA TROPICAL

CURITIBA

2020

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Orientador: Prof. Dr. Rodrigo Barbosa Gonçalves

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Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em CIÊNCIAS BIOLÓGICAS (ENTOMOLOGIA) da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de CAMILA CRISTINA FERREIRA DA COSTA intitulada: Efeito dos microambientes sobre a estrutura da guilda de abelhas e vespas que nidificam em ninhos-armadilha e em seus inimigos naturais em área de floresta tropical, sob orientação do Prof. Dr. RODRIGO BARBOSA GONÇALVES, que após terem inquirido a autora e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

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Dedico esta tese à minha família
sanguínea e de coração, em especial à
meus pais Tereza e Lourival.

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RESUMO

Microambiente é uma pequena área que difere dos seus arredores em relação a fatores abióticos e bióticos. Florestas tropicais são complexas e as espécies se distribuem em três dimensões espaciais, os gradientes horizontais e o vertical. Como exemplo de variação nas dimensões horizontais, clareiras naturais são locais que devido a maior incidência de luz sofrem alterações climáticas e estas alterações resultam em modificações ambientais e biológicas. Padrões semelhantes ocorrem na estratificação vertical, porém as alterações biológicas são mais acentuadas quando comparadas com as horizontais. Abelhas e vespas solitárias que nidificam em ninhos-armadilha são sensíveis a mudanças ambientais. Por tal motivo, são consideradas bons modelos para estudos ecológicos e de conservação ambiental. Considerando o presente cenário, o principal objetivo deste estudo foi compreender como a guilda de abelhas e vespas solitárias que nidificam em ninhos-armadilha em uma área de floresta tropical variam entre três microambientes (clareira, dossel e sub-bosque). Para responder esta questão o desenho amostral foi feito da seguinte maneira: em uma área de Mata Atlântica localizada na Reserva Guaricica, Paraná, município de Antonina, há dez parcelas amostrais permanentes, em cada um destes pontos foram inseridos três estações de ninhos-armadilha, cada qual representando um microambiente. Cada estação era composta com 20 ninhos-armadilha confeccionados de bambu inseridos dentro de um tubo PCV. As coletas foram feitas mensalmente, com exceção do primeiro verão que foram feitas de 20 em 20 dias. Todos os ninhos finalizados, eram transportados para laboratório e mantidos em câmara de criação até a conclusão do ciclo de vida. A tese se divide em dois capítulos: o capítulo 1 que aborda as respostas da estrutura da guilda aos diferentes microambientes; o capítulo 2 trata das diferenças dos traços biológicos, morfológicos e de arquitetura de ninho de uma espécie de vespa, *Podium* sp.1, nos três microambientes. No total foram coletadas 1037 células de cria correspondentes a dez espécies de vespas e cinco de abelhas. A menor abundância e diversidade foram encontradas no sub-bosque, o que indica que existe uma preferência de nidificação por microambientes com maior incidência solar. A composição de espécies era bastante similar entre os microambientes, uma vez que todas as espécies mais comuns estão amplamente distribuídas, este resultado é contrastante com vários outros existentes na literatura. A taxa de parasitismo foi maior no dossel e possivelmente está relacionada

com a maior disponibilidade de hospedeiros neste microambiente. Em relação aos traços biológicos de *Podium* sp.1 apenas a razão sexual variou entre dossel e sub-bosque (estratificação vertical). Possivelmente este resultado está relacionado com a maior disponibilidade de provisão no sub-bosque, já que as fêmeas desta espécie são muito maiores que os machos e por isso mais custosas para serem produzidas. Este estudo foi pioneiro em vários aspectos, mesmo diante da grande popularidade da metodologia de ninhos-armadilha. O trabalho contribuiu significativamente para o entendimento da estrutura da guilda de abelhas e vespas em relação aos micro-ambientes, além disto, também auxiliou na compreensão da complexidade espacial em uma área de floresta tropical.

Palavras-chave: Guilda, abundância, estratificação vertical, clareiras, história de vida.

ABSTRACT

Micro-environment is considered a small area that differed from its surroundings by abiotic and biotic factors. Tropical forests are complex and species distribution is three-dimensional, they are distributed along the horizontal gradients and along the vertical gradient. For example in horizontal dimensions, gaps are places in understory that it has higher sunlight incidence and there are climate changes. These climate changes cause environments and biologicals alteration. Similar pattern occurs in vertical stratification however biological responses are stronger than on horizontal gradients. Trap-nesting bees and wasps are very sensitive to environmental and ecological changes. Because that they are considered good models for ecological and environments conservation studies. Considering the introduced scenario, the main aim of this study is to investigate how trap-nesting bees and wasps in the tropical forest vary among three micro-environments (gap, canopy and understory). Our sampled design was: in an area of the Atlantic Forest within Reserva Natural Guaricica, in the Paraná State, city of Antonina, in ten permanent plots, three trap-nest stations were installed in all micro-environments. Each trap-nest station consisted of a PVC tube filled with a random mix of 20 bamboos internodes. The stations were inspected every month and except in first summer, they were inspected every 20 days. All completed nests were brought to the laboratory and maintained in a growth chamber until the emerging of adults. This doctoral dissertation has two chapters: the chapter 1 investigates the responses of trap-nesting Hymenoptera guild structure in three micro-environments; the chapter 2 addresses to biological, morphological and nest architecture traits differences in a wasp species, *Podium* sp.1, in three micro-environments. We found 1037 brood cells of the ten wasps species and five bees species. The abundance and diversity were lower in understory, wasps and bees showed preference to nest in micro-environment with higher sunlight intensity. Species composition is similar among micro-environments since almost all of common species were in all environments. This result partiality disagrees with various previous studies. Parasitism rate is larger in canopy and could be correlated with higher resources available. Among biological traits of *Podium* sp.1 only sex ratio varies between canopy and understory (vertical stratification). This result could be explained by the higher prey availability in understory since females this species are bigger than males and more food resources are used to brood cells. This study was pioneer in many aspects even

considering that the trap-nest methodology is very popular. The work brings a significant contribution to understanding of the trap-nesting bees and wasps guild on micro-environments, besides that, about spatial complex in an area of tropical forest.

Key-words: Guild, abundance, vertical stratification, gaps, life history.

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1. INTRODUÇÃO

1.1 HYMENOPTERA

Hymenoptera, a ordem que abriga os insetos popularmente conhecidos como abelhas, vespas e formigas, faz parte das quatro ordens megadiversas de insetos (Manson *et al.*, 2006). O número de espécies descritas é de aproximadamente 153 mil (Grimaldi & Engel, 2005), porém estima-se que este número esteja acima de 1 milhão de espécies (Grimaldi & Engel, 2005; Forbes *et al.*, 2018), o que a tornaria a ordem mais diversa de insetos (Forbes *et al.*, 2018). Estima-se que a diversificação de Hymenoptera se iniciou há aproximadamente 283 milhões de anos, durante o Permiano (Peters *et al.*, 2017).

Além da grande diversidade de espécies, Hymenoptera também se destaca pela grande diversidade morfológica e ecológica; sendo poucas as sinapomorfias compartilhadas em todo o grupo (Manson *et al.*, 2006). Os himenópteros apresentam espécies com variados nichos: fitófagas, parasitoides e predadores (Grimaldi & Engel, 2005; Manson *et al.*, 2006). As fitófagas se alimentam de várias formas, de tecidos vegetais verdes interna e externamente, são brocadores de madeira, indutores de galhas ou utilizam pólen e nectar (Gauld & Bolton, 1988; Grimaldi & Engel, 2005). Os parasitoides e predadores usam uma gama de espécies de artrópodes como hospedeiros e presas. Além disto, os parasitoides apresentam diferentes hábitos, tais como ectoparasitismo (idiobiontes ou cenobiontes), endoparasitismo (cenobiontes) e cleptoparasitismo (Gauld & Bolton, 1988; Manson *et al.*, 2006). Há também diferentes hábitos de vida, variando deste o solitário, o qual pertence a maioria das espécies; o eussocial e outras variações intermediárias (comunais, quasissociais e semissociais) (Grimaldi & Engel, 2005; Manson *et al.*, 2006).

Os Hymenoptera são fundamentais nos ecossistemas terrestres, uma vez que prestam importantes serviços ecossistêmicos; como exemplo, as abelhas são consideradas o grupo de polinizadores mais importante na natureza (Michener, 2007). Ademais vespas também são polinizadores, porém é mais evidente sua função como

predadores e parasitoides, agindo no controle biológico de vários artrópodes (Harris, 1994).

Por mais que os grupos que constroem ninhos sejam os mais populares, dentre os Hymenoptera, apenas Aculeata *s.s* (superfamílias tradicionais Apoidea e Vespoidea) possui este comportamento (Peters *et al.*, 2017; Sann *et al.*, 2018). Aculeata *s.s* também abrigam espécies eussociais, no entanto diferentemente do que se pensa, a maioria das espécies deste grupo é solitária (O'Neill, 2001; Garófalo *et al.*, 2012).

Os ninhos de himenópteros solitários são feitos de diversas maneiras, podem ser escavados no solo ou em material vegetal verde (gramíneas e ramos verdes); expostos ou livres; em cavidades preexistentes no solo, pedras, madeira e caules; ou em outros substratos (construções humanas, conchas de Mollusca, madeira em decomposição) (Gess, 1981; O'Neill, 2001; Sheffield, 2017).

1.2 NINHOS-ARMADILHA

Por volta de 5% das espécies de Aculeata *s.s*. nidificam em cavidades preexistentes na madeira, e para coleta destas espécies podem ser utilizadas cavidades artificiais que são chamadas de ninhos-armadilha (Krombein, 1967). Estas armadilhas podem ser feitas com diversos materiais, os mais comuns são os confeccionados com gomos de bambu, tubos de cartolinas inseridas em uma placa de madeira (Camillo *et al.*, 1995; Araújo *et al.*, 2016) ou blocos de madeira perfurados (Krombein, 1967; Buschini, 2006).

As abelhas e vespas coletadas com ninhos armadilhas são consideradas uma guilda, uma vez que compartilham o mesmo recurso (Wilson, 1999; Costa & Gonçalves, 2019; Costa & Gonçalves em produção), mas formam um grupo monofilético (Wilson, 1999; Peters *et al.*, 2017). São registradas para ninhos-armadilha duas superfamílias (Vespidae e Apoidea), sendo uma das abelhas (Apidae *s.l.*) e outras cinco de vespas (Ampulicidae, Crabronidae *s.l.*, Sphecidae, Vespidae e Pompilidae) (Costa & Gonçalves, 2019; Costa & Gonçalves em produção).

A técnica de ninhos-armadilhas se popularizou no mundo no fim dos anos 60 depois da publicação do livro “Trap-nesting wasps and bees: life histories, nests, and associates” de Krombein (1967). Trabalhos com esta metodologia se tornaram bem

comuns e usados para responder diversas questões ecológicas (Buschini *et al.*, 2007; MacIvor & Packer, 2015; Campbell *et al.*, 2017; Staab *et al.*, 2018), principalmente porque a fauna coletada com ninhos-armadilha é útil para avaliar mudanças ambientais e qualidade ambiental (Tscharntke *et al.*, 1998). Esta metodologia já foi usada com sucesso para responder várias perguntas ecológicas, tais como o impacto da fragmentação florestal, do uso da terra na agricultura, urbanização, entre outros (MacIvor, 2017).

Esta metodologia também tem como característica relevante, além da coleta de informações sobre a estrutura comunidade de vespas e abelhas, a coleta de dados sobre biologia de nidificação, história de vida e interação com inimigos naturais (parasitoides e cleptoparasitas) das espécies amostradas. É um método simples, eficiente e com baixo custo para amostrar as espécies que vivem em determinada área, evitando aquelas que estejam apenas transitando pelo local (Camillo *et al.*, 1995; Tscharntke *et al.*, 1998; MacIvor, 2017), além disto, o método permite padronizar as amostragens (tempo e espaço), desta forma evitando diferenças no esforço amostral (Tscharntke *et al.*, 1998; MacIvor, 2017).

Como qualquer metodologia, a de ninhos-armadilha também apresenta suas limitações e uma delas é número restrito de espécies coletadas. Para região Neotropical em ninhos-armadilha atualmente há 140 espécies de abelhas registradas (Costa & Gonçalves, 2019) e o total são de 5000 (Moure *et al.*, 2007), 42 espécies de vespas Apoidea (Costa & Gonçalves em preparação) e o total são de 1834 espécies (Amarante, 2002). Comparando com outras metodologias utilizadas para coleta de abelhas e vespas como pratos coloridos ou coleta ativa com rede entomológica observamos que os resultados obtidos, principalmente em relação a riqueza de espécies, é várias vezes maior (Krug & Alves-dos-Santos, 2008).

1.3 MICROAMBIENTES (CLAREIRA, DOSSEL E SUB-BOSQUE)

Florestas tropicais são muito heterogêneas e por isso proporcionam ambientes com diferentes características bióticas e abióticas (Basset *et al.*, 2015). Pequenos ambientes como ocos em árvores (Christie *et al.*, 2013), clareiras (Schliemann & Bockheim, 2011), bromélias (Lopez *et al.*, 2011), bordas (Matlack, 1993) podem manter

distintas comunidades de animais e plantas (Matlack, 1993; Schliemann & Bockheim, 2011)

Em florestas tropicais a distribuição de espécies tem três dimensões espaciais, deste modo as espécies ocorrem longo do espaço de forma vertical e horizontal (Basset *et al.*, 2015). Para abordar esta variação, neste estudo são utilizados três microambientes, clareira, dossel e sub-bosque, os quais nos permitem avaliar a estratificação vertical e horizontal do ambiente.

Clareiras são aberturas no dossel, causadas pela queda de árvores ou seus galhos (Whitmore, 1989; Schliemann & Bockheim, 2011). A queda dessas árvores ou suas partes são devido principalmente ao vento, doenças, insetos e fogo (Schliemann & Bockheim, 2011). Clareiras desempenham um importante papel em florestas, principalmente em sucessão tardia, uma vez que, a alteração microclimática, principalmente pelo aumento da luz, está correlacionado com o aumento da diversidade florística (Lorimer & Frelich, 1989; Schliemann & Bockheim, 2011; Chen *et al.*, 2019).

Clareiras naturais abrigam uma maior diversidade de plantas e também uma composição de espécies diferente dos seus arredores (Whitmore, 1989; Schliemann & Bockheim, 2011). Para alguns grupos de animais isso também é observado, por exemplo, em aves (Fuller, 2000; Siri *et al.*, 2019), anfíbios (Horn *et al.*, 2005), répteis (Greenberg, 2001) e insetos (Gorham *et al.*, 2002; Taki *et al.*, 2008). Além das alterações diretas nas comunidades bióticas, as clareiras alteram também a estrutura destes ecossistemas como um todo, causando modificações no solo, ciclo dos nutrientes e microtopografia das florestas (Schliemann & Bockheim, 2011).

As dimensões horizontais em florestas tropicais apresentam uma menor variação na distribuição de espécies e características intraespecíficas por distância, em comparação com a dimensão vertical (Basset *et al.*, 2015; Nice *et al.*, 2019). Dossel e sub-bosque apresentam características abióticas, como luminosidade, umidade e temperatura, muito distintas (Ashton *et al.*, 2015; Basset *et al.*, 2015). Esta distância entre dossel e sub-bosque forma vários estratos ao longo desta distância, uma vez que a variação climática ocorre gradualmente (Allaby & Park, 2013; Nakamura *et al.*, 2017). Desta forma o meio biótico também se sub-divide nestes estratos, formando várias comunidades (Allaby & Park, 2013). Este gradiente de estratos é chamado de estratificação vertical (Allaby & Park, 2013). Em florestas tropicais a estratificação vertical é mais pronunciada do que em outros ecossistemas e é considerada parte

essencial da complexidade espacial e do aumento da biodiversidade nestes ambientes (Gardner *et al.*, 2009; Basset *et al.*, 2015).

A variação vertical nas comunidades já foi registrada para vários grupos de animais, tais como vertebrados e invertebrados. Em vertebrados, como aves (Culbert *et al.*, 2013), anfíbios (Oliveira & Scheffers, 2019), mamíferos (Vieira & Monteiro-Filho, 2003) e invertebrados, como insetos (Basset *et al.*, 2015; Stangler *et al.*, 2016; Weiss *et al.*, 2016) e outros artropódes (Basset *et al.*, 2015). Além das alterações entre espécies nas comunidades, também já foi indicada a variação genética entre populações (Nice *et al.*, 2019).

Mesmo com as dificuldades clássicas para se realizar coletas no dossel, pela dificuldade para alcançá-lo (Nakamura *et al.*, 2017), o conhecimento da guilda de ninhos-armadilha é maior neste microambiente do que em clareiras naturais (Morato, 2001; Taki *et al.*, 2008; Stangler *et al.*, 2016; Torretta & Marrero, 2019). Estudos feitos com abordagem em estratificação vertical com a guilda de abelhas e vespas que nidificam em ninhos-armadilha já foram realizados em diferentes biomas de florestas tropicais (Morato, 2001; Stangler *et al.*, 2016; Torretta & Marrero, 2019). Porém, vários resultados encontrados são controversos entre os estudos, por isso ainda é necessário compreender melhor como este fator afeta este grupo. Em relação ao efeito das clareiras, apenas observações não sistematizadas foram feitas em relação ao tema (Taki *et al.*, 2008; Costa, 2015).

Os três microambientes selecionados neste estudo, como descritos acima possuem diferenças já relatadas na literatura. Como diferenças nos microambientes deste estudo, as clareiras selecionadas mediam no mínimo um metro quadrado, a temperatura máxima era de 25,8°C e a mínima de 24,1°C, a umidade máxima relativa do ar de 72,1% e a mínima de 69,3%. A altura do dossel variava entre 19 metros e 9,1, a temperatura máxima de 25,5°C e a mínima de 24,2°C, umidade máxima de 72,5% e mínima de 69,3%. O sub-bosque tinha temperatura máxima de 25,1°C e mínima de 23,8°C, umidade máxima de 72,1% e mínima de 69,6%.

Desta forma, esta tese configura-se como um estudo da relação da fauna que nidifica em ninhos-armadilhas e seus inimigos naturais em diferentes microambientes. Avaliaremos as diferenças sobre a estrutura da guilda e suas relações com inimigos naturais em três diferentes microambientes (clareira, dossel e sub-bosque) (Capítulo I)

assim como dados de história de vida, estrutura de ninhos e morfologia da espécie mais abundante do estudo (*Podium* sp.1 - Sphecidae) (Capítulo II).

2. OBJETIVOS

2.1 OBJETIVO GERAL

Determinar a composição de espécies e características de estrutura das guildas de abelhas e vespas que nidificam em ninhos-armadilha, assim como também as interações com inimigos naturais em três microambientes (clareira, dossel e sub-bosque).

2.2 OBJETIVOS ESPECÍFICOS

(I) Descrever a abundância de células de cria, diversidade e composição de abelhas e vespas que nidificam em ninhos-armadilha, e as taxas de parasitismo e mortalidade para cada microambiente (Capítulo I).

(II) Descrever a abundância de células de cria, a frequência, a razão sexual, a taxa de mortalidade e a distância intrategular da espécie mais abundante (*Podium* sp.1) para cada microambiente (Capítulo II).

(IV) Verificar se existe alguma resposta dos descritores ao padrão espacial dos pontos de amostragem utilizados (Capítulo I e II).

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CAPÍTULO I

MICRO-ENVIRONMENTS WITH HIGHER INTENSITY OF SUNLIGHT IN ATLANTIC FOREST HAVE MORE ABUNDANCE AND DIVERSITY OF TRAP-NESTING HYMENOPTERA

* formatted for submission to *Ecological entomology*

Abstract 1. Tropical forests are complex three-dimensional environments because they exhibit horizontal and vertical gradients, creating many micro-environments. Treefall gaps and canopy have higher intensity of sunlight, because they are lighter and drier than understory. Environments with higher intensity of sunlight in forest have higher trap-nesting Hymenoptera abundance and richness than environments with lesser intensity of sunlight.

2. Trap-nesting Hymenoptera is key elements in ecosystems and they are sensitive to environmental changes. Despite the use of trap-nest methodology in ecological and conservation studies, there is still many gaps in knowledge about trap-nesting fauna. Our main aim is to investigate the trap-nesting bees and wasps responses to three micro-environments (gap, canopy and understory).

3. The sampling was conducted in 10 permanent plots in an area of the Atlantic Forest; with three trap-nest stations in each one. A trap-nest station is a set of 20 bamboo trap-nests placed inside of a PVC tube. Brood cells abundance, diversity, mortality and parasitism rate on micro-environments, were analyzed using rarefaction curves, ordination and analysis of variance.

4. We found 1037 brood cells from ten wasps species and five bees species. While the lower abundance and diversity is found in understory, abundance and parasitism rates are higher in canopy and these differences are significant between those two micro-environments.

5. Trap-nesting bees and wasps prefer environments with higher intensity of sunlight, such gap and canopy. These micro-environments are more diverse than understory. However, this difference occurs only in abundance and diversity but not in the species composition. Gap guild is not different from canopy and understory, which may be explained through the small dimension of gaps. Parasitism rate is associated with host abundance, the more abundant is micro-environment the higher is the rate.

Key words. Tropical forest, brood cells, parasitism rate, species composition.

INTRODUCTION

Tropical forests are very complex habitats, contributing significantly to global biodiversity (Basset *et al.*, 2012; Weiss *et al.*, 2019). Tropical forests arthropods represent majority terrestrial eukaryote diversity on Earth (Basset *et al.*, 2012, 2015; Weiss *et al.*, 2019). Besides, diversity of arthropod functional groups is also incomparable with any other group (Basset *et al.*, 2012, 2015). A key part of tropical forest spatial complexity is the horizontal (DeVries *et al.*, 1997) and vertical gradients of biodiversity (Basset *et al.*, 2015; Nice *et al.*, 2019).

Species distribution in tropical forests is three-dimensional occurring along the horizontal gradients and the vertical gradient (Basset *et al.*, 2015). The vertical gradient is strongly structured in tropical forests (Basset *et al.*, 2003; Weiss *et al.*, 2019), while horizontal gradient show lesser impacts on micro-environments (Basset *et al.*, 2015; Nice *et al.*, 2019). This contrast between gradients reflects the difference of canopy and understory, specially related to abiotic conditions (Ashton *et al.*, 2015). Various strata are formed along the vertical stratification, each one with different biotics and abiotics characteristics (Richards, 1983). Despite horizontal stratification has less variation than vertical, edges and gaps bring important heterogeneity in horizontal gradient (DeVries *et al.*, 1997; Rocha-Filho *et al.*, 2017; Torretta & Marrero, 2019) and should not neglected.

Gaps play an important role in maintaining plant biodiversity (Saiful & Latiff, 2017), with increasing on diversity and changes on species composition. The same applies to insects, as reported for some groups, such as Auchenorrhyncha (Hemiptera) from American hardwood forests (Gorham *et al.*, 2002), trap-nesting wasps (Hymenoptera) from Canadian forests fragments and crops (Taki *et al.*, 2008) and Brazilian Atlantic forests (Costa, 2015).

Even with canopy sample limitations, mainly due to the limited accessibility in forests (Nakamura *et al.*, 2017), the insect knowledge on canopy is higher than on gaps (Basset *et al.*, 2015; Stangler *et al.*, 2016; Whitworth *et al.*, 2016; De Smedt *et al.*, 2019; Weiss *et al.*, 2019). Despite the evidence of differences on vertical gradient environments, it is not known yet which vertical strata contains the greatest insect biodiversity (Whitworth *et al.*, 2016). This uncertainty is also noticed in trap-nesting Hymenoptera (Morato, 2001; Stangler *et al.*, 2016; Torretta & Marrero, 2019).

Trap-nest Hymenoptera are sensitive to environmental change (Tscharntke *et al.*, 1998). This group offers different ecosystem services, since bees are the most important group of pollinators in the world (Michener, 2007), for both native plants (Ollerton *et al.*, 2011) and crops (Klein *et al.*, 2003), while wasps are predators and parasitoids, frequently used in biological control (Harris, 1994).

Trap-nests are a good tool to study community, ecological interactions and biological information. Because of that, many works address conservation, crops managements and community structure using this method (Tylianakis *et al.*, 2006a; Buschini & Woiski, 2008; Batista Matos *et al.*, 2013; Steckel *et al.*, 2014), but few studies have investigated the trap-nesting Hymenoptera in gaps and vertical stratification (Stangler *et al.*, 2014, 2016; Moure-Oliveira *et al.*, 2017; Torretta & Marrero, 2019).

Considering the presented scenario, the main purpose of this study is to investigate the responses of the trap-nesting Hymenoptera to three micro-environments: gap, canopy and understory. Micro-environment is considered a specific small area in this work, differed from its immediate surroundings by such factors as the light, humidity and temperature (Allaby & Park, 2013). Our hypotheses were the following: (i) trap-nesting Hymenoptera is more abundant and diverse in micro-environments with higher intensity of sunlight (Buschini & Woiski, 2008; Batista-Matos *et al.*, 2013); (ii) mortality rate is higher in understory than in gap and canopy (Stangler *et al.*, 2016); (iii) the parasitism rate is lower in the micro-environment with higher abundance of trap-nesting Hymenoptera (Tylianakis *et al.*, 2006b; Veddeler *et al.*, 2010); (iv) trap-nesting Hymenoptera species composition is different in each micro-environment (Morato, 2001; Stangler *et al.*, 2016).

MATERIALS AND METHODS

STUDY AREA

Trap-nesting Hymenoptera and their parasites were sampled with trap-nest from October 2016 to May 2018 in an area of the Atlantic Forest within Reserva Natural Guaricica (25°19'15"S and 45°42'24"W), in the city of Antonina, Paraná State, southern Brazil. The local climate is humid subtropical (Cfa, Köppen classification), the average

temperature is 22 °C, the average annual rainfall is 2545 mm and the altitude varies from 0 to 600 m (Ferretti & Britez, 2005).

Study area was divided in 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 it we established a subplot with a corridor of 20 × 250 m in the middle of the subplot (Fig. 1).

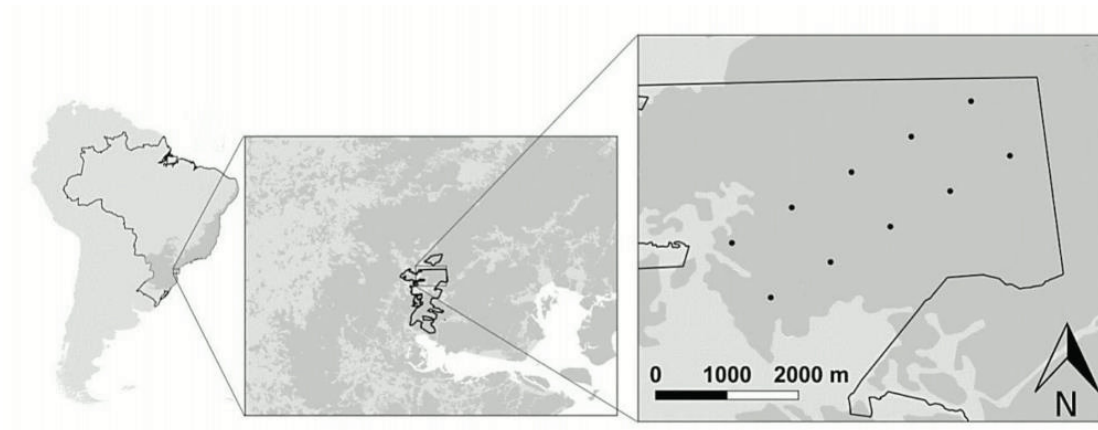


Fig. 1. Map of the study area with highlight to the RAPELD module. Each black point represents a permanent plot (modified from De La Torre, 2018).

SAMPLING DESIGN

In each permanent plot there were three trap-nests stations, a station in understory placed in a tree at approximately 1.5 meters height; other in a gap fixed in a wooden post at 1.5 meters height; and in canopy suspended with nylon thread in a tree (max height 19.0 meters, min height 9.1) (Fig. 2). In the canopy trap-nest stations, we decided to not standardize height among plots, because the trees height strongly varies within the sample area. Each trap-nest station consisted of a modified PVC tube filled with different diameters (0.3 cm – 3 cm) of about 20 bamboo internodes. The bamboos were cut longitudinally in half and then held together with adhesive tape to allow the examination of the cavities.

The stations were inspected every and during each inspection, the traps that contained completed nests, which are easily distinguishable by the characteristic nest-closing plug, were removed and immediately replaced with empty traps of the similar diameter. The nests were then brought to the laboratory and moved to plastic bottles closed with cotton wool. They were maintained in a growth chamber accompanied with the weekly historic temperature mean of Antonina city, 50-75% relative humidity and photoperiod of 12:12 hours to complete the life-cycle (death or emergence of adult).

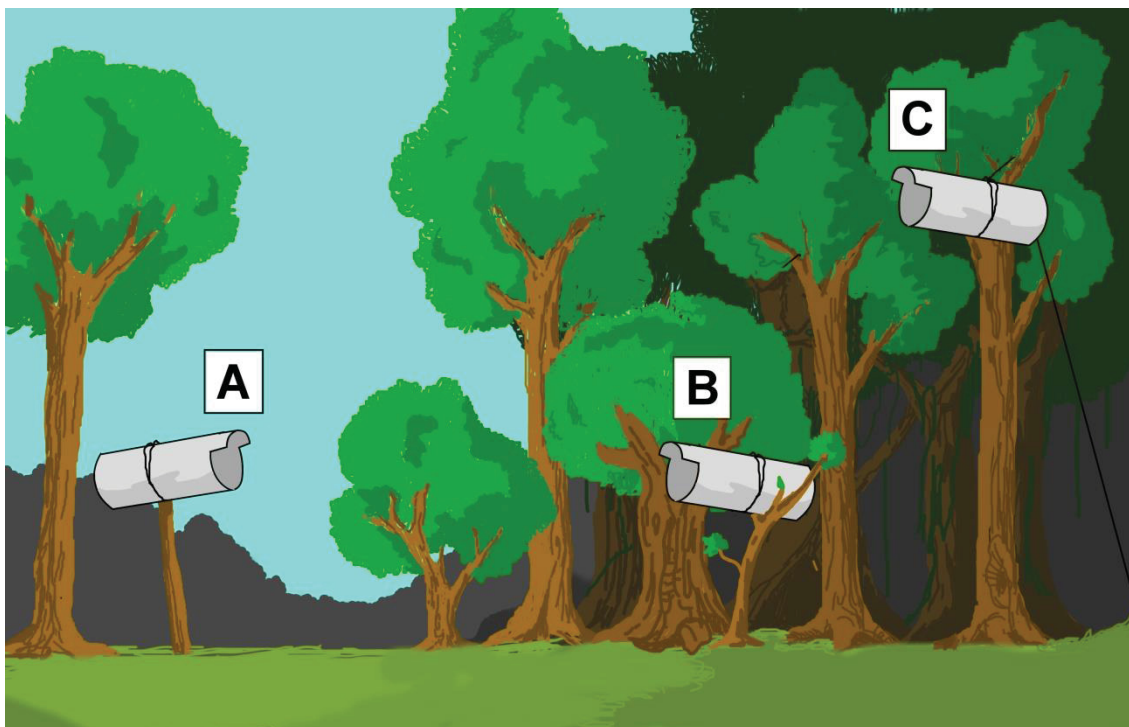


Fig. 2. Overview of the sampling design. Trap-nest stations each one with 20 bamboo internodes. (A) gap, placed in wooden post at 1.5m height; (B) understory, placed in a tree at approximately 1.5 meters height; (C) canopy, suspend with thread in a tree (height between 19.0 and 9.1 meters).

SPECIES IDENTIFICATION

For trap-nesting Hymenoptera, wasps were identified until genus level using the key made by Menke and Fernández (1996) and bees using Silveira *et al.* (2002). Species level determination was carried out by comparison with museum collection and by specialists listed in the acknowledgements section. Voucher specimens were deposited at the Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba (DZUP).

DATA DESCRIPTION

For every nest, we recorded the number of brood, vestibular and intercalary cells. After the adult emergence, we documented the number of dead cells and the number of attacked by natural enemy cells. Value of trap-nesting Hymenoptera abundance is based on the number of brood cells following previous authors (Stangler *et al.* 2016, 2014).

Parasitism rate is the ratio of brood cells per number of parasitized cells and mortality rate is the ratio of brood cells per number of cells where any adult emerged (parasite or host).

STATISTICAL ANALYSIS

We calculated species richness curves for three Hill numbers (0, 1, 2) using the package *iNext* version 2.0.19 (Hsieh *et al.*, 2019) for the three micro-environments. For interpolated curves the endpoint was the lowest observed abundance (65 brood cells), and for extrapolated curves the endpoint was double the highest observed abundance (790 brood cells). The interpolated and extrapolated curves were calculated using individual-based rarefaction curves.

Non-metric multidimensional scaling (nMDS) and analysis of similarity (ANOSIM) were used for testing hypotheses about species abundance differences among micro-environments. These analyses were conducted using Hellinger transformation for reducing the impacts of rare species (Legendre & Gallagher, 2001) and the Bray-Curtis distance based on abundance. The nMDS and ANOSIM were computed using the package *vegan* version 2.5-5 (Oksanen *et al.*, 2019) and the nMDS graphics were plotted using the package *ggord* version 1.0.0 (Beck, 2017). The nMDS ordination was generated only for species sample more than once.

For the following variables: brood cells abundance; richness; Simpson's index; parasitism rate; and mortality rate, we calculated ANOVA one way or Kruskal-Wallis for the factor micro-environments. ANOVA was used for residuals with normal distribution and Kruskal-Wallis for residuals with non-normal distribution. Tukey's contrasts were used for back-comparisons a posteriori.

A Mantel test was conducted to test spatial autocorrelation. The test was based on Pearson correlations, using a distance matrix from geography coordinates (Euclidian)

and abundance of brood cells (Bray-Curtis). We found no spatial autocorrelation (Gap: $r = -0.10$ and $p = 0.66$; Canopy $r = -0.5$ 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).

RESULTS

We found 1037 brood cells of the ten wasps species (Crabronidae and Sphecidae) and five bees species (Apidae) in the three micro-environments (Table 1 and S1). A total of 24.2% of brood cells adults do not emerge and other 16.2% were parasitized (Table 1).

Table 1. Total number of brood cells, wasp and bee species, 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 three micro-environments in Atlantic forest, Brazil.

	Brood cells	Wasps species	Bees species	Mortality rate	Parasitism rate
Gap	386	7	3	19.4%	13.1%
Canopy	543	9	2	22.6%	30%
Understory	108	4	1	30.6%	5.5%
TOTAL	1037	10	5	24.2%	16.2%

DIVERSITY IN MICRO-ENVIRONMENTS

The richness and diversity ($q=0;1;2$: Fig. 3), and abundance (Fig. S2) were lower in understory than in the gap and canopy. About canopy and gap, in canopy richness species ($q=0$) was higher than gap, and Shannon diversity and inverse of Simpson diversity were lower. However the difference is not significantly between canopy and gap, because in all curves ($q=0;1;2$) the confidence intervals overlap. Only understory curve reaches the asymptote (Fig. 3), suggesting that we sampled a substantial proportion of the species present in the area. Extrapolation curves (Fig. S1) have similar results as interpolated curves.

For the frequently species the ordination did not show separation among micro-environments. The common species are shared among the micro-environments and only rare species are specific (Fig. 4; $k=3$, stress =0.077).

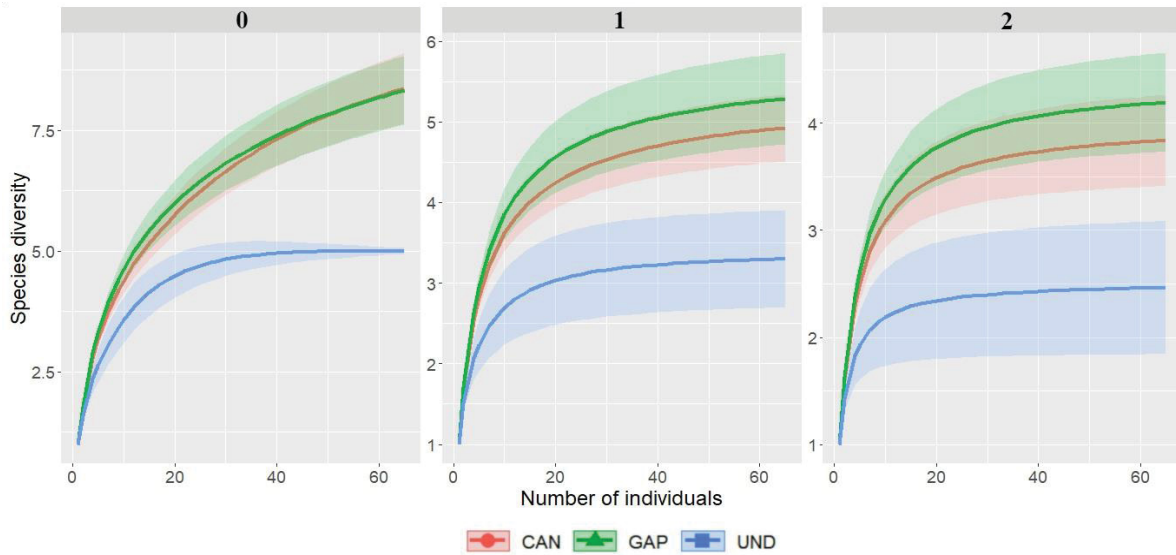


Fig. 3. Interpolation curves of the richness and diversity of trap-nesting Hymenoptera (Atlantic forest, Brazil) in relation to the lowest observed abundance brood cells sampled and assessed for three Hill numbers (0, 1 e 2). CAN= canopy; GAP = gap and UND= understory.

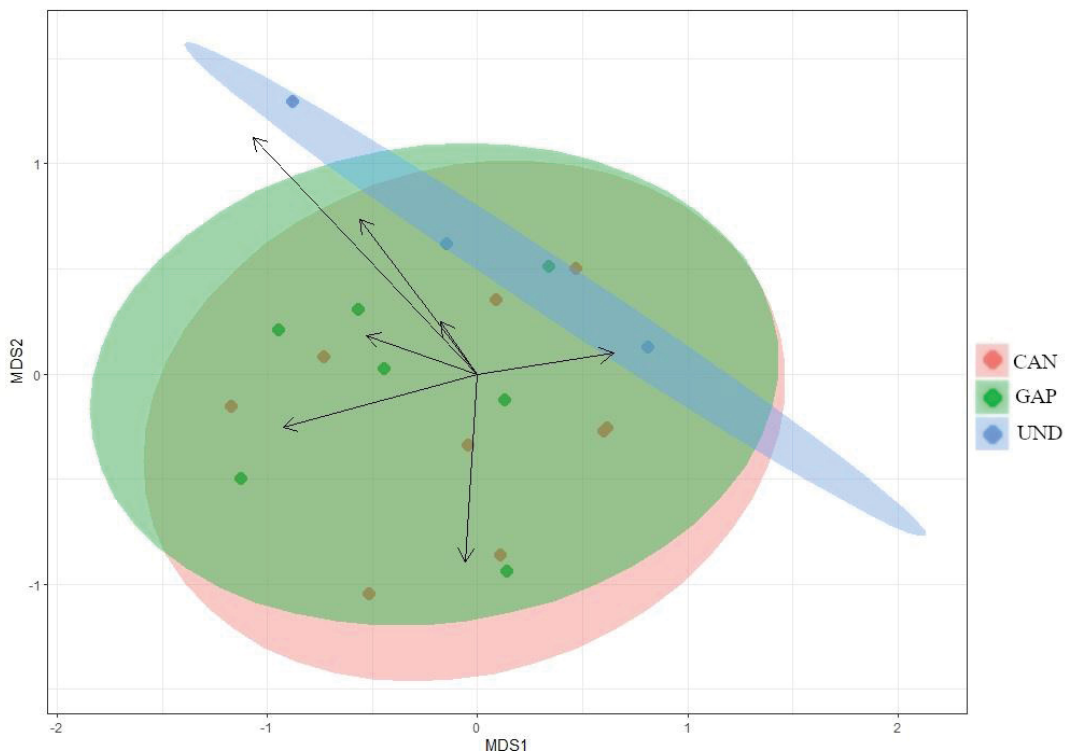


Fig. 4. Non-metric multidimensional scaling (nMDS) ordination for most frequent trap-nesting Hymenoptera species (Atlantic forest, Brazil). Number of dimensions = 3; stress = 0.077. CAN= canopy; GAP = gap and UND= understory.

EFFECTS OF THE MICRO-ENVIRONMENTS

Micro-environments had influence on brood cells and parasitism rate (Table 2). Mortality rates, richness and inverse of Simpson's diversity index don't have influence from micro-environments (Fig. S2, S3 and S4). Tukey test shows that the understory is significantly different from the other micro-environments in relation to brood cells and parasitism rate (Fig. 5 and 6). Gap and canopy are not significantly different.

Table 2. Effects of micro-environment on abundance of brood cells, parasitism and mortality rates, trapping Hymenoptera richness and Simpson's diversity index and parasites richness and Simpson's diversity index.

Response variable	F-statistic ¹ or Chi-squared ²	p-value
Brood cells	4.962 ¹	0.02*
Species richness	1.286 ¹	0.29 <i>ns</i>
Simpson's diversity	3.1964 ²	0.20 <i>ns</i>
Parasitism rate	9.5432 ²	0.008**
Mortality rate	0.0683 ¹	0.93 <i>ns</i>

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

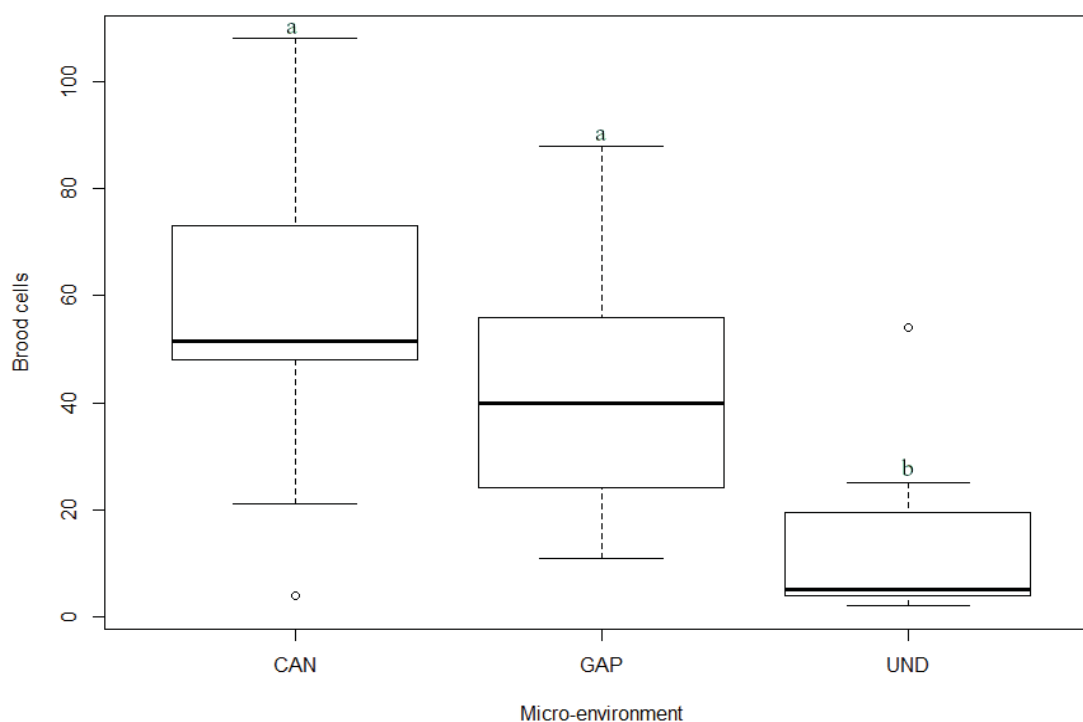


Fig.5. Boxplot and Tukey HSD post-hoc test showing difference on the brood cells among micro-environments. CAN = canopy; GAP = gap and UND = understory.

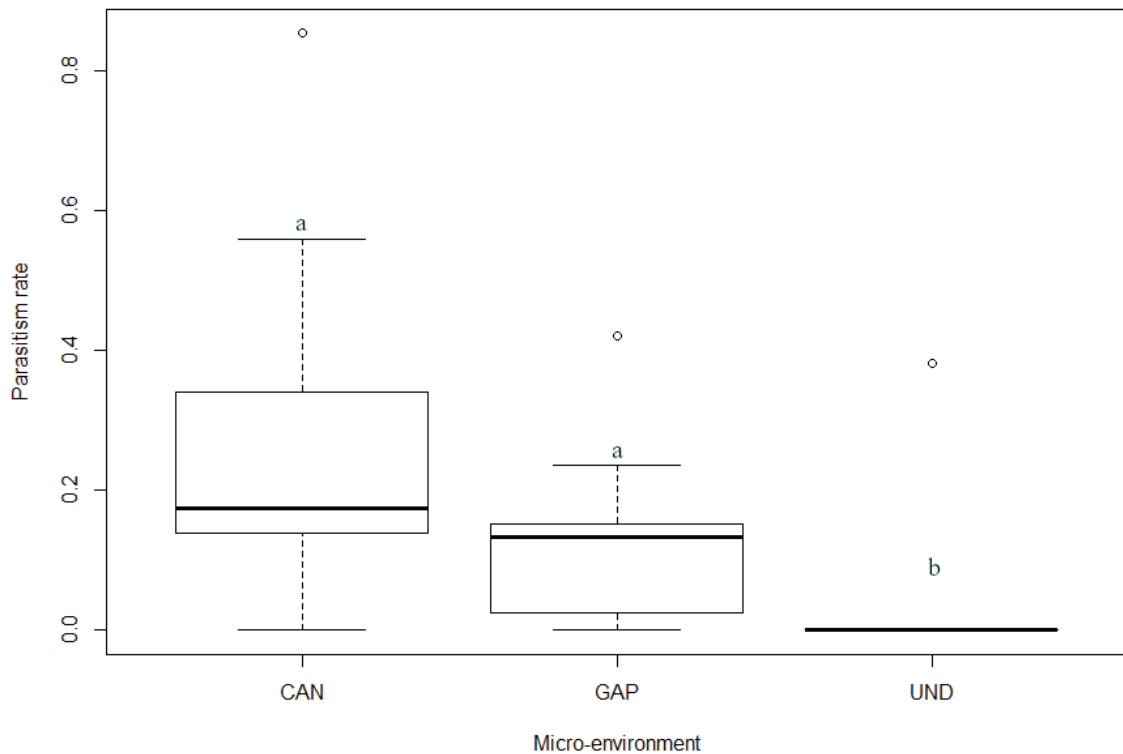


Fig.6. Boxplot and Tukey HSD post-hoc test showing difference on the parasitism rate among micro-environments. CAN = canopy; GAP = gap and UND = understory.

DISCUSSION

We found significant difference in the abundance of trap-nesting Hymenoptera guild between canopy and understory in Atlantic Forest. Similarly, Morato (2001) in tropical rainforests of Brazil and Sobek *et al.* (2009) in temperate deciduous forests, Germany found the higher abundance and diversity in canopy. In contrast, Torretta and Marrero (2019) observed no difference between canopy and understory in riparian forests and savannas, Argentina, while Stangler *et al.* (2016) study showed the higher abundance and diversity in understory, in the Costa Rica, only for bees.

We found that gap and canopy, micro-environments with higher sunlight intensity, they have more abundance and diversity, supporting to our working hypothesis (i). Previous studies in Neotropical region have reported that trap-nesting bees and wasps are more abundant in open and sunnier areas (Morato & Campos, 2000; Buschini, 2006; Buschini & Woiski, 2008; Batista Matos *et al.*, 2013; Stangler *et al.*, 2016). Besides the temperature and humidity, light also could be an important factor due to influences in

visual ability (Warrant *et al.*, 2004). The homing is guided mainly by the vision and it is required the use of visual marks next of the nest to find its entrance (Fauria *et al.*, 2004; Warrant *et al.*, 2004). In this sense, it might be easier to find the nest entrance in micro-environments with more sunlight intensity, such as gap and canopy.

Treefall gaps, one of the key forms of disturbance in closed canopy forest, they are important to maintain diversity and abundance (Shelly, 1988; Schnitzer & Carson, 2001). Gap creates resources heterogeneity in understory to allow for resource partitioning and niche differentiation (Kern *et al.*, 2013; Blonder *et al.*, 2018), and also it releases resources such as light, soil moisture and nutrients that permit the establishment or reproduction of pioneers plant species (Chazdon & Fetcher, 1984; Denslow *et al.*, 1998; Schnitzer & Carson, 2001). Besides of plants, gaps also impact the understory insect community (Gorham *et al.*, 2002; Horn *et al.*, 2005; Richards & Coley, 2007) and trap-nesting wasps and bees guild (Taki *et al.*, 2008; Costa, 2015). This micro-environment affected abundance and richness or change insects species composition (Horn *et al.*, 2005; Richards & Coley, 2007; Taki *et al.*, 2008; Costa, 2015).

Despite, gap was not significantly different from canopy or understory, what may be related with gap dimensions. Sizes of gaps are important because they determine the light levels and consequently the other abiotics factors, such as temperature and humidity (Denslow *et al.*, 1998; Whitmore, 1998). Climate and light intensity could explain Whitmore (1998); small gaps are more similar to understories, while larger than canopies. In this study the three micro-environments have very similar climate, what probably allows the composition and diversity without much variation.

In canopies, dry natural cavities are possibly more abundant due to sunlight exposure whereas higher humidity in understories leads to a higher activity of fungi (Morato & Martins, 2006). Yet many other biotic resources are important in nest activity, as plant abundance and richness (Loyola & Martins, 2008; Batista Matos *et al.*, 2013), food and nest building-material availability (Morato & Martins, 2006). Beyond the presence of these resources, the distance between them and the nesting place is also important (Klein *et al.*, 2004; Morato & Martins, 2006).

The most abundant and rich species is *Podium* sp.1 that occur in all micro-environments. Their nest is built mainly of mud and brood cells are provisioned by cockroaches, both resources are more common in understory than gap and canopy

(Schal & Bell., 1986). Considering the correlation between brood-cell density and foraging time (Klein *et al.*, 2004) It is expected that nests would be more common in areas with more abundant prey. Foraging distance in solitary bees ranges from 100 to 6040 meters (Zurbuchen *et al.*, 2010). Foraging distance is correlated to the intertegular distance for bees (Greenleaf *et al.*, 2007) and probably these mechanisms may also apply for solitary wasps. The most of trap-nesting Hymenoptera sampled in this work is medium size and they can forage around 1000 meters (Zurbuchen *et al.*, 2010), this distance exceed the plot size. Because that we believe which the distance among micro-environments is short for sampled wasps and bees in this study.

Common species are in all micro-environments because composition is very similar. Only rare species as bees of the genus *Megachile* and wasps, *Podium* sp.2, *Trypoxylon* (*Trypoxylon*) sp.1 and *Auplopus pratens* were micro-environment specific, but most were sampled only once. By contrast, other studies reported differences in composition between canopy and understory. In Euglossini bees, species occur only in specific strata, some species are only in understory and others in intermediary height (12 meters) (Oliveira & Campos 1996). According to Stangler *et al.* (2016) and Thiele (2005), *Centris labrosa* Friese, 1899 (Centridini) is also a bee strata specific, since their nests occur just in understory. Morato (2001) found some species more abundant in canopy and others more abundant in understory, but no species is exclusive of a vertical strata. For other insects, as moths and butterflies, species composition were also related to vertical strata (Fermon *et al.*, 2005; De-Smedt *et al.*, 2019).

Trap-nesting Hymenoptera death is caused by multiple causes, including parasitoids and kleptoparasites attack and other unknown factors (Tepedino & Frohlich, 1982; Garcia & Adis, 1993). In this study, we measured death causes by mortality rate (unknown multiple causes) and parasitism rate (natural enemies attack). Authors postulated that the increase on mortality rates are correlated with temperature and humidity (Jesus & Garófalo, 2000; Morato & Martins, 2006; Stangler *et al.*, 2016). Stangler *et al.* (2016) found that mortality rate is higher in understory because wetter conditions help to increase infestations by fungi. Despite these expectations, no significant differences were found 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 & Marrero, 2019). We believe mortality rate is not a good indicator for ecological studies because in most cases we could not identify the

death causes (Tepedino & Frohlich, 1982; Garcia & Adis, 1993). In this sense, it is impossible to correlate mortality with abiotics or biotics factors. Regarding that laboratorial conditions were not equal to those of the field, mortality rate must be interpreted carefully (Torretta & Marrero, 2019).

Parasitism rate is significantly superior in canopy, micro-environment with more abundance, which does not match to our hypothesis (III). Previous studies showed conflicting results: Sobek *et al.* (2009) found the higher parasitism rate in canopy; Stangler *et al.* (2016) in understory; while Torretta & Marrero (2019) observed no difference. Many effects could be related to parasitism, such as host abundance and diversity (Rand *et al.*, 2006; Rocha-Filho *et al.*, 2017), plant diversity (Sobek *et al.*, 2009) and natural enemy abundance and diversity (Tylianakis *et al.*, 2006b; Sobek *et al.*, 2009). Besides higher trophic levels are more sensitive to environmental changes (Klein *et al.*, 2006; Tylianakis *et al.*, 2006b) and because of that they depend indirectly on the same resources of their hosts (Sobek *et al.*, 2009).

In conclusion, we could observe that micro-environments with higher intensity of sunlight have the highest trap-nesting Hymenoptera abundance, richness and diversity. Regarding other ecological variables, we found only few significantly differences among micro-environments, which partly agrees with reported by other studies. However, evaluating the existing knowledge it is noticed that there are many divergences in the trap-nesting Hymenoptera responses, mainly in tropical forest studies. This divergence could be caused by two methodological problems. Firstly most of studies during only two years (MacIvor, 2017) and secondly, the trap-nest protocol usually sampled a few number of individuals and of species. Therefore, we recommend for further studies a more extensive sampling.

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SUPPLEMENTARY MATERIAL

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= GAP; C= Canopy; U= Understory

	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10	
<i>Trypoxylon</i> (<i>Trypoxylon</i>) spn.1	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trypoxylon</i> (<i>Trypargilum</i>) spn. 1	15	0	0	5	0	0	5	6	0	0	0	5	11	0	0	0	0	0	0	0	0	0	5	8	0	0	0	0	0	0	0
<i>Trypoxylon</i> (<i>Trypargilum</i>) <i>agamemnon</i>	18	0	15	44	0	0	6	0	16	0	0	0	0	0	0	0	0	11	7	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trypoxylon</i> (<i>Trypargilum</i>) <i>opacum</i>	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0
<i>Trypoxylon</i> (<i>Trypargilum</i>) <i>nitidum</i>	0	0	0	0	0	0	4	0	0	0	0	0	6	0	0	22	9	23	0	0	0	0	5	0	0	0	0	0	0	0	0
<i>Trypoxylon</i> (<i>Trypargilum</i>) <i>lactitarse</i>	1	0	0	0	37	0	0	0	0	0	73	0	18	7	5	0	9	0	30	0	0	0	0	0	0	0	0	0	0	0	0
<i>Podium</i> sp.1	0	19	32	7	3	0	3	17	0	0	10	43	0	34	20	10	3	0	0	0	0	34	4	0	5	0	0	1	0	3	
<i>Podium</i> sp.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Auplopus basalis</i>	0	0	0	12	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Auplopus pratens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	2	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Euglossa</i> (<i>Glossura</i>) <i>annectans</i>	0	0	3	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

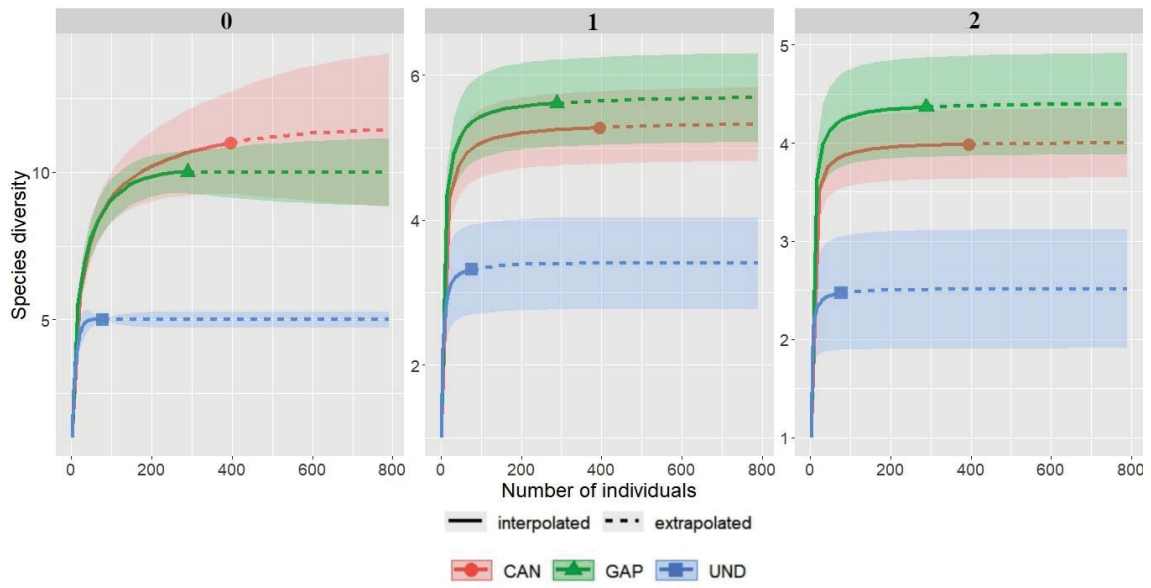


Fig S1. Extrapolation curves of the number of species of trap-nesting Hymenoptera found in relation to the double of the highest observed abundance brood cells sampled asses for three Hill numbers (0, 1 e 2). CAN= canopy; GAP = gap and UND= understory

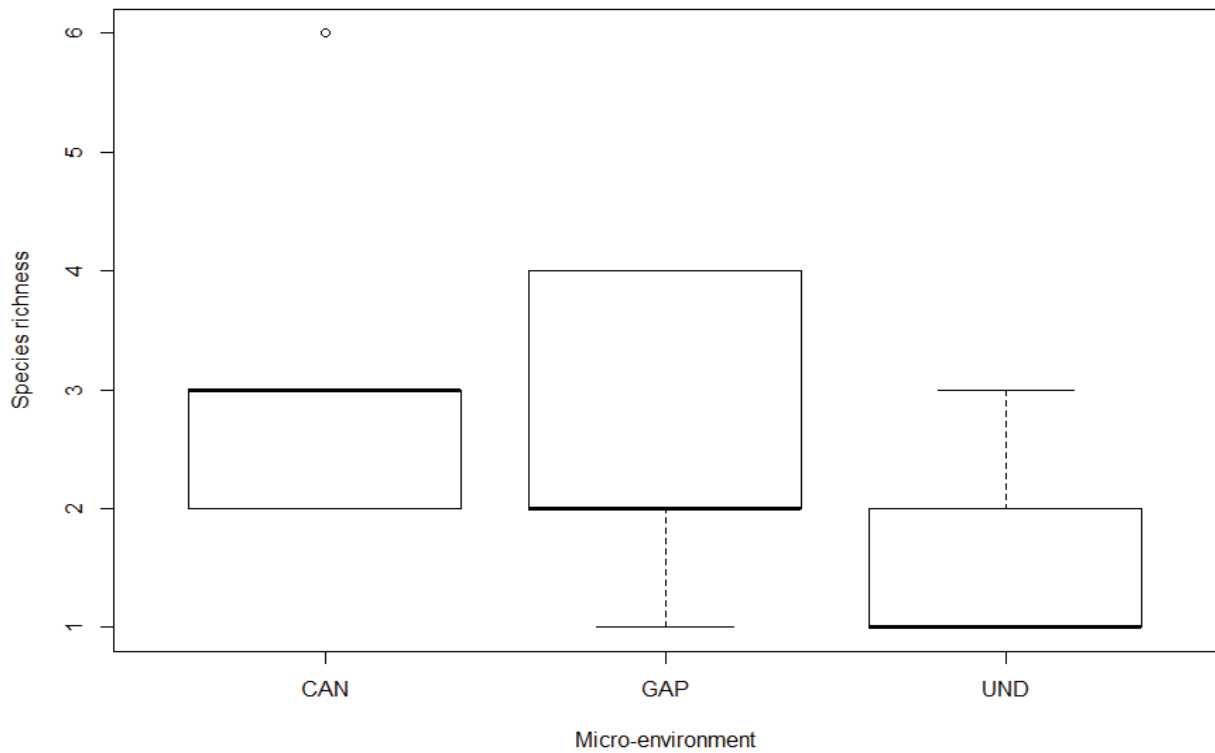


Fig. S2. Micro-environment distribution of species richness. CAN= canopy; GAP = gap and UND= understory.

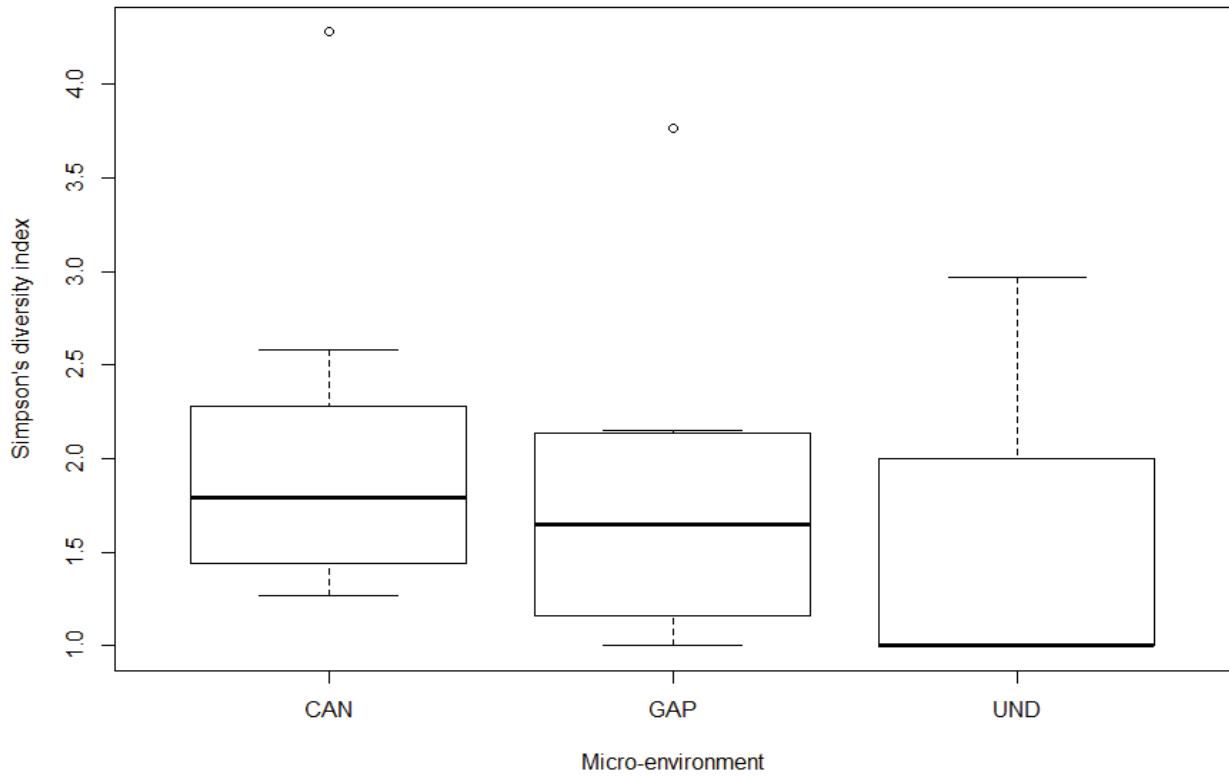


Fig. S3. Micro-environment distribution of Simpson's diversity index. CAN= canopy; GAP = gap and UND= understory.

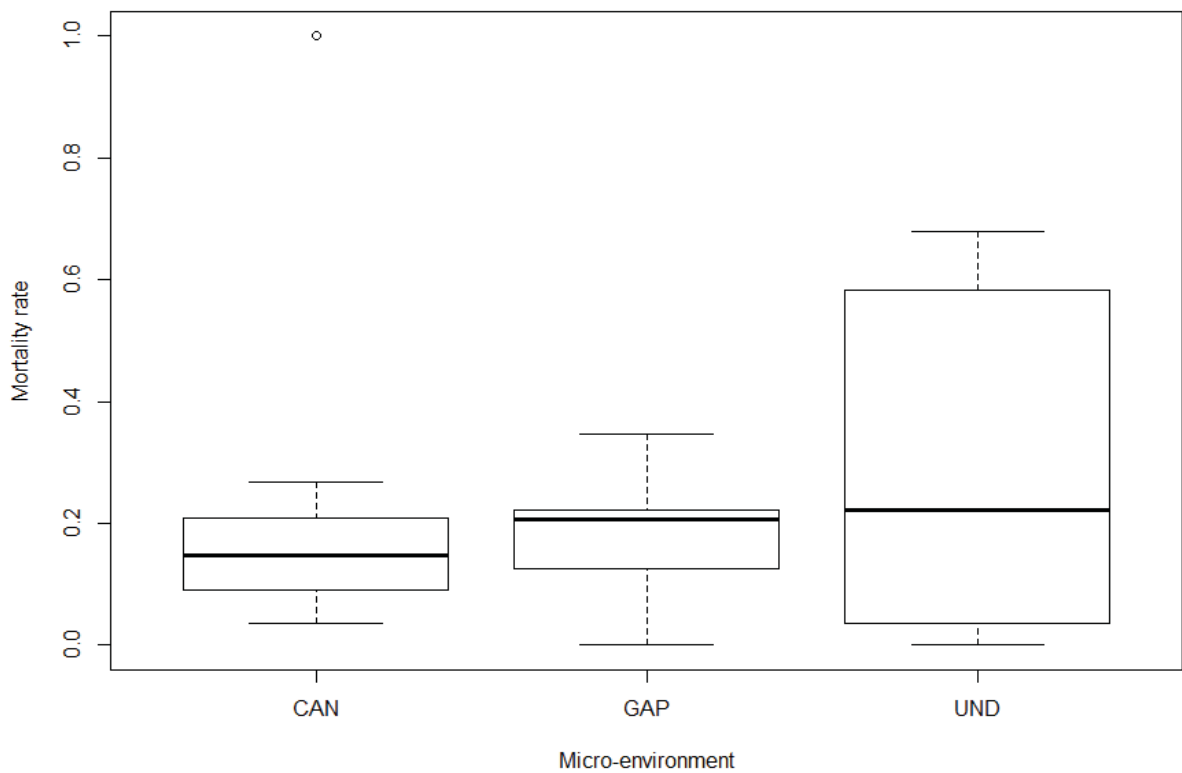


Fig. S4. Micro-environment distribution of mortality rate. CAN= canopy; GAP = gap and UND= understory.

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CAPÍTULO II

WHERE ARE THE GIRLS AND BOYS? VERTICAL DISTRIBUTION OF WASP SEX RATIO IN A BRAZILIAN TROPICAL FOREST

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ABSTRACT

In tropical forests species distribution is three-dimensional. Trap-nesting Hymenoptera fauna is sensitive environmental changes and a good model for ecological studies. The main objective of this study was to analyzed biological and morphological traits of the focal species were driven by micro-environments, these environments vary in three scales; vertical, horizontal or light stratification. We chose *Podium* sp. as focal species. This species is a common and abundant trap-nesting wasp in this region. The sampling was conducted with trap-nest from October 2016 to May 2018 in 10 permanent plots in an area of the Atlantic Forest. The following biological traits: number of broods cells, nesting frequency, mortality rate, female and male intertegular size were analyzed using a general linear model (GLM). Sex ratio varied significantly between canopy and understory, with more females in understory and males in canopy. Possibly this result was correlated with higher prey abundance in understory since female production is costly. Other biological traits tested here did not differ among micro-environments. Most of our predictions were rejected contrasting with information about trap-nesting fauna reported by others studies. This study is pioneer and it is a move to understand variation in population of trap-nesting wasp in vertical and horizontal distribution.

Keywords: Brazilian tropical forest, trap-nesting wasp, vertical stratification, sex ratio.

1. INTRODUCTION

Tropical forests harbor most of the biodiversity of the world [1,2]. A key part of this huge biodiversity is environment heterogeneity, caused by dimensional species distribution [2,3]. We know that species distribution in these landscapes is three-dimensional [2]. However, the mechanisms that cause generates this high species diversity are poorly understood [2,4]. The knowledge of these mechanisms is very important since the anthropogenic deforestation is very fast and we need effective management of conservation [1,3].

Trap-nest technique is used to collect solitary bees and wasps that nesting in pre-existent cavities [5]. This method is popular worldwide and very useful, it enables to sample information about nesting community, their interactions and biological traits (life history, interactions, and nest architecture) [6–8]. Besides that, trap-nesting fauna offers important ecosystem services, bees are the most important pollinator [9,10] and wasps are predator and parasitoids, contributing to the biological control [11,12]. This fauna are sensitive environmental changes and they are used as bio-indicators in many studies [7,13].

Vertical stratification, treefall gaps and edges are factors what change community structure in trap-nesting wasps and bees [14–18]. However, it not only community structure changes , but also population. In population level variation on traits such as male and female size; life span; number of generations; sex ratio; mortality and parasitism rate were observed in trap-nesting wasp species, driven by horizontal stratification [19]. In vertical stratification was observed a huge population genetics differences on butterfly species [20].

Our main objective was to compare biological and morphological traits (nest structure, life history and intertegular size) of the *Podium* sp. in three dimensions; vertical stratification (comparing canopy with understory), horizontal stratification (comparing gap with understory), and light stratification (comparing gap with canopy) in an area of tropical forest.

We predict that (1) This wasp species is more abundant and frequent in one of the scales [14,16]; (2) it has difference in sex ratio among these scales [19]; (3) the mortality rate is higher in the understory than in the canopy due to environmental conditions [14]; (4) it has difference in adult intertegular sizes among scales; (5) it has vertical stratification

in some of analyzed traits; and (6) there are more abundance or frequency in environments with higher intensity of sunlight [17,21].

2. MATERIAL AND METHODS

(a) STUDY AREA AND TRAP-NEST SAMPLING

Sampling was conducted in an Atlantic Forest area within the Reserva Natural Guaricica (25°19'15"S and 45°42'24"W), city of Antonina, southern Brazil. Study area was divided in 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, for more details see Chapter 1).

Wasps and bees were sampled with trap-nest from October 2016 to May 2018. Each trap-nest station consisted of a PVC tube filled random mix of 20 bamboos internodes ranging from 0.3 cm to 3.0 cm in diameter. In each plot were installed three trap-nest stations, each in an environment (gap, canopy and understory). The gap station was fixed in a wooden post at 1.5 meters height; canopy station was suspended with nylon thread in a tree (max height 19.0 meters, min height 9.1 meters); and understory station was placed in a tree at approximately 1.5 meters height.

(b) FOCAL SPECIES

Podium sp. is a common trap-nesting wasp in this region, it was the most abundant species in two studies, here (Chapter I) and in [23] study that was conducted in the same environmental protection area, but in other reserve. The genus *Podium* is a cockroach hunter and build its nest mainly with mud, and closing plug could be covered with resin [25,26].

(c) DATA DESCRIPTION

We considered brood cells as all cells that contained provision, larvae, pupae or dead adult wasp imprisoned. Intertegular size was measured in females and males as a measure of distance between tegulae [24]. For wasps and bees the intertegular distance have been used as a proxy to adult body size [24–26].

The mortality rate was obtained by the ratio between the number of cells without emerged individuals (host and/or parasitic species) per total number of brood cells; parasite rate by number of the parasitized cells per number of the brood cells; and sex ratio by number of females per total of adults emerged.

(d) STATISTICAL ANALYSIS

Analyses were conducted in RStudio 1.1.463 [27]. We tested the effect of vertical, horizontal and light dimensions, micro-environments, elevation and plots using a general linear model (GLM). Statistical significance of model compared to the null model was analyzed using Anova test. Additional details of families of error distribution are describing in Table S1.

3. RESULTS

The following measures: number of broods cells, nesting frequency, mortality rate, female and male intertegular size were lesser in understory than in gaps and canopy (Figure S1, S2, S3, S4, S5). However, all traits mentioned above were not significantly variable among vertical, horizontal and light, stratification (Table 1). Sex ratio is the only trait that was significantly variable, being higher in understory than in canopy. This result showed that vertical stratification effect sex distribution, with more females in understory and males in canopy (Figure 1, table 1). Environments, plots and elevation had no influence traits variation on wasp, only in female intertegular size (Table S2).

Table 1. Effects of vertical, horizontal and light stratification on a trap-nest wasp species nest architecture and life history.

Response variables	Explanatory variables	F value	p value
Brood cells	Vertical stratification	2.624	0.14
	Horizontal stratification	0.926	0.36
	Light stratification	0.63	0.445
Frequency	Vertical stratification	2.223	0.17
	Horizontal stratification	1.608	0.236
	Light stratification	0.037	0.849
Sex ratio	Vertical stratification	24.059	0.0008*
	Horizontal stratification	4.145	0.072
	Light stratification	0.489	0.5
Mortality rate	Vertical stratification	0.717	0.419

	Horizontal stratification	1.818	0.21
	Light stratification	0.581	0.463
	Vertical stratification	0.119	0.73
Female intertegular size	Horizontal stratification	0.0019	0.966
	Light stratification	0.12	0.729
	Vertical stratification	0.023	0.879
Male intertegular size	Horizontal stratification	0.052	0.82
	Light stratification	0.038	0.846

Results derived from independent GLMs. Vertical stratification = Canopy and understory; horizontal stratification = Gap and understory; light stratification = Gaps and canopy.

*p<0,05

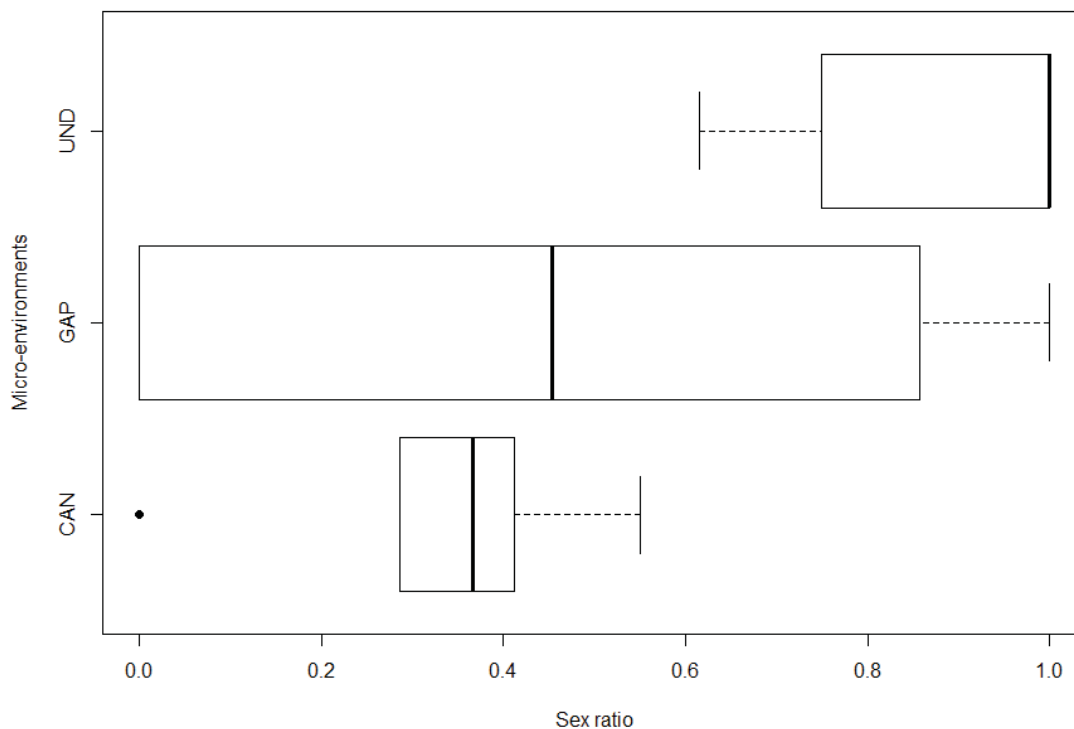


Figure1. Sex ratio in the three micro-environments. UND = understory; GAP = Gap; CAN = Canopy.

4. DISCUSSION

As *Podium* sp. is a cockroach hunter with nest built mainly with mud, and all the nest resources are more common in the understory, because that we expected that the females nesting closer to the ground, however nests were found in all micro-environments in this study and other *Podium* species was report in a variety of vertical stratum in Amazon Forest [15,28].

We found that nests, life history and morphological traits did not significantly vary among vertical, horizontal and light dimensions (disagree with prediction 1, 3, and 4). Mostly of the studies about effects of vertical stratification or environments with

different quantities of light in trap-nesting guild showed difference in abundance (brood cells or nests) and mortality rate among environments, so we expected to behave like this our focal species [15,29,30]. Likewise, as the explanatory variables above; environments, plots and elevation; also did not vary significantly in relation to the biological and morphological traits, except by female intertegular size along plots. However, variation about female size was related neither to the geographical position nor to the stage of forest succession of the plot. The only study about biological and morphological traits among different populations significantly changes [19]. These populations were from different cities (around of 1700 kilometers away) and showed variation in morphological (males and females sizes) and life history (sex ratio, life span, nest season, number of generation per year, mortality rate, parasitism rate) [19]. When individuals are changed of the city they preserve part of the life history and this suggests genetic differences between populations [19].

Only sex ratio varies between canopy and understory (prediction 5). In tropical forest vertical stratification is considered more pronounced than others ecosystems [3,31] and shows more variation than horizontal dimensions [2,20]. Sex distribution, with more females in understory and more males in canopy could be correlated the higher cost to produce females and environment with more resources. *Podium* females are larger than males (Figure 1) and requiring more food to develop [5,32]. Cockroach, prey used as provision, is more abundant and rich in understory (litter) [33], then there are more resource availability for the investment in females [34].

Environments with higher intensity of sunlight influence guild structure of trap-nesting Hymenoptera [17,18,35]. Open and sunnier areas within forests with closed canopy have more abundance and diversity [17,18,35] and it caused by changes on abiotics conditions (microclimate) (Richards, 1983, Marthews et al., 2008), as low humidity and high temperature caused by sunlight [15,33,34].

Most of our predictions were rejected contrasting with information about trap-nesting fauna reported by others studies [15,17,19,30,36]. Indeed, our study is pioneer in understand of the biological traits variation in population of trap-nesting wasp in vertical and horizontal distribution, especially regarding effects of the sunlight. We believe that studies with population genetics and more delimited abiotics variables could show most satisfactory results. Much remains to be learned about what playing

the higher biodiversity in tropical forests [2], as also biological responses of trap-nesting wasps [36].

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(doi:10.1007/s13744-019-00696-3)

SUPPLEMENTARY MATERIAL

Table S1. The families used in the analysis distribution of residual data.

Model	Family
Brood cells~Environments*	Gaussian
Brood cells~Elevation *	Gaussian
Brood cells~Plots*	Gaussian
Brood cells~Vertical stratification*	Gaussian
Brood cells~Horizontal stratification*	Gaussian
Brood cells~Light stratification	Gaussian
Frequency~Environments	Poisson
Frequency~Elevation	Poisson
Frequency~Plots	Poisson
Frequency~Vertical stratification	Poisson
Frequency~Horizontal stratification	Poisson
Frequency~ Light stratification *	Gaussian
Sex ratio~Environments	Binomial
Sex ratio~Elevation	Binomial
Sex ratio~Plots	Binomial
Sex ratio~Vertical stratification*	Gaussian
Sex ratio~Horizontal stratification	Binomial
Sex ratio~ Light stratification	Gaussian
Mortality rate~Environments	Binomial
Mortality rate~Elevation	Binomial
Mortality rate~Plots	Binomial
Mortality rate~Vertical stratification	Gaussian
Mortality rate~Horizontal stratification	Binomial
Mortality rate~Light stratification *	Gaussian
IS female~Environments	Gaussian
IS female~Elevation	Gaussian
IS female~Plots	Gaussian
IS female~Vertical stratification	Gaussian
IS female~Horizontal stratification	Gaussian
IS female~ Light stratification	Gaussian
IS male~Environments	Gaussian
IS male~Elevation	Gaussian
IS male~Plots	Gaussian
IS male~Vertical stratification	Poisson
IS male~Horizontal stratification*	Gaussian
IS male~ Light stratification	Gaussian

*log transformed

IS= Intertegular size

Table S2. Effects of environments, elevation and plots on a trap-nest wasp species nest architecture and life history.

Response variables	Explanatory variables	F value	p value
Brood cells	Environments	1.39	0.281
	Elevation	0.199	0.661
	Plots	1.1	0.45
Frequency	Environments	1.13	0.35
	Elevation	0.41	0.531
	Plots	0.849	0.589
Sex ratio	Environments	4.836	0.025*
	Elevation	0.000	0.98
	Plots	2.790	0.084
Mortality rate	Environments	1.208	0.328
	Elevation	1.819	0.197
	Plots	1.401	0.322
Intertegular size female	Environments	0.083	0.920
	Elevation	0.317	0.574
	Plots	3.460	0.004*
Intertegular size male	Environments	0.04	0,96
	Elevation	0.518	0.819
	Plots	0.6	0.729

Results derived from independent GLMs.

* $p < 0,05$

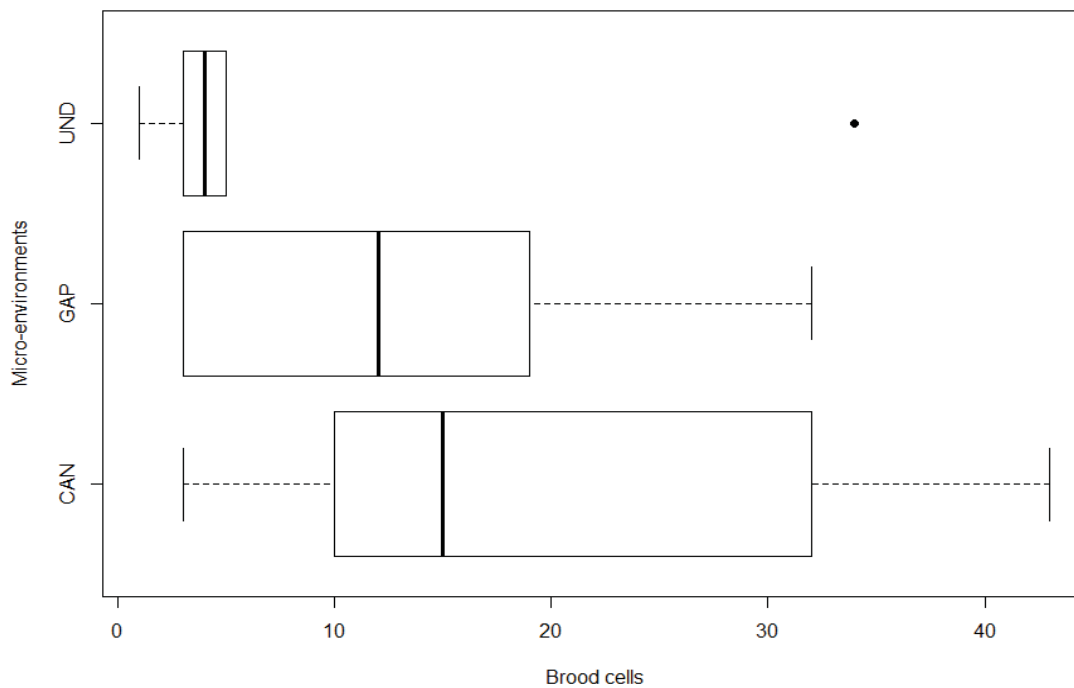


Figure S1. Brood cells in the three micro-environments. UND = understory; GAP = Gap; CAN = Canopy.

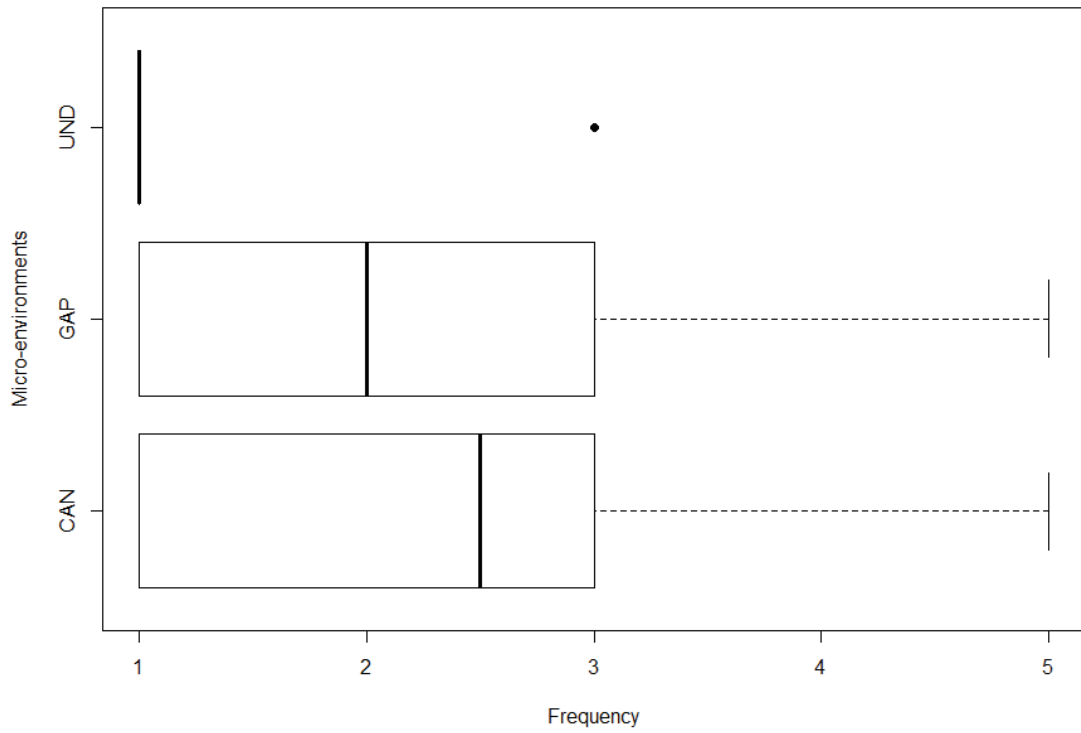


Figure S2. Frequency in the three micro-environments. UND = understory; GAP = Gap; CAN = Canopy.

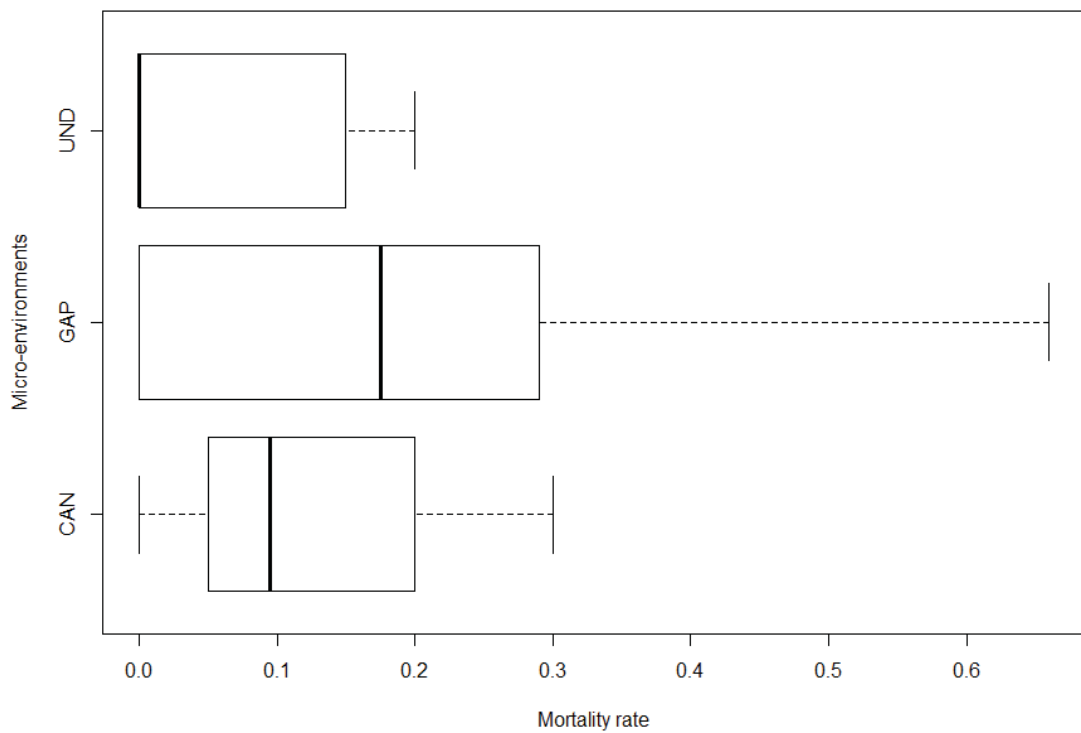


Figure S3. Mortality rate in the three micro-environments. UND = understory; GAP = Gap; CAN = Canopy.

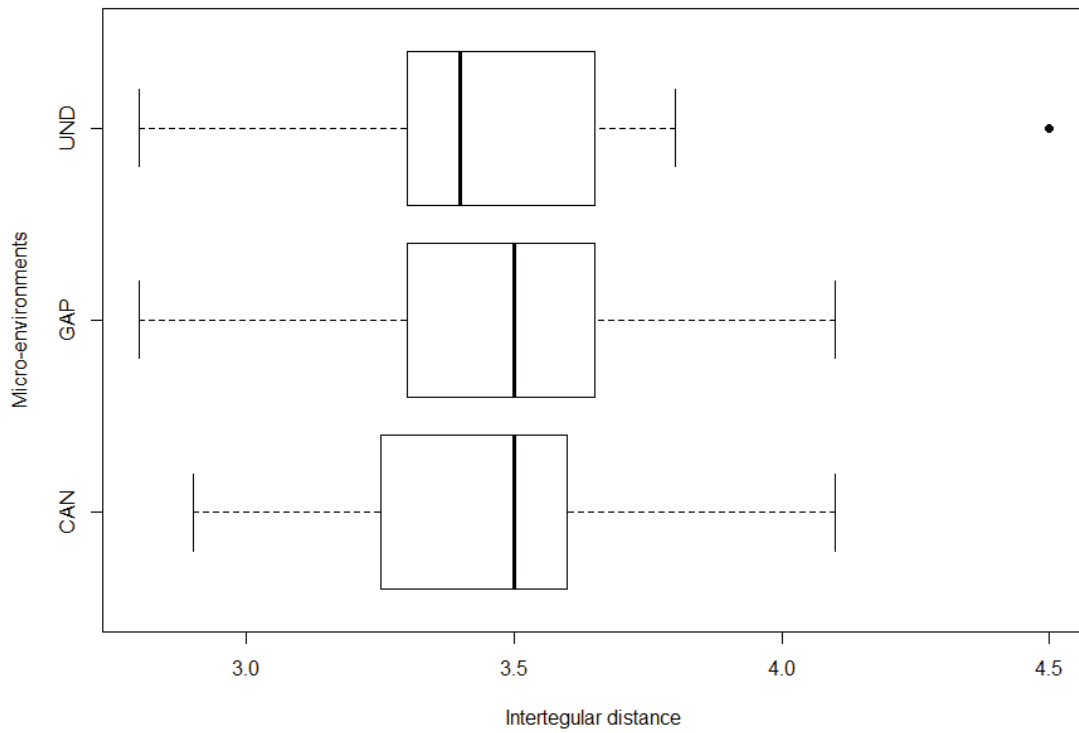


Figure S4. Female intertegral distance in the three micro-environments. UND = understory; GAP = Gap; CAN = Canopy. Intertegular distance in mm.

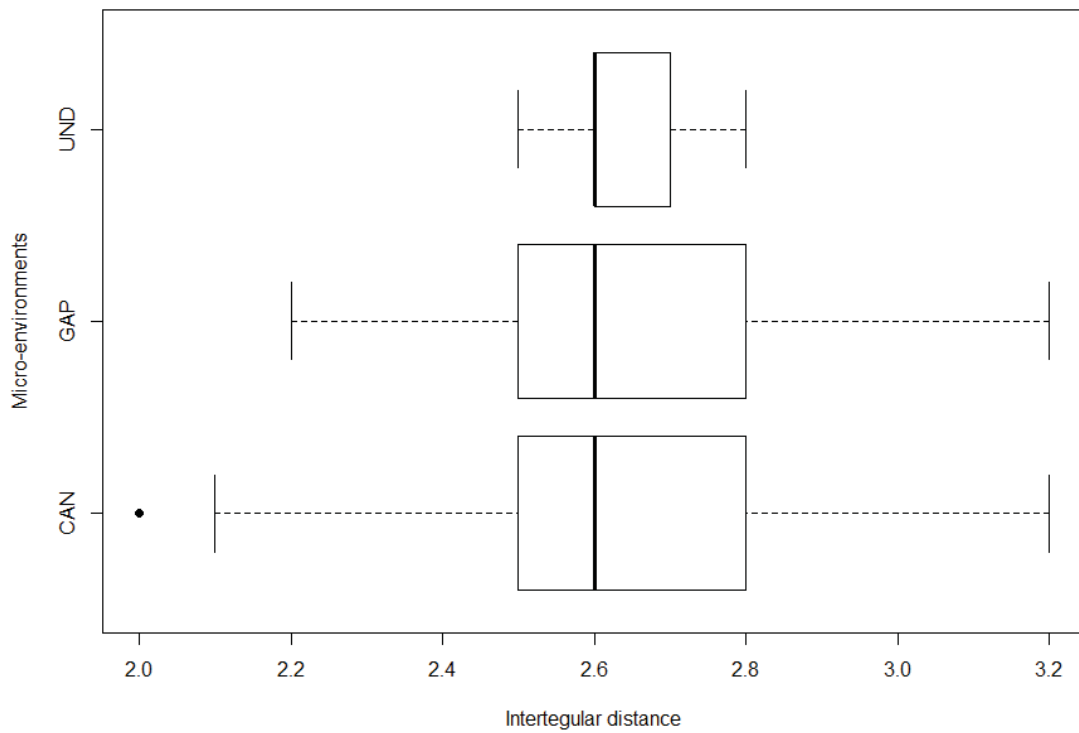


Figure S5. Male intertegral distance in the three micro-environments. UND = understory; GAP = Gap; CAN = Canopy. Intertegular distance in mm.

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CONSIDERAÇÕES FINAIS

O presente trabalho contribuiu para o entendimento de como a estrutura da guilda de abelhas e vespas que nidificam em ninhos-armadilha e em sua taxa de parasitismo e mortalidade varia entre os microambientes em floresta. Além disto, o estudo auxiliou também na compreensão da complexidade espacial em uma área de floresta tropical, a qual é um fator importante na manutenção da biodiversidade.

O entendimento dos mecanismos citados acima são importantes para embasar futuros projetos com enfoque em conservação ambiental por dois motivos. Primeiro, a fauna de ninhos-armadilha é considerada um bioindicador e é utilizada em muitos trabalhos com finalidades ecológicas, no entanto, muitas vezes as respostas obtidas são contraditórias ou incertas, principalmente em áreas tropicais e subtropicais. Por isso, o conhecimento do microambiente nos elucida várias questões ecológicas, principalmente o quão sensível às mudanças ambientais é este grupo de himenópteros, facilitando assim a compreensão em macroescalas. Segundo motivo é o entendimento da complexidade existente nas florestas tropicais e dos fatores geradores de biodiversidade, o que poderá subsidiar melhores propostas de manejo florestal, principalmente para a Mata Atlântica que é um dos biomas mais ameaçados do mundo.

Os microambientes mais ensolarados apresentaram um maior abundância e diversidade, tanto nos nidificantes, como na taxa de parasitismo. Porém não houve tanta distinção entre a estrutura da guilda entre os microambientes. Em relação a composição, muitas espécies eram compartilhadas entre os microambientes, sendo que apenas espécies raras com frequência baixa eram específicas.

Analisando traços de arquitetura de ninhos, história de vida e morfologia de *Podium* sp.1, que foi a espécie mais abundante e frequente do estudo, apenas a razão sexual é significativamente distinta entre os microambientes. Ademais, os traços biológicos não variaram em nenhum das escalas espaciais observadas, o que mostra haver uma grande dispersão da população na área.

Por fim, como panorama sabemos que áreas com maior intensidade de luz solar afetam a estrutura desta guilda em florestas com dossel fechado, porém não se sabe quais fatores microclimáticos afetam propriamente as abelhas e vespas, tais como umidade; luz ou temperatura. Além disto, sabemos que apesar da área de forrageamento das espécies ser ampla, existe uma fidelidade no local de construção dos ninhos. Neste

sentido, estudos genéticos poderiam explicar quanto isoladas ou não estão as populações.

Este trabalho é pioneiro, primeiramente no estudo do efeito de clareiras em himenópteros e também na utilização de dados biológicos desta mesma fauna para responder questões em relação ao microambiente. E exatamente por este motivo, alguns aspectos não puderam ser tão aprofundados pela falta de informação na literatura. No entanto, para suprir esta lacuna tentei utilizar referências correlatas, como sobre a estrutura de comunidades da fauna de ninho-armadilha ou trabalhos sobre outros grupos de insetos com objetivos semelhantes, além da minha experiência na área que tem enfoque no entendimento da biologia de abelhas e vespas solitárias. Mesmo com essa dificuldade, pudemos compreender padrões sobre a comunidade e responder a maioria das questões propostas deste projeto de doutorado.

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