UNIVERSIDADE ESTADUAL DO MARANHÃO
CENTRO DE CIÊNCIAS AGRÁRIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM AGROECOLOGIA
CURSO DE DOUTORADO EM AGROECOLOGIA

COMPOSIÇÃO DA COMUNIDADE DE VESPAS E ABELHAS SOLITÁRIAS EM VEGETAÇÃO DE RESTINGA DE SERGIPE

DANÚBIA MARIA DA COSTA

SÃO LUÍS - MA

2019

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Tese apresentada ao Programa de Pós-Graduação em Agroecologia da Universidade Estadual do Maranhão, para a obtenção do título de doutora em Agroecologia.

Orientador: Prof. Dr. Adenir Vieira Teodoro

Co-orientadora: Dra. Michela Costa Batista

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2019

Costa, Danúbia Maria da.
Composição da comunidade de vespas e abelhas solitárias em vegetação de restinga de Sergipe / Danúbia Maria da Costa. – São Luís, 2020.

88 f

Tese (Doutorado) – Curso de Agroecologia, Universidade Estadual do Maranhão, 2020.

Orientador: Prof. Dr. Adenir Vieira Teodoro.

1.Ninhos-armadilha. 2.Controle biológico natural. 3.Polinizadores. 4.Mata Atlântica. I.Título

CDU: 632.937(813.7)

Elaborado por Giselle Frazão Tavares - CRB 13/665

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Tese defendida e aprovada em 26 /09 /2019

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2019

O conhecimento emerge apenas através da invenção e reinvenção, através da inquietante, impaciente, contínua e esperançosa investigação que os seres humanos buscam no mundo, com o mundo e uns com os outros.

Paulo Freire

Dedico

Aos meu familiares, em especial aos meus pais Gláucia e Antônio, aos meus irmãos Henrique e Mariana e minha cunhada Fabíola por todo apoio.

AGRADECIMENTOS

Agradeço primeiramente à minha família, aos meus pais Gláucia e Antônio, aos meus irmãos Henrique e Mariana e minha cunhada Fabíola por todo o apoio e compreensão pela ausência e distância.

Ao Profº. Drº. Adenir Vieira Teodoro pela orientação, ensinamentos, confiança, disposição e paciência. À Dr.ª Michela Costa Batista pela co-orientação, ensinamentos disposição e paciência. Ao Dr.º José Guedes Sena Filho, por toda contribuição, motivação e ensinamentos.

Aos técnicos responsáveis pela RPPN do Caju Sr. Erivaldo e Cleverson por todo auxílio no trabalho de campo, disponibilidade e paciência.

Aos amigos do laboratório de Entomologia da Embrapa Tabuleiros Costeiros, Shênia, Clézia, Adriano, Amaury, Luís, Vanessa, Gisele, Alex, Igor, Eliana, Mariana, Jacilene, Taynara, Dalton, Ruan, e em especial Carol e Flaviana (que cuidaram de mim), Tatiana, Marina e Adriele (Laboratório de Genética) pela amizade, risadas, companheirismo, paciência.

Aos amigos de longa data Juliana, Michele, Bruna, João Paulo e Flávio (primos) Laércio, Jéssica, e aos novos Júnior, Mayane e Netinho que mesmo à distância continuam presentes.

Aos colegas, professores e funcionários do curso de Pós-Graduação em Agroecologia da Universidade Estadual do Maranhão.

À Rayanne que que por incontáveis vezes salvou minha vida junto à coordenação do Programa de Pós-Graduação.

Ao Programa de Pós-Graduação em Agroecologia da UEMA e à Embrapa Tabuleiros Costeiros pela oportunidade de desenvolver a pesquisa, à CAPES pela concessão da bolsa.

À todas as pessoas que de forma direta e indireta contribuíram para a realização deste trabalho, gratidão.

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RESUMO

Abelhas e vespas solitárias são himenópteros que nidifcam em cavidades pré-existentes em ambientes naturais, exercem um papel chave no funcionamento dos ecossistemas promovendo serviços ambientais como, polinização e controle biológico natural. O objetivo do estudo foi avaliar a composição da comunidade de abelhas e vespas solitárias em vegetação de restinga, e determinar como as condições climáticas influenciam na nidificação em restinga da Reserva Particular do Patrimônio Natural do Caju (RPPN). Usamos ninhos-armadilha para a coleta de ninhos e as avaliações foram mensais no período de dois anos. Foram coletados 735 ninhos de 4 espécies de abelhas e 15 de vespas. A nidificação ocorreu principalmente em áreas abertas durante a estação seca, reduzindo na estação chuvosa. A composição de espécies diferiu entre área aberta e vegetação secundária, e no geral, a contribuição dos componentes da beta diversidade (turnover e aninhamento) foi similar entre os tipos de vegetação, no entanto, na estação seca o turnover foi maior em vegetação secundária e arbustiva. Por outro lado, vegetação arbustiva foi completamente aninhada à área aberta em ambas estações e o turnover foi o principal responsável pela beta diversidade ao longo do tempo. Além disso, nós avaliamos como as condições climáticas, o tipo de vegetação e o estrato arbóreo influenciam na nidificação pela abelha *Centris tarsata* . A nidificação foi maior durante a estação seca, em áreas abertas a 1.5m de altura. No entanto, em vegetação arbustiva e secundária a nidificação parece ser favorecida por uma variação específica de temperatura e pluviosidade. Além disso, a quantidade de células de cria, adultos e comprimento de ninho foram maiores em áreas abertas que outros tipos de vegetação. Os resultados sugerem que abelhas e vespas solitárias respondem diretamente às condições climáticas e preferem nidificar em locais com grandes quantidades de recursos como material de construção dos ninhos e alimento para as crias.

Palavras-chave: ninhos-armadilha, controle biológico natural, polinizadores, Mata Atlântica.

ABSTRACT

Cavity-nesting bees and wasps are himenopterans that nest in pre-existing cavities in natural environments, and play a key role in ecosystem functioning providing environmental services such as pollination, and biological control. Here, we aimed at assessing the species composition of cavity-nesting bee and wasp community in restinga vegetation, and determine how climatic conditions influence nesting and assembly composition in restinga vegetation from Reserva Particular do Patrimônio Natural do Caju (RPPN). We used trap-nests and evaluations were conducted monthly over two years. We collected 735 nests from 4 bee species and 14 wasp species. Mostly nesting occurred in open areas during dry season, and decreased in the rainy season. The species composition differed for open areas and secondary vegetation, overall, contribution of beta diversity components turnover and nestedness was similar between vegetation types, but, in the dry season turnover was higher in secondary and shrubby vegetation. Conversely, shrubby vegetation was completely nested to open areas in both seasons and turnover was the main responsible for beta diversity over the time. In addition, we assessed how climatic conditions, vegetation type and arboreal strata influence *Centris tarsata* nesting, the most abundant bee species in RPPN do Caju. Overall, nesting was higher during the dry season, mostly in open areas at 1.5m height. However, in shrubby and secondary vegetations nesting seems to be favored by a specific rainfall and temperature range. Furthermore, the amount of brood cells, total number of adults and nest length were higher in open areas than other vegetation types. The results suggest that bees and wasps respond directly to climate conditions, and these arthropds show preference for nesting in places with greater resource availability such as building materials and food for their offspring.

Keywords: trap-nests, natural biological control, pollinators, Atlantic Rainforest.

CAPÍTULO 1

Referencial teórico

1 - REFERENCIAL TEÓRICO

1.1 - Vegetação de restinga

A Mata Atlântica já foi uma das maiores florestas tropicais das Américas, originalmente cobriu cerca de 150 milhões de hectares em condições ambientais altamente heterogêneas. Extende do Rio Grande do Norte ao Rio Grande do Sul por todas as formações florestais ao longo da costa brasileira (LANDIM & SANTOS, 2001). No Brasil, apesar da constante exploração, por mais de 500 anos ainda abriga uma alta biodiversidade (RIBEIRO *et al.*, 2009; ROCHA-FILHO *et al.*, 2017). Dentro deste bioma está inserido o ecossistema de restinga, o qual é considerado como uma vegetação de regiões costeiras tropicais e subtropicais que cresce em planícies arenosas sob influência marinha. No entanto, esse ecossistema está em constante ameaça devido à expansão urbana e especulação imobiliária (NOGUEIRA JUNIOR, *et al*, 2013; OLIVEIRA & LANDIM, 2014; SERRA *et al.*, 2016).

A composição florística das restingas ao longo do litoral brasileiro é altamente variável, tanto em escala regional quanto local. Os diferentes tipos de vegetação variam desde formações herbáceas, passando por formações arbustivas abertas ou fechadas, chegando a florestas, cujo dossel varia em altura, geralmente não ultrapassando 20m (SILVA, 2000).

As formações herbáceas ocorrem nas faixas de praia e locais que podem ser atingidos pelas marés mais altas ou depressões alagáveis. Nestas, predominam espécies herbáceas, em alguns casos com pequenos arbustos e árvores que podem ocorrer de forma isolada ou formando agrupamentos mais densos, com variações fisionômicas, composição e graus de cobertura (SILVA, 2000). Formações arbustivas são os tipos fisionômicos que mais chamam atenção, variando desde densos emaranhados de arbustos misturados (trepadeiras, bromélias terrícolas e cactáceas) a moitas com extensão e altura variáveis, intercaladas por áreas abertas expondo diretamente a areia que forma o substrato (ZICKEL *et al.*, 2004).

Já as formações florestais variam ao longo de toda a costa, tanto em aspectos florísticos como estruturais, sendo inflenciadas pela vegetação adjacente e pelas características do substrato (origem, composição e condições de drenagem). Esse tipo de vegetação a altura do estrato superior pode variar de 15 a 20m de altura (SILVA, 2000).

1.2 - A Reserva Particular do Patrimônio Natural (RPPN) do Caju

A Reserva Particular do Patrimônio Natural (RPPN) do Caju é uma Unidade de Conservação pertencente à Embrapa Tabuleiros Costeiros criada em 17 de janeiro de 2011, era uma antiga propriedade conhecida regionalmente como Fazenda do Caju. Atualmente, são realizadas atividades de pesquisas científicas, visitas de educação ambiental e atividades com comunidades ao entorno. A RRPN do Caju está localizada no município de Itaporanga D'Ajuda (11°06'16.19"S; 37°11'05.89"O) a 29 km de Aracaju - SE, abrangendo uma área de 763,37 hectares, sendo 416,08 de zona de proteção (Figura 1). O clima da região é tropical com verão seco, estação chuvosa no outono e precipitação acima de 1.250 mm^3. O bioma em que está inserida é o de Mata Atlântica, em seu interior são encontrados apicuns (áreas sem vegetação com substrato de areia que recebem influência direta do regime de marés), mangue e vegetação de restinga em mosaico. O relevo é predominantemente plano com pequenas áreas onduladas, solos arenosos e baixa fertilidade natural (NOGUEIRA JUNIOR *et al.*, 2013).

A vegetação de restinga da RPPN do Caju pode ser caracterizada em três tipos:

Vegetação de área aberta - incidência direta de luz solar, presença de vegetação herbácea, predominância de gramíneas como o capim-gengibre (*Paspalum maritimum* Trind), plantas herbáceas, o cacto coroa-de-frade (*Melocactus zehntneri* Britton & Rose), e presença esparsa de espécies arbóreas.

Formação de vegetação arbustiva - sombreamento parcial com alta luminosidade, predominância de espécies arbustivas e em menor número espécies arbóreas de porte médio como o murici (*Byrsonima crassifolia* L. Kunth), cambuí (*Myrciaria tenella* D.C. Berg), aroeira da praia (*Schinus terebinthifolius* Raddi), piaçava (*Attalea funifera* Martius) e gramíneas esparsas.

Formações florestais (vegetação secundária) - composta por vegetação secundária com solo coberto por grande quantidade de serapilheira, sombreamento com baixa luminosidade e alta umidade relativa do ar, vegetação densa com predominância de espécies arbóreas de médio a grande porte como o cajueiro (*Anacardium occidentale* L), mangaba (*Hancornia speciosa* Gomes), pau-pombo (*Tapira guianensis* Aublet) e ingá (*Inga* sp.).

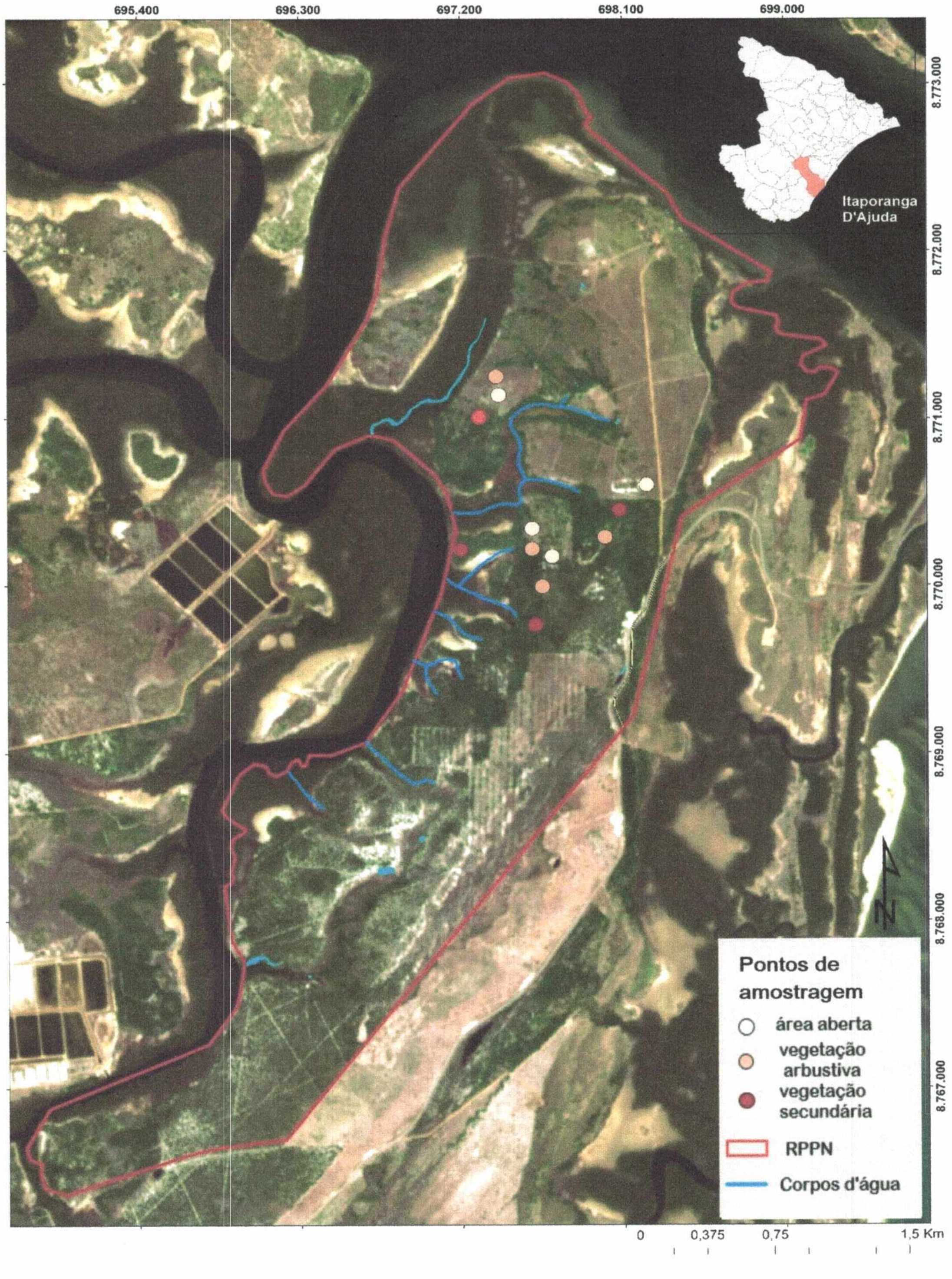

Figura 1 - Mapa da RPPN do Caju, localizada em Itaporanga D'Ajuda, SE, usando imagem do satélite Sentinel-2.

1.3 - Escalas de diversidade

Compreender os padrões de diversidade de espécies é vital para avaliar os impactos do manejo florestal e para desenvolver estratégias de conservação (RUBENE *et al.*, 2014). A diversidade de espécies em sistemas naturais e paisagens fragmentadas é afetada por múltiplos processos operando em múltiplas escalas (GAVISH *et al.* 2019). Whittaker (1972) definiu três importantes escalas de diversidade: alfa (riqueza de espécies no habitat), beta (variação nas identidades das espécies entre os habitats), e a diversidade gama que é a riqueza de espécies regional, entre uma variedade de habitats (uma paisagem, área geográfica, ilha).

O estudo da diversidade beta permite testar diferentes hipóteses sobre os processos que direcionam a distribuição de espécies e há duas formas em que as comunidades de espécies podem ser "diferentes". A primeira é a substituição de espécies (turnover) em um local por diferentes espécies em outro local, de modo que as duas comunidades são diferentes entre si (BASELGA, 2012). A segunda é a perda (ou ganho) de espécies em somente um dos locais, o que implica a eliminação (ou adição) de espécies, fazendo com que a comunidade mais pobre seja um subconjunto da mais rica (um padrão chamado aninhamento) (BASELGA & ORME, 2012), a ocorrência de espécies tende à sobrepor uma à outra e compartilhar locais em comum (ULRICH & GOTELLI, 2007) (Figura 2).

Portanto, a seleção da medida de dissimilaridade para quantificar as diferenças entre as assembléias é crucial pois, existem diferentes maneiras de medi-la (BASELGA & ORME, 2012). Nesse sentido, Baselga (2010, 2012) propôs um método para a partição da dissimilaridade total (beta diversidade) em dois componentes separados: a dissimilaridade da substituição de espécies (turnover) e a dissimilaridade do aninhamento (BASELGA & ORME, 2012). Na natureza, a substituição de espécies pode refletir a separação de espécies pelo meio ambiente ou a dispersão, enquanto o aninhamento é frequentemente relacionado à dinâmicas de extinção-colonização ordenadas (SI *et al.,* 2016, SOININEN *et al.*, 2017). Portanto, a diversidade beta interage com os gradientes de diversidade alfa (riqueza), e ambos os componentes da biodiversidade (alfa e beta) resultam da montagem da comunidade por meio de filtros locais e regionais. Assim, a diversidade beta pode capturar a natureza dinâmica dos padrões de diversidade melhor do que medidas simples de diversidade alfa (SOININEN, *et al.,* 2017).

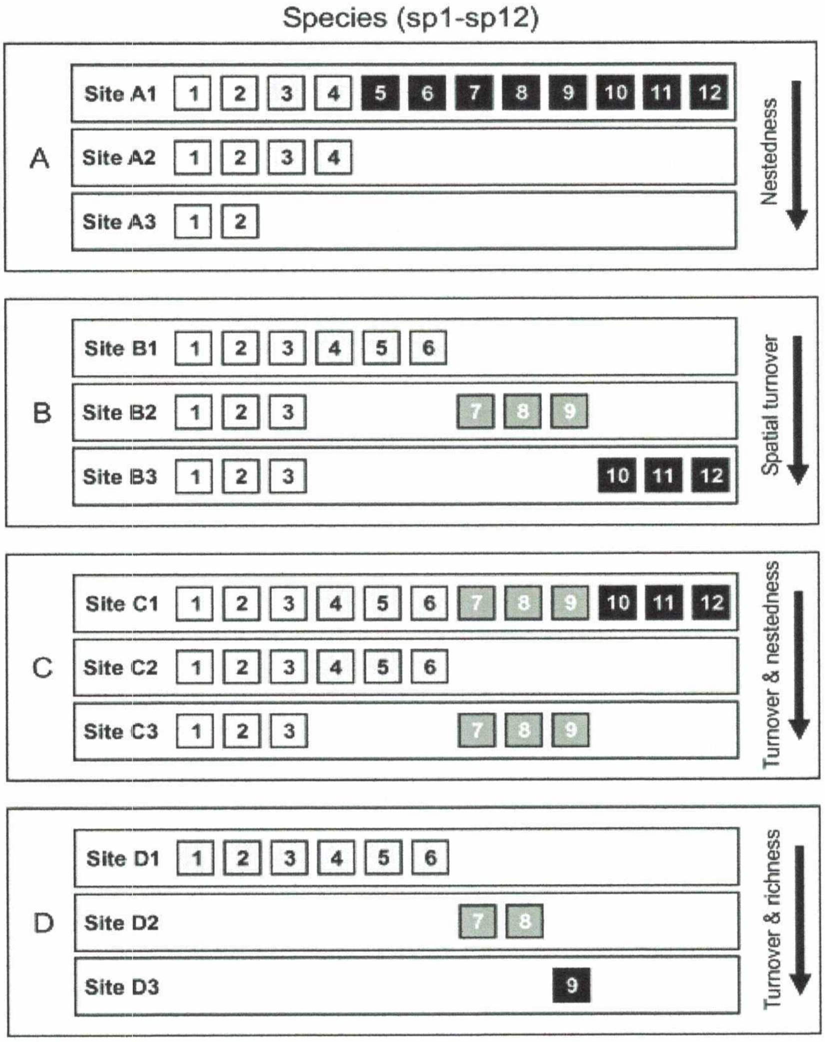

Figura 2 - Exemplos hipotéticos envolvendo quatro ilhas (A - D) e três sítios amostrais em cada. Biotas dos sítios A1 - A3 são completamente aninhadas, porque biotas pobres são subconjuntos das biotas ricas. Sítios B1 - B3 têm a mesma riqueza (seis espécies cada) com três espécies em comum a todos os três locais e três espécies exclusivas para cada sítio, ou seja, exibindo um padrão de turnover espacial. Sítios C1 - C3 ambos padrões presentes, porque C2 e C3 são subconjuntos de C1 (aninhamento), mas algumas espécies são substituídas entre C2 e C3, que não são subconjuntos uma da outra. Sítios D1 - D3 turnover espacial e não são obviamente aninhada, mas apresentam diferenças na riqueza (BASELGA, 2010).

2.4 - Abelhas e vespas solitárias

As interações plantas-polinizadores são relações mutualísticas de extrema importância, ao coletar recursos florais como pólen, néctar e óleos, os polinizadores facilitam a reprodução das plantas, proporcionando a formação de frutos e sementes (GIANNINI *et al.*, 2015). As abelhas são os mais importantes e efetivos polinizadores (KLEIN *et al.*, 2007), são ecologicamente e funcionalmente diversas, forrageiam uma ampla variedade de formas florais e nidificam em diversos substratos (MICHENER, 2007).

Apesar de sua importância, os números de riqueza de abelhas são imprecisos por diversas razões como erros de identificação, sinonímias, homonímias, muitas áreas a serem amostradas (FREITAS *et al.*, 2009). Estima-se que o número de espécies de abelhas descritas está em torno de 18.000, mas que o número total pode ser em torno de 20.000 a 30.000 espécies (MICHENER, 2007) sendo que 85% são solitárias (SILVA *et al.*, 2001; BUSCHINI, 2006). A fêmea de espécies de abelhas solitárias constroi seu próprio ninho, abastece as células de cria sem ajuda de outras abelhas, e geralmente morre ou deixa o ninho antes da emersão de sua cria (MICHENER, 2007).

Quanto às vespas, cerca de 26.000 espécies foram descritas no mundo todo, sendo 90% consideradas de hábito solitário (LOYOLA & MARTINS, 2006; BUSCHINI & WOISKI, 2008; BATISTA, 2010). Várias destas espécies de vespas solitárias são consideradas inimigos naturais de artrópodes atuando no controle biológico natural de insetos (afídeos, ortópteros e lepidópteros) (TYLIANAKIS, *et al.*, 2005; HOLZSCHUH *et al.*, 2009, CAMPBELL, *et al.*, 2017), e outros artrópodes (baratas e aranhas) (EBELING *et al.* 2012, ROCHA-FILHO, *et al.*, 2017).

Vespas e abelhas solitárias podem nidificar em cavidades pré-existentes no solo, em troncos e galhos ocos ou perfurados, podendo ser estudadas por meio de ninhos-armadilha (TSCHARNTKE *et al.*, 1998; MORATO & CAMPOS, 2000; AGUIAR & MARTINS, 2002; MENDES & RÊGO, 2007). Ninhos-armadilha são espaços tubulares, os quais espécies de abelhas e vespas solitárias podem usar para nidificação (Figura 3) (TSCHARNTKE *et al.*, 1998; MORATO & CAMPOS, 2000; AGUIAR & MARTINS, 2002; TYLIANAKIS *et al.* 2005; KLEIN *et al.* 2007). Ninhos-armadilha são um sistema adequado para estudar interações multitróficas complexas devido à abelhas e vespas solitárias possuírem tamanho pequeno, riqueza de espécies alta, complexidade trófica, e por sua importância no funcionamento do ecossistema (TSCHARNKE *et al.*, 1998; KLEIN *et al.* 2007). Cerca de 5% de todas as abelhas e vespas são potenciais espécies que nidificam em cavidades (Figuras 3, 4 e 5) (GATHMANN, 1998), e os recursos alimentares para ambas guildas dependem da diversidade de plantas presentes no habitat. Há evidências de que a abundância e a riqueza local das espécies de abelhas e vespas correlacionam-se com a diversidade de recursos alimentares como flores, néctar e presas.(TSCHARNKE *et al.*, 1998).

Segundo Morato & Martins (2006) abelhas e vespas solitárias gastam muito tempo de sua vida adulta construindo ninhos e coletando alimento para suas crias e, fatores que afetam essas atividades como local de nidificação e disponibilidade de alimento são por sua vez afetados pela estrutura ambiental. Consequentemente, mudanças na diversidade e abundância desses insetos podem afetar as relações do ecossistema através de seus papéis como predadores e polinizadores (TAKI *et al.* 2008). Algumas espécies de abelhas e vespas têm requerimentos de habitats específicos, para a construção de seus ninhos necessitam de cavidades pré-existentes, que por sua vez dependem da estrutura da vegetação (FLORES *et al.*, 2018). O período de nidificação é uma fase crítica no ciclo de vida de abelhas e vespas solitárias (MORATO & MARTINS, 2006; FLORES *et al.*, 2018) pois, esses himenópteros são sensíveis aos efeitos de perturbações ambientais (MORATO & CAMPOS, 2000) portanto, têm sido usadas como bioindicadores da qualidade do ambiente em diferentes ecossistemas (TYLIANAKIS *et al.*, 2005).

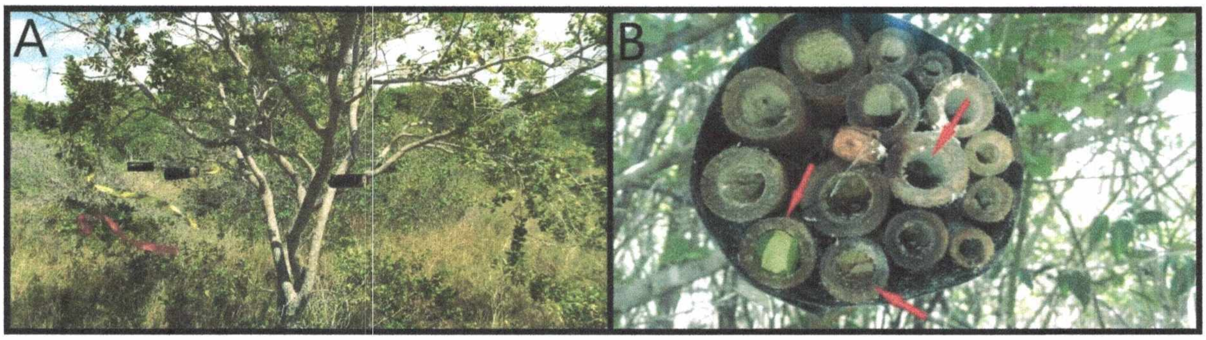

Figura 3- (A) Ninhos-armadilha instalados na RPPN do Caju; (B) ninhos fundados por abelhas (setas vermelhas) em cavidades de ninhos-armadilhas.

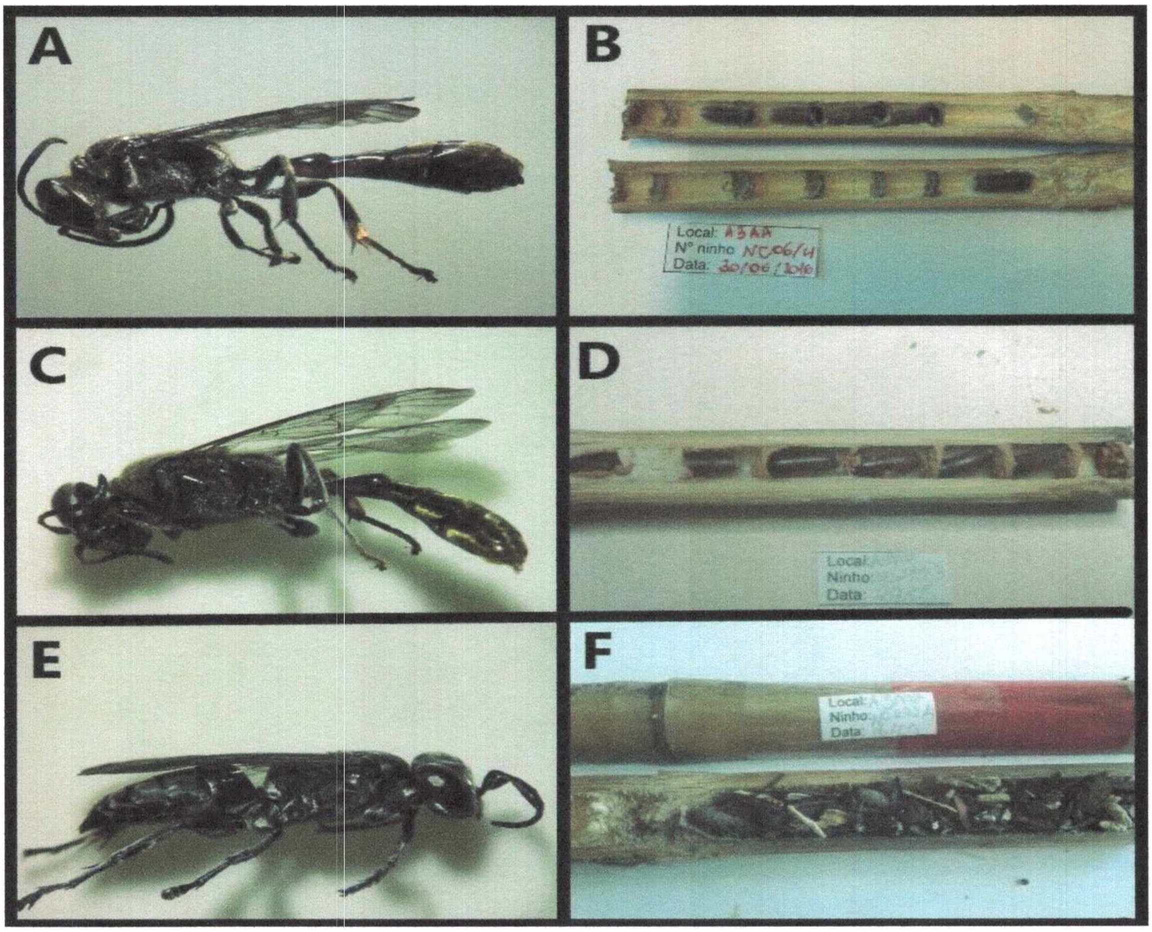

Figura 4 - Espécies e ninhos de vespas solitárias em vegetação de restinga na RPPN do Caju: Adulto (A) e ninho com pupas (B) de *Trypoxylon aff. nitidum*; Adulto (C) e ninho fundado (D) por *T. ausuncicola*; Adulto (E) e ninho com pupas (F) de *Liris* sp.

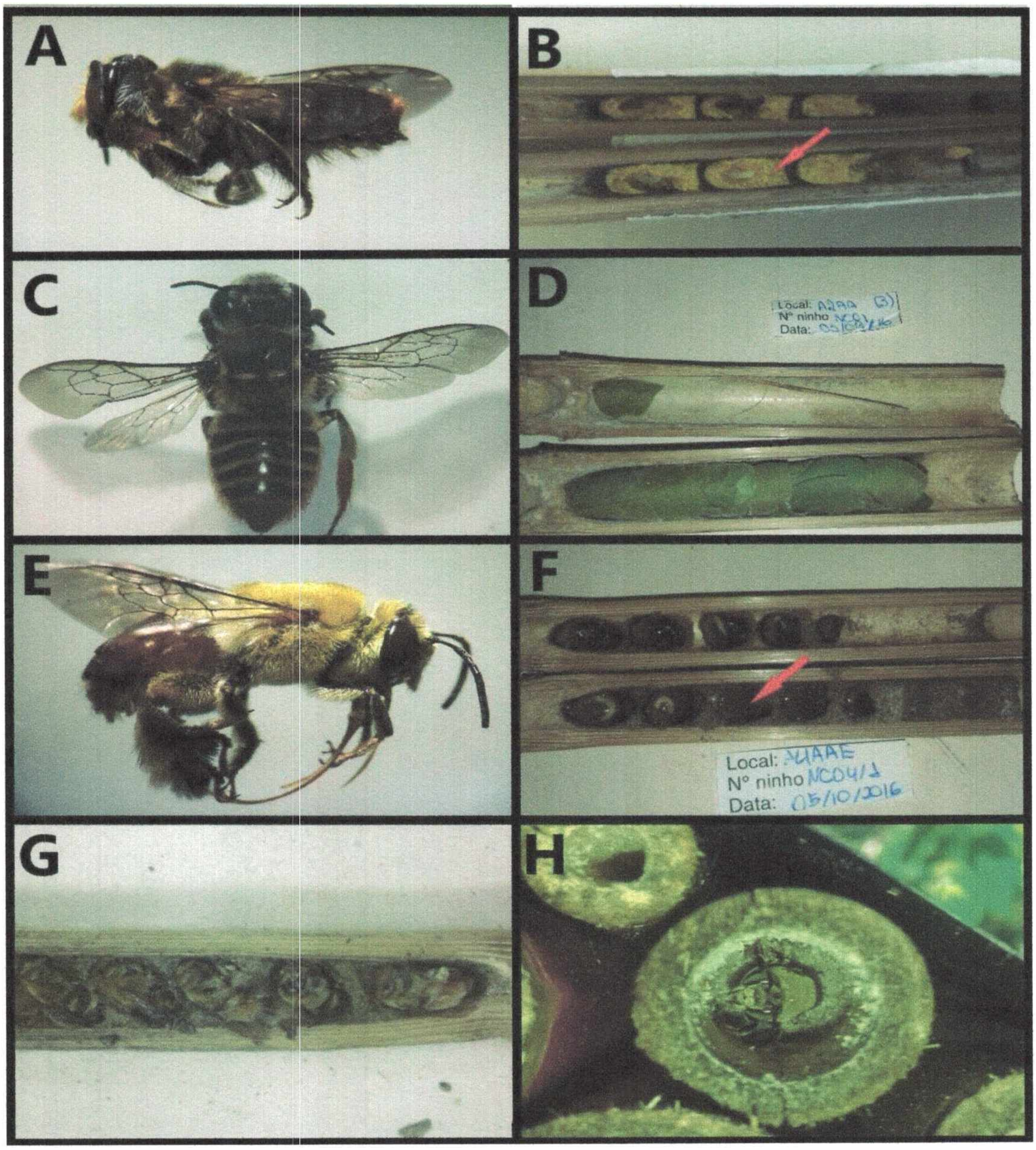

Figura 5- Espécies e ninhos de abelhas solitárias registrados em vegetação de restinga na RPPN do Caju: Adulto (A) e ninho (B) de *Centris* sp., é possível observar pólen disposto nas células como fonte de alimento para as larvas; Adulto (C) e ninho (D) de Megachilidae; Adulto (E) e ninho (F) de *C. tarsata*, nota-se a alimentação das larvas nas células, (G) Pré-adultos de *C. tarsata* dispostos nas células de cria antes da emergência; e (H) Ninho sendo construído por fêmea de *C. tarsata*.

2 - OBJETIVOS

2.1 Objetivo geral

Avaliar a composição de espécies da comunidadede vespas e abelhas solitárias em áreas abertas, vegetação arbustiva e secundária de restinga.

2.2– Objetivos específicos

- Investigar como as condições climáticas e o tipo de vegetação influenciam a nidificação e a composição de espécies da comunidade de vespas e abelhas solitárias em restinga.

- Investigar se a associação entre tipo de vegetação e condições climáticas influenciam na nidificação da abelha *Centris tarsata*, bem como nas características biológicas e de arquitetura dos ninhos dessa espécie.

3 - ESBOÇO DOS CAPÍTULOS

O presente estudo apresenta os resultados de uma pesquisa de dois anos com início em maio de 2016, com abelhas e vespas solitárias nidificantes em vegetação de restinga na RPPN do Caju no município de Itaporanga D'Ajuda, Sergipe.

Capítulo 2 – Aborda padrões de diversidade e estrutura da comunidade de espécies de abelhas e vespas solitárias que nidificam em ambiente de restinga por meio da partição da diversidade beta nos componentes substituição de espécies (turnover) e aninhamento. Foram abordados neste estudo os seguintes questionamentos: condições climáticas são fatores determinantes na riqueza e abundância de abelhas e vespas solitárias? A diversidade beta e seus componentes, substituição de espécies e aninhamento, são influenciados pelos diferentes tipos de vegetação? Os padrões de diversidade da comunidade de vespas e abelhas solitárias mudam ao longo do tempo?

Capítulo 3 - Investiga se a vegetação em mosaico de restinga e as condições climáticas regionais têm efeito sobre a nidificação de *Centris tarsata*, a abelha solitária mais abundante na região estudada abordando as seguintes questões: há uma associação entre as condições climáticas, tipo de vegetação e nidificação por *C. tarsata*? A arquitetura dos ninhos, características biológicas e o parasitismo por outros artrópodes variam com o tipo de vegetação? *Centris tarsata* apresenta preferências de nidificação nos diferentes estratos da vegetação?

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CAPÍTULO 2

Community composition of cavity-nesting bees and wasps according to restinga vegetation type

Manuscrito escrito de acordo com as normas da revista Biotropica

Community composition of cavity-nesting bees and wasps according to restinga vegetation type

ABSTRACT

Solitary bees and wasps are himenopterans that nest in pre-existing cavities in natural environments, and play a key role in ecosystem functioning providing important ecosystem services such as pollination and natural biological control. Here, we aimed to to assess the species composition of cavity-nesting bees and wasps community in restinga vegetation, and determine how climatic conditions influence nesting and assembly composition in three vegetation types (open-areas, shrubby and secondary vegetation) of Brazilian restinga. The hymenopterans were sampled with trap-nests and evaluations were conducted monthly over two years. We collected 735 nests belonging to 4 bee species and 15 wasp species. Most nesting occurred in open areas followed by secondary vegetation in the dry season, decreasing in the rainy season. Species composition differed between open areas and secondary vegetation. Overall, the contribution of beta diversity components, turnover and nestedness, was similar among vegetation types. However, in the dry season, turnover was higher in secondary and shrubby vegetations. Conversely, a completely nested pattern occurred in open areas in both seasons. Turnover was the main responsible for beta diversity between the first and second years, being high in secondary and shrubby vegetations. Accordingly, climatic conditions influence species composition of cavity-nesting bees and wasps in restinga vegetation favouring nesting activity in open areas and secondary vegetations. Furthermore, secondary vegetation playing the role of shelter during warm and dry season, contributing for the conservation of these essential ecosystem service providers.

Key-words: Atlantic Rainforest, beta diversity; climatic conditions; trap-nests

1. INTRODUCTION

Habitat fragmentation and land use intensification has led to the decline of global biodiversity. The Brazilian Atlantic Forest biome, famed for its high biodiversity, has been continuously exploited over the past 500 years and replaced by agriculture, livestock and urban areas. The restinga is an ecosystem contained within the Atlantic forest biome, which is characteristic of tropical and subtropical coastal regions, composed of herbaceous plants, shrubs and an arboreal stratum growing in sandy plains under a marine influence. However, this ecosystem is under constant threat as urban sprawl, real estate speculation and deforestation directly affects the local flora and fauna (Fischer & Lindenmayer, 2007; Oliveira & Landim, 2014; Rocha-Filho et al., 2017; Serra et al., 2016).

Bees and wasps are important in ecosystem functioning, play the role of providing ecosystem services, are effective pollinators, ecologically and functionally diverse and they forage a wide variety of floral plant species. Otherwise, several wasps species are considered natural enemies of diverse arthropod species, thereby acting as natural biological control of phytophagous species (Buschini & Woiski, 2008; Ebeling et al., 2012; Holzschuh et al., 2009; Klein et al., 2007; Michener, 2007; Tylianakis et al., 2005).

Around 5% of all bees and wasps are potential cavity-nesting species that use hollow trunks and branches to nest, and therefore can be studied using trap-nests (Aguiar & Martins, 2002; Mendes & Rêgo, 2007; Morato & Campos, 2000; Tscharntke et al., 1998, Veddeler et al., 2010). These insects require pre-existing cavities to build their nests, which means that they rely on the availability of particular vegetation structure and, therefore, they can be used as indicators of environmental quality or changes (Flores et al., 2018; Tscharntke et al., 1998). Understanding and preserving the habitats of cavity-nesting bees and wasps is important for the maintenance of these populations of Aculeata (Morato & Martins, 2006). Therefore, recognising diversity patterns and how biotic and abiotic factors influence the community structure of these arthropods is essential for their management and conservation.

Beta diversity is defined as the variation in community composition between sites and it may capture the dynamic nature of diversity patterns more thoroughly than measurements of alpha diversity (species richness) (Soininen et al., 2017; Tuomisto & Ruokololainen, 2006). Analysing beta diversity allows different hypotheses regarding the processes driving species distribution to be tested. Therefore, Baselga (2010, 2012) proposed a method for partitioning total dissimilarity (beta diversity) into two components accounting for the dissimilarities derived from turnover and from nestedness. Turnover is the replacement of species in one site with different species in another site. Nestedness is the species loss (or gain) resulting from the elimination (or addition) of species in one location, making the poorer community a subset of the richer (Baselga & Orme, 2012). In nature, species turnover may reflect species segregation by environment or dispersal, while nesting is often related to ordered extinction-colonization dynamics (Si et al., 2016; Soininen et al., 2017).

Here, we addressed the following questions: (a) whether climatic conditions influence the nesting periods and vegetation type preferences of cavity-nesting bees and wasps; (b) what the relative contributions are of turnover and nestedness to variation in the community composition of cavity-nesting bees and wasps; (c) whether there is a relationship between climatic conditions and turnover and nestedness for communities of cavity-nesting bees and wasps within the restinga.

2. METHODS

2.1 Study Area

The study was carried out in a protected area (763.37-ha) belonging to the Brazilian Agricultural Research Corporation (Embrapa Tabuleiros Costeiros) in the municipality of Itaporanga D'Ajuda (11° 06' 16.19" S, 37° 11' 05.89" W), in the north-eastern Brazilian State of Sergipe. According to the Köppen-Geiger classification, the predominant climate in the region is tropical with marked dry (September to February) and rainy (March to August) seasons, with average annual rainfall above 1250 mm. The biome is Atlantic rainforest composed of a matrix of mangrove, restinga and apicum (sandy open areas influenced by the tidal regime). The study was conducted within the restinga domain and rainfall and temperature, respectively, were obtained from a meteorological station located in the area and from the Instituto Nacional de Meteorologia (2018), on a per-month basis.

2.2 Sampling

Trap-nests were constructed from 15 pieces of hollow bamboo cane (20.0 cm long), with one node in the middle, forming two internodes (9.0 to 11.0 cm deep). Bamboo canes had internal diameters ranging from 0.3 to 2.0 cm evenly distributed (5 hollow bamboo canes of 0.3 to 0.8 cm, 5 of 0.9 to 1.4 cm and 5 of 1.5 to 2.0 cm diameter) and they were wrapped together with a 22.0 cm-wide plastic sheet and wire, making a total of 30 cavities (Batista Matos et al., 2012). Trap-nests were set up in three vegetation types in the restinga: (a) open areas, with dominance of grasses, such as *Paspalum maritimum* Trind., weeds, cactus (*Melocactus zehntneri,* Britton & Rose) and some sparsely distributed trees, direct sunlight; (b) shrubby vegetations, with dominance of shrubs and a few tree species, such as *Anacardium* *occidentale* L., *Byrsonima crassifolia* (L.) Kunth, *Myrciaria tenella* (D.C.) O.Berg, grasses, partial shading with high luminosity; and (c) secondary vegetations, with dominance of medium to large tree species such as *A. occidentale, Hancornia speciosa* Gomes, *Tapirira guianensis* Aublet and *Inga* sp., dense vegetations, soil covered by a thick litter layer, shaded with low luminosity. Four replicates for each vegetation type were chosen, totalling 12 sampling areas. Study sites were usually clustered in groups of three vegetation types to avoid spatial autocorrelation. Four trap-nests were hung by a wire at each study site and attached to a tree branch, 1.5 m above the ground and distanced 1.0 m from each other. Sampling areas were at least 100 m distant from each other. Entomological glue was applied to the wire monthly to deter crawling arthropods. Trap-nests were inspected monthly for two years (from July 2016 to June 2018) and nested bamboo canes were removed and replaced by empty ones with similar internal diameter. Nested bamboo canes were placed in a plastic cage individually and kept indoors at 27°C (± 2°C) for three months. After adult emergence, cavity-nesting bees and wasps were separated according to morphotype and identified using Goulet & Huber (1993), Michener (2007) and DNA sequencing. Voucher specimens were deposited in the collection of Laboratório de Entomologia, Embrapa Tabuleiros Costeiros, Aracaju, Brazil, and Laboratório de Genética Evolutiva e de Himenopteros, Universidade Federal de São Carlos, São Carlos, Brazil.

2.3 Data Analysis

Species richness was calculated using the estimators Chao1 and ACE (Abundance-based Coverage Estimator) to verify the sufficiency of sampling effort using EstimateS software version 9.1.0 (Colwell, 2013). Afterwards, sample-based accumulation curves were plotted for observed and expected richness using SigmaPlot software version 12.5 (Systat Software, 2011). We also performed the Spearman correlation between observed and estimated richness using the *ISwR* package (Dalgaard, 2015). Shannon-Wiener diversity (H') and Pielou's evenness index (J') were calculated for cavity-nesting bees and wasps and submitted to analysis of variance (ANOVA). Also, the number of singletons/doubletons in the vegetation types was obtained using the *vegan* package (Oksanen et al., 2019). General linear models (GLMs) with Poisson (discrete variables) error distributions were constructed in order to assess differences among vegetation types for species richness. The models were subjected to ANOVA, and *a posteriori* contrasts were carried out to assess differences among treatments (Crawley 2007).

Regression tree analyses addressed how climatic conditions and vegetation type influenced the nesting of bees and wasps. Temperature (°C), rainfall (mm^3) and vegetation type (open areas, shrubby and secondary vegetations) were treated as exploratory variables and the number of nests built as the response variable. The root node represented total sampling, which was further divided into two or more sets called decision nodes and into sub-nodes and/or terminal nodes. Analyses were performed using the *rpart* package (Therneau et al., 2019).

The contribution of beta diversity components was assessed using the dissimilarity partition method (Baselga, 2010), which separates the total beta diversity (Sørensen dissimilarity index) into two components (turnover and nestedness), using the *betapart* package. The Sørensen dissimilarity index (presence/absence) is expressed by the formula: $\beta_{SOR} = \beta_{SIM} + \beta_{NES}$, where β_{SIM} is the Simpson dissimilarity (the turnover component of Sørensen dissimilarity) and β_{NES} is the nestedness component of Sørensen dissimilarity. In order to establish the components of beta diversity between the first and the second year of evaluation, we used the *beta.temp* function which calculates the dissimilarity values (turnover and nestedness) between the combined sites of two data sets (x, y) describing presence and absence at the same set of locations for two separate times. Also, we calculated pairwise dissimilarity, which computes beta diversity and components using the *beta.pair* function (Baselga & Orme, 2012). Unless otherwise stated, the analyses described above were performed using R software version 3.3.1 (R Development Core Team 2016). Additionally, we used the Mantel test to explore the possible relationship between spatial distance and species dissimilarity, using Jaccard distance (presence/absence) for bees' and wasps' species composition and Euclidean distance for the spatial distance matrix, using Pearson's correlation and 999 permutations (Perillo et al., 2017).

Non-metric multidimensional scaling (NMDS) analysis was performed to verify differences in the community composition of cavity-nesting bees and wasps among vegetation types using the Bray-Curtis similarity index (abundance). Moreover, similarity analyses (ANOSIM) were conducted to compare the differences between two or more groups of vegetation using the Bray-Curtis similarity index and Bonferroni correction at the 5% level. Analyses were performed using the software PAST (Hammer et al., 2001).

3. RESULTS

A total of 735 nests and 2.147 individuals were collected, of which 1.353 were wasps, comprising 15 species and/or morphospecies (Table 1), belonging to the families Crabronidae and Sphecidae. The remaining 794 individuals that emerged were bees, encompassing 4 species from the families Apidae and Megachilidae (Table 1).

In open areas, we found 607 individuals from 11 wasp species and 441 from 4 bee species. In shrubby vegetations, there were 328 individuals belonging to 5 species of wasps and 277 individuals from 3 bee species. In secondary vegetations 418 individuals of 10 wasp species and 76 comprising 3 bee species were found. Secondary vegetations also presented more singletons (7) compared to open areas (5) and shrubby vegetations (4), whereas doubletons were found only in open areas and secondary vegetations (2 and 1, respectively).

Sample-based accumulation curves show that the observed species richness of bees and wasps increased with the number of individuals (Figure 1). Observed and estimated species richness were highly correlated with the Chao1 and ACE estimators (Spearman correlation; *rho* = 0.99, $P < 0.0001$), with 97.56% and 91.86% efficiency, respectively, suggesting that sampling effort was sufficient. However, the Shannon-Wiener (H') and Pielou (J') indexes did not differ among vegetation types (open areas: H' = 1.64; J' = 0.74; shrubby vegetations: H' = 1.28; J' = 0.74; secondary vegetations: H' = 1.21; J' = 0.71; $P > 0.05$). In contrast, vegetation types influenced species richness, in that open areas had more species in comparison with shrubby and secondary vegetations ($\chi^2 = 26.51$, $df = 1$, $P < 0.0001$; $\chi^2 = 20.76$, $df = 1$, $P < 0.001$, respectively).

Cavity-nesting bees and wasps preferred to nest in open areas during the dry season, followed by shrubby and secondary vegetations. Nesting peaked from November to December 2016 and from November 2017 to June 2018 (Figure 2). The regression tree revealed 5 levels of depth and 15 nodes, these being 7 decision nodes and 8 terminals. Two groups were formed according to temperature and vegetation types. In the first group, nesting was favoured at temperatures below 27°C in shrubby and secondary vegetations, with 0.25 nests in 33% of the samples. On the other hand, in open areas, for temperatures below 27°C and rainfall lower than 148 mm^3 the mean number of nests was 0.72 in 11% of the samples. However, when rainfall increased, average nesting was 1.8 in 6% of the samples. In the second group (temperature ≥ 27 °C), the mean number of nests was 1.2 in 33% of the samples in shrubby and secondary vegetations. Conversely, nesting in open areas was favoured in temperatures below 28°C. Dry periods with rainfall ranging from 41 to 132 mm^3, led to a mean number of 3.4 nests in 4% of the samples. For rainfall below 41 mm^3, the mean number of nests was 1.4 in 6% of the samples (Figure 3).

Overall, the components of beta diversity indicated that species turnover and nestedness contributed similarly (51.4% and 48.6%, respectively), which was also true during the dry season (57.1%, and 42.9%, respectively) (Figure 4A). However, during the rainy season, nestedness (65.8%) overrode species turnover (34.2%) (Figure 4B). Between the first and second years of evaluation, higher bee and wasp species turnover was recorded in secondary vegetations (84.4%), followed by shrubby vegetations (70.8%), while in open areas (53.3%) species composition variation matched the nestedness pattern (46.7%) (Table 2).

According to the pairwise dissimilarity, shrubby vegetations was completely nested within open areas (100%). Secondary vegetations and open areas had high species turnover (82.5%) while between shrubby and secondary vegetations (62.5%) was lower. During both the dry and rainy seasons, open areas and shrubby vegetations remained completely nested (100%), unlike open areas and secondary vegetations where nestedness was 13.2 % during the dry season and 63.6 % in the rainy season. Conversely, during the dry season species turnover between open areas and secondary vegetations was high (86.1%), as well as during the rainy season between shrubby and secondary vegetations (57.1%) (Table 2). The Mantel test showed that there was no relationship between spatial distance and species dissimilarity (Pearson correlation; $r = -0.09013$; $P > 0.05$).

The NMDS revealed that open areas and secondary vegetations were dissimilar in their cavity-nesting bee and wasp community composition, while shrubby and secondary vegetations, and open areas and shrubby vegetations, were similar (stress = 0.13, Figure 5). However, according to ANOSIM, there was no difference in the rank similarities for the 12 sites in the three vegetation types ($P > 0.05$).

4. DISCUSSION

Our results showed that wasp species richness was higher than bee species richness for the three restinga vegetation types, which has also been observed in tropical regions in Indonesia, Costa Rica, Amazonia and north-east Brazil. This pattern may be due to bees being more sensitive than wasps to habitat modification (Batista Matos et al., 2012; Klein et al., 2002; Morato & Campos, 2000; Stangler et al., 2015).

Open areas harboured greater species richness and diversity of cavity-nesting bees and wasps, followed by secondary vegetations, possibly due to the influence of generalist species on the overall species richness. Generalist species may benefit from a wide variety of resources and thus are prone to be less sensitive to simplified habitats (Flores et al., 2018). In addition, open areas may provide greater availability of resources such as exposed nest building materials like clay, sand grains, resins, leaves, filaments, twigs, and organic matter, as well as food resources such as pollen, nectar, floral oils and prey (Loyola & Martins, 2006; Morato & Martins, 2006).

Overall, the nesting of cavity-nesting bees and wasps seems to be affected by climatic conditions, as it was higher during the dry season in open areas, followed by secondary vegetations. As rainfall increased, nesting decreased, except for in shrubby vegetations, where nesting was higher during the rainy season. Nesting was lower during the first year compared to the second, possibly due to higher rainfall during the latter (INMET, 2018).

However, the regression tree showed that there are ranges of temperature and rainfall that may be beneficial to cavity-nesting bees and wasps nesting. Nesting in shrubby and secondary vegetations was favoured by higher temperatures in drier periods, while in open areas were temperatures below 28°C and rainfall up to 132 mm^3. Seasonal changes in temperature and relative humidity can affect the population density of several arthropod species, including cavity-nesting bees and wasps, and play an important role in determining species' preference for a given habitat, (Buschini et al., 2006; Matos et al., 2016; Philpott et al., 2006; Teodoro et al., 2009; Tylianakis et al., 2005). Additionally, climatic conditions can directly affect resource availability, and the higher humidity inside forests can negatively influence the activity of cavity-nesting bees and wasps due to their limited ability to thermoregulate (Loyola & Martins, 2006; Stangler et al., 2015).

In a study on differential habitat occupation by *Trypoxylon* spp. wasps, Santoni et al. (2009) observed a synchronic temporal occurrence of these species, especially in the warm and rainy season. According to these authors, the influence of seasonality on nesting biology of neotropical cavity-nesting species is possibly associated with monthly average temperature. Moreover, in a study of *Trypoxylon lactitarse* from southern Brazil (pronounced dry season, mild summers and frosts in the winter), Buschini & Wolff (2006) observed that this species started nesting in forested areas during spring and summer and switched to grassland and swamps during autumn and winter. However, *Centris tarsata*, the most abundant oil-collecting bee in the present study, showed a preference for nesting during the dry season, a pattern observed in several studies in different regions of Brazil (Aguiar & Martins, 2002; Buschini & Wolff, 2006; Mendes & Rêgo, 2007; Costa et al., 2019).

The species composition was dissimilar between open areas and secondary vegetations, endorsing results obtained in other regions of Brazil that species composition of cavity-nesting bee and wasp assemblages varies along a habitat complexity gradient (Buschini & Woiski, 2008; Flores et al., 2018).

Total beta diversity among vegetation types was low and nestedness and species turnover made similar contributions. However, when it was calculated for each season, different contributions from turnover and nestedness were observed. Species replacement (turnover) was favoured during the dry season, unlike the rainy season, when species richness was low and the poorer cavity-nesting bees and wasps community became nested within the richer. Regardless of season, the community of cavity-nesting bee and wasp species from shrubby vegetation was completed nested within that of the open areas and secondary vegetations, but, in the latter case only during the dry season. Additionally, species replacement was higher than nestedness for the two years, possibly due to the high rainfall recorded during the second year of sampling.

The relationship between precipitation and variation in fauna composition may explain the covariation between species richness and precipitation variation (Baselga, 2008). A study of the structure of bee and wasp diversity in burned and unburned areas in clear-cut forest in Sweden demonstrated that 72% to 90% of beta diversity was explained by species turnover, while nestedness explained only 10% to 28% (Rubene et al., 2015). Furthermore, Perillo et al. (2017), investigating the species composition of the bee and wasp community over an altitude gradient in the neotropical region, found that beta diversity partitioning was mainly influenced by species turnover (81%). According to these authors, species turnover was influenced by the high rate of singletons and doubletons, a pattern commonly seen in tropical arthropod studies. In fact, in our study, secondary vegetations presented a higher number of singletons and doubletons compared to the other vegetation types, and that environment had species turnover as the most representative component of beta diversity.

Our results indicate that solitary wasps and bees in the restinga respond strongly to climatic conditions and vegetation type. These species prefer to nest during the warmer dry season in open areas and secondary vegetations. Although the variation in species composition was low for open areas, shrubby and secondary vegetations, the patterns that drive species distribution varied according to vegetation type and climatic conditions. Therefore, understanding the species composition of cavity-nesting bees and wasps is crucial for the management and conservation of these essential ecosystem service providers.

ACKNOWLEGMENTS

We thank to Dr. Felipe Vivallo from the Rio de Janeiro National Museum for his collaboration in identifying *C. tarsata* bee species and Dr. Marco Antonio Del Lama and MSc. Camila Sabadini from the Universidade Federal de São Carlos for their collaboration in identifying *Trypoxylon* wasps. This work was supported by the Coordenação de Aperfeiçoamento de Pessoal (CAPES) wich granted the fellowship for DMC and ASB, and Embrapa Tabuleiros Costeiros for the permissions to conduct the research on the study area and for providing logistical support.

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Table 1 - Total number of cavity-nesting bees (Apidae and Megachilidae) and wasps (Sphecidae and Crabronidae) in open areas, shrubby and secondary vegetations in restinga domain in Caju RPPN, Itaporanga D'Ajuda, Sergipe.

Family	**Morphospecies**	**Nests founded**	**Total emerged adults**		
			Open area	**Shrubby vegetation**	**Secondary vegetation**
Sphecidae	Sphecidae 1	15	15	25	5
	Sphecidae 2	1	0	0	2
	Sphecidae 3	2	10	0	0
	Liris sp	87	69	44	31
	Isodontia sp 1	1	1	0	0
	Isodontia sp2	1	1	0	0
	Isodontia sp3	2	0	0	2
	Isodontia sp4	8	7	0	0
Crabronidae	*Trypoxylon lactitarse*	71	16	0	46
	Typoxylon nitidum	199	238	220	280
	Trypoxylon ausuncícola	47	119	9	17
	Trypoxylon sp	83	94	30	27
	Trypoxylon sp1	1	0	0	6
	Trypoxylon sp2	9	37	0	0
	Trypoxylon sp 3	2	0	0	2
Apidae	*Centris tarsata*	162	363	217	61
	Centris sp 1	1	1	0	0
Megachilidae	*Megachile* sp	27	33	40	8
	Anthidiini	16	44	20	7
Total		**735**	**1048**	**605**	**494**

Table 2 - Proportion of Beta diversity components for cavity-nesting bee and wasp community in restinga domain. Bold numbers indicate contribution over 50% in beta diversity. βSIM (Simpson dissimilarity, i.e. species turnover), βNES (nestedness) and βSOR Sørensen dissimilarity, i.e. total beta diversity).

Solitary bees and wasps communities	**Beta diversity components**		**Total beta diversity**
	βSIM	βSNE	βSOR
First and secondy year of sampling			
Open areas	**0.22 (53.3%)**	0.19 (46.7%)	0.42 (100%)
Shrubby vegetation	**0.12 (70.83%**	0.05 (29.17%	0.17 (100%)
Secondary vegetation	**0.37 (84.37%**	0.07 (15.65%	0.44 (100%)
Pairwise among vegetation types			
Open areas – Shrubby vegetation	0 (0%)	**0.30 (100%)**	0.30 (100%)
Open areas – Secondary vegetation	**0.33 (82.5%)**	0.07 (17.5%)	0.40 (100%)
Shrubby vegetation - Secondary vegetation	**0.25 (62.5%)**	0.15 (37.5%)	0.40 (100%)
Pairwise among vegetation for dry season			
Open areas – Shrubby vegetation	0 (0%)	**0.25 (100%)**	0.25 (100%)
Open areas – Secondary vegetation	**0.33 (86.1%)**	0.049 (13.2%	0.36 (100%)
Shrubby vegetation - Secondary vegetation	0 (0%)	**0.18 (100%)**	0.18 (100%).
Pairwise among vegetation for rainy season			
Open areas – Shrubby vegetation	0 (0%)	**0.20 (100%)**	0.20 (100%)
Open areas – Secondary vegetation	0.16 (36.4%)	**0.27(63.6%)**	0.44 (100%)
Shrubby vegetation - Secondary vegetation	**0.16 (57.1%)**	0.12 (42.9%)	0.28 (100%)

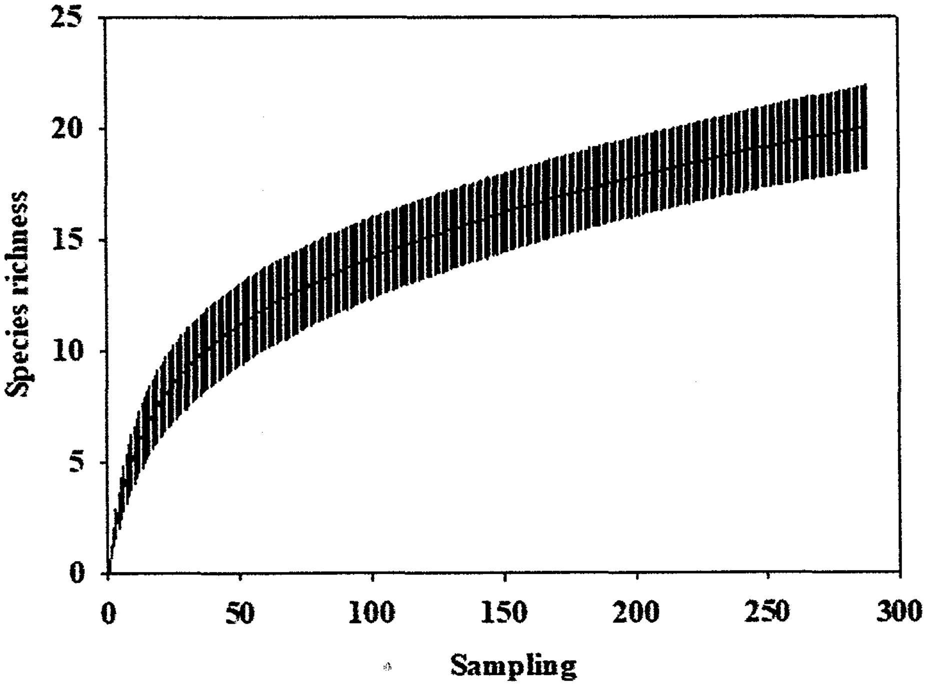

Figure 1 - Sample-based species accumulation curve for cavity-nesting bees and wasps in restinga domain. Error bars denote 95% *CI*.

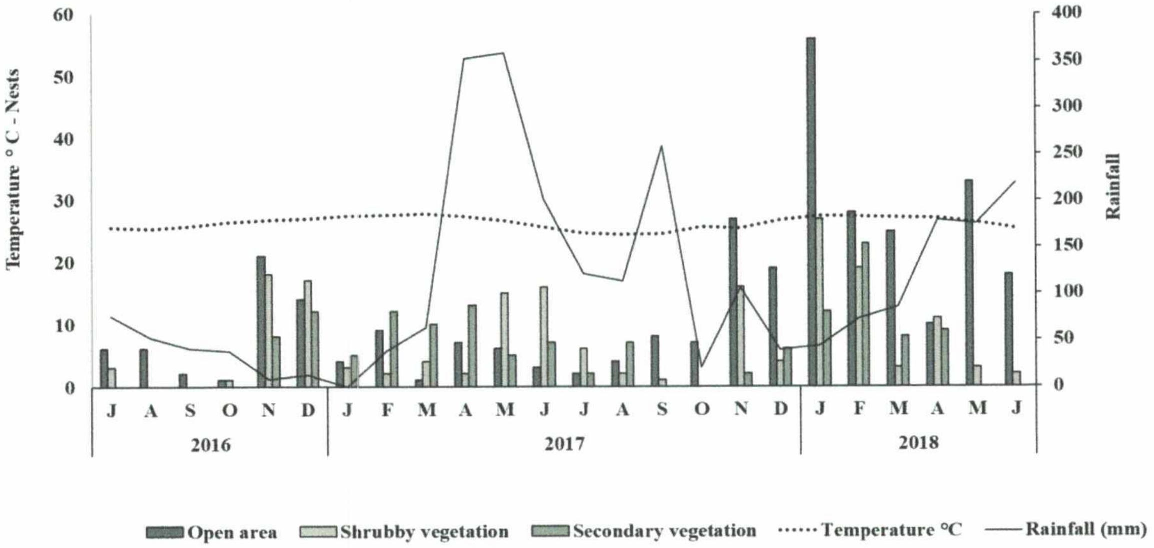

Figure 2 - Temperature (°C), rainfall (mm^3) and nests founded by cavity-nesting bees and wasps in open areas, shrubby and secondary vegetation in restinga domain over two year.

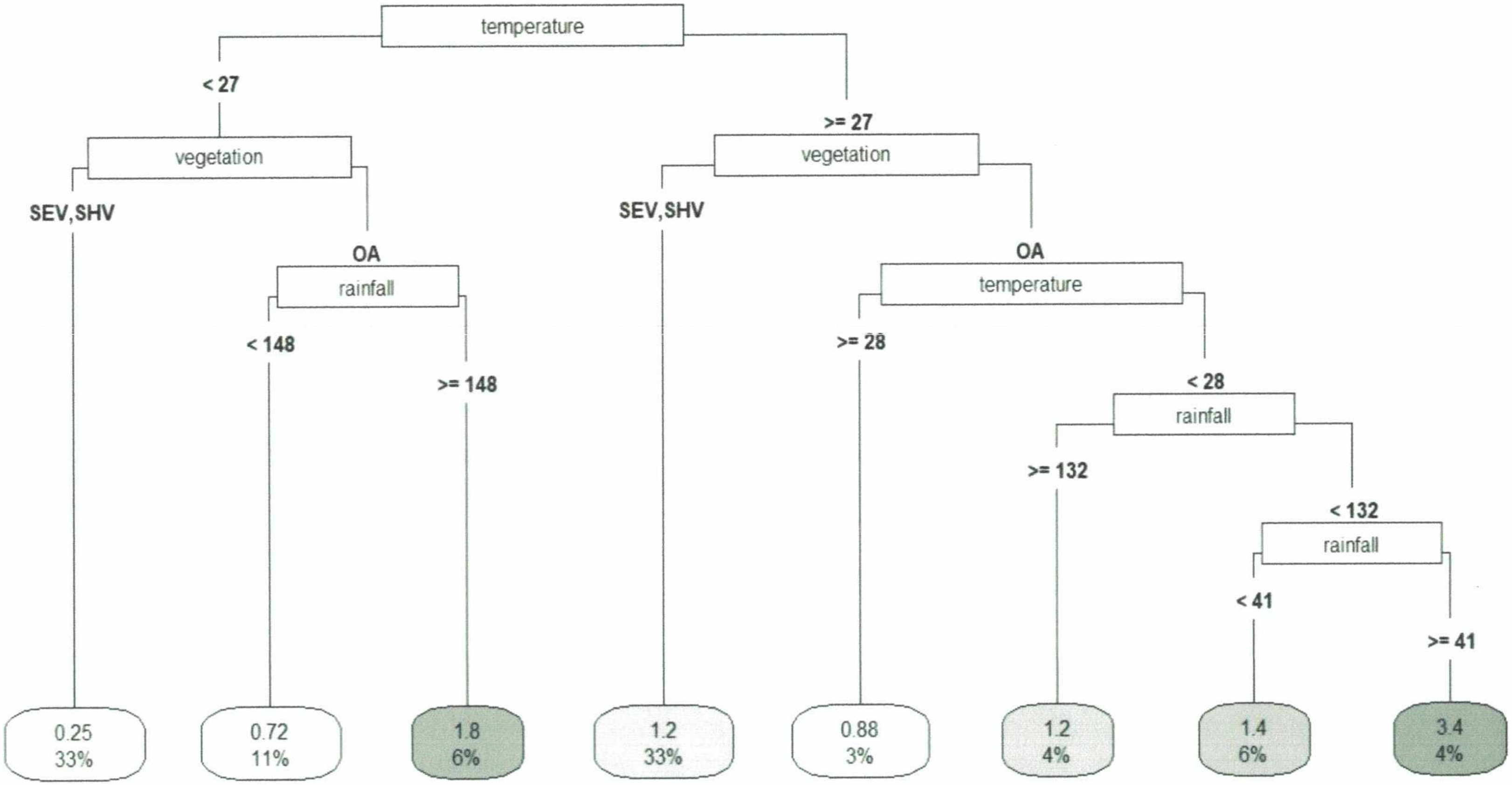

Figure 1 - Regression tree showing the influence of climatic conditions and vegetation types (OA- open area; SHV – shrubby; SEV - secondary vegetation) on nesting by cavity-nesting bees and wasps in restinga domain over two year.

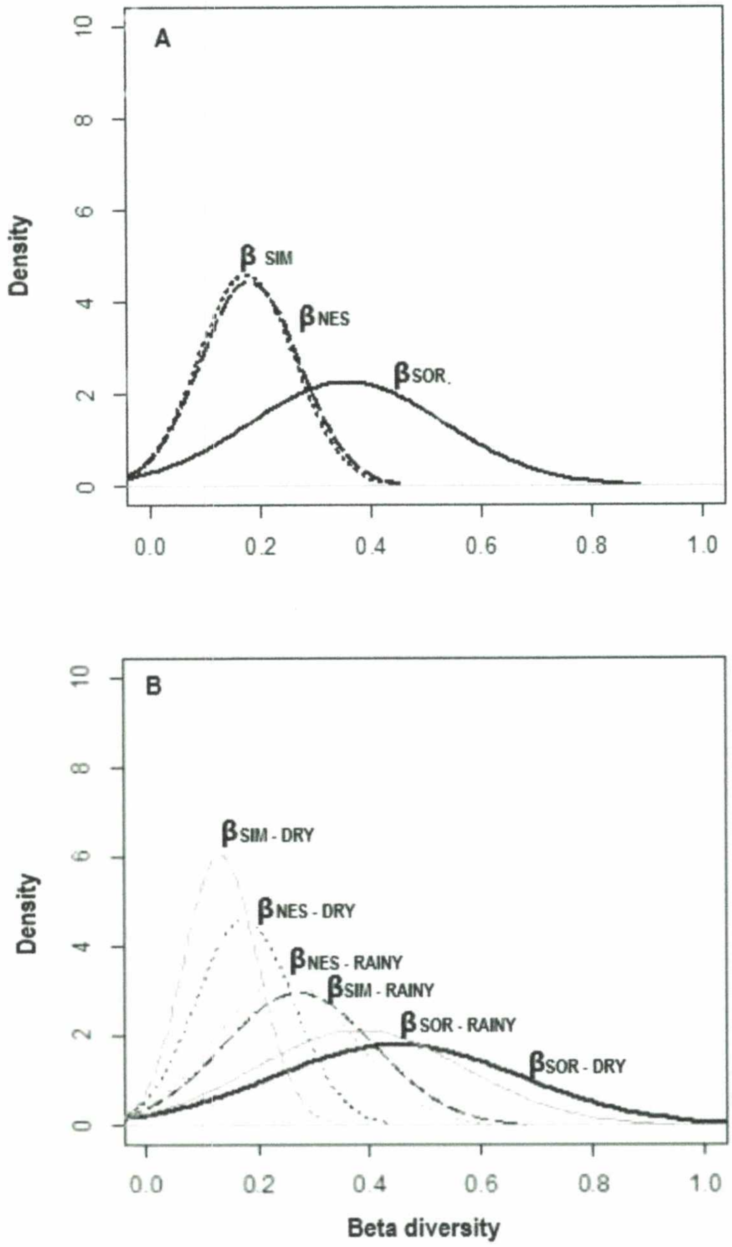

Figure 2 - Beta diversity components for cavity-nesting bee and wasp community. (A) Among the vegetations types of restinga domain (open area, shrubby and secondary vegetation); (B) During dryer and rainy season. βSIM (Simpson dissimilarity, i.e. species turnover), β_{NES} (nestedness) and β_{SOR} (Sørensen dissimilarity, i.e. total beta diversity).

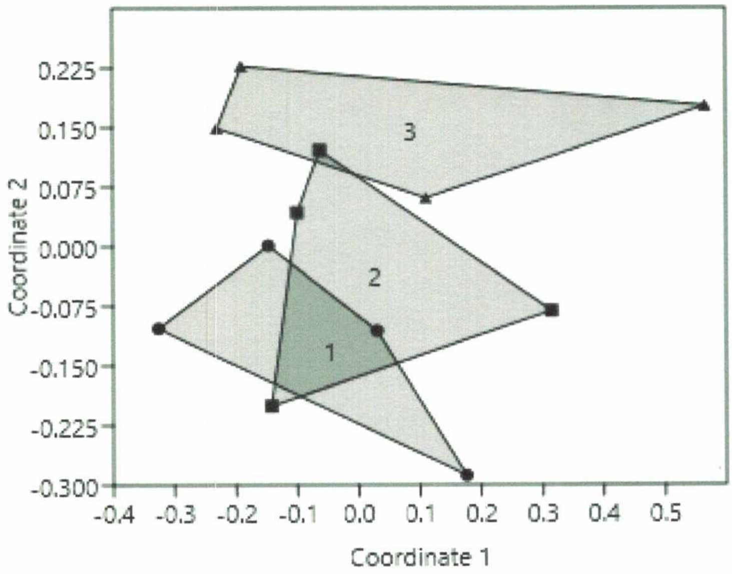

Figure 3- Non-metric scaling analysis of similarity (NMDS) ordination for species abundance of cavity-nesting bees and wasps in open areas (1), shrubby (2) and secondary vegetation (3) in restinga domain. NMDS were calculated based on Bray-Curtis similarity and Bonferroni correction at 5% level.

CAPÍTULO 3

Rainfall, temperature and vegetation type influence nesting by the oil-collecting bee *Centris* (*Hemisiella*) *tarsata* in Brazilian restinga

Manuscrito aceito pelo periódico Apidologie

Rainfall, temperature and vegetation type influence nesting by the oil-collecting bee *Centris* (*Hemisiella*) *tarsata* in Brazilian restinga

Nesting by *Centris tarsata* in restinga

Abstract

Solitary bees are the main pollinators of native plant species and crops, therefore understanding how they respond to environment is essential to maintain ecosystem function and services. Here, we assessed how climatic conditions and vegetation type influence *Centris tarsata* nesting in Brazilian restinga. Evaluations were conducted using trap-nests placed in open areas, shrubby and secondary vegetations, and at understory and canopy in open areas and secondary vegetations. Overall, nesting was higher during the dry season, mostly in open areas at 1.5m height. However, in shrubby and secondary vegetations nesting seems to be favored by a specific rainfall and temperature range. Furthermore, the amount of brood cells, total number of adults and nest length were higher in open areas compared to shrubby and secondary vegetations. Therefore, our results show that rainfall, temperature and vegetation structure are determining factors in *C. tarsata* nesting in the Brazilian restinga.

Keywords: **Trap-nests / cavity-nesting bees / pollinators / climate conditions / Malpighiaceae**

1 – INTRODUCTION

Mutualistic interactions between plants and pollinators play a fundamental role in the maintenance of ecosystem functions and services. Plants provide food resources such as pollen and nectar to pollinators, which in turn help fruit and seed formation through pollination services (Giannini et al. 2015). Bees are the most important and effective pollinators. Furthermore, they are ecologically and functionally diverse, forage on a wide variety of floral forms and nest on a myriad of substrates (Klein et al. 2007). The number of bee species worldwide could be as high as 30.000 species (Michener 2007), from which 85% have a solitary habit (Silva et al. 2001; Buschini & Wolff 2006). Solitary bee species have specific habitat requirements such as pre-existing cavities for nesting as well as flower resources (pollen, nectar and oil), and thus, they heavily rely on vegetation structure (Ebeling et al. 2012; Flores et al. 2018). Additionally, the reproductive success of solitary bees can be indirectly affected by climatic conditions owed to their influence on host plant community richness, composition, physiognomy and bee nesting biology. Therefore, habitat simplification has adverse effects on bee diversity, which makes preservation efforts pivotal for the maintenance of Aculeata populations (Morato & Campos 2000, Morato & Martins 2006; Faria & Gonçalves 2013; Flores et al. 2018).

Several studies evaluating solitary bee communities in areas with well-defined dry and rainy seasons revealed that *Megachile* sp. (Megachilidae), *Eufriesea nordestina* Moure, *Euglossa cordata* Linnaeus, *Tetrapedia diversipes* Klug, *Xylocopa frontalis* Olivier, and species belonging to the genus *Centris* such as *Centris tarsata* Smith, *C. analis* Fabricius and *C. vittata* Lepeletier (Apidae) are the most common species (Aguiar & Martins 2002; Aguiar et al 2005, Mesquita &

Augusto 2011, Flores et al 2018). The genus *Centris* encloses medium to large sized solitary bee species, it is predominantly occidental, and distributed from tropical areas of Argentina and Bolivia to the United States (Silveira et al. 2002; Michener 2007). These species need a rich flora to obtain food resources such as nectar, pollen and floral oils for both larvae and adults. *Centris* (*Hemisiella*) *tarsata* (Smith), 1874 is widely distributed in Brazil and it has been recorded in different biomes and climatic conditions countrywide (Silva et al. 2001; Aguiar & Martins 2002; Aguiar & Garófalo 2004; Buschini & Wolff 2006, Mendes & Rêgo 2007, Mesquita & Augusto 2011, Flores et al. 2018).

Although some studies have investigated the vertical nesting of bees in tropical forests (Morato 2001; Mendes & Rêgo 2007; Stangler et al. 2015), they were carried out in the Amazon forest and in semi-deciduous vegetation in Brazil, and in forest remnants in Costa Rica. Information on bee nesting preference for understory or canopy is scarce, and to our knowledge no study has addressed the vertical nesting behavior of solitary bees in restinga. This tropical and subtropical ecosystem is typical on coastal regions, and it is composed by herbaceous plants, shrubs and arboreous strata on sandy plains under marine influence (Souza et al. 2008; Serra et al. 2016). Accordingly, we addressed the following questions: (1) is there an association among climatic conditions, type of vegetation and *C. tarsata* nesting behavior? (2) Do nest architecture (brood cell number built, nest length, cavity width, thickness of entrance and partition walls, and volume of cell) biological characteristics and parasitism vary among vegetation types? (3) Is there preference for *C. tarsata* nesting at different vegetation strata?

2 – MATERIAL AND METHODS

2.1 – Study area

The study was carried out in a protected area (763.37 ha) belonging to Empresa Brasileira de Pesquisa Agropecuária (Embrapa) in the municipality of Itaporanga D'Ajuda (11° 06'16.19 "S; 37° 11'05.89" W), in the northeastern Brazilian State of Sergipe. According to Köppen classification, predominant climate in the region is tropical with marked dry (September to February) and rainy (March to August) seasons, with average annual rainfall above 1250 mm. The biome is Atlantic rainforest composed by a matrix of mangrove, restinga and apicum (sandy open areas influenced by the tidal regime). The study was conducted within the restinga domain (Nogueira Junior et al. 2013). Rainfall and temperature were respectively obtained from a meteorological station located in the area and from the Instituto Nacional de Meteorologia (INMET), on a per-month basis.

2.2 - Sampling

Trap-nests consisted of 15 pieces of hollow bamboo canes (20.0cm long) with one node in the middle, forming two internodes (9.0 to 11.0cm deep). Bamboo canes had internal diameters ranging from 0.3 to 2.0cm evenly distributed (5 hollow bamboo canes of 0.3 to 0.8cm, 5 of 0.9 to 1.4cm and 5 of 1.5 to 2.0cm of diameter) and they were wrapped together with a 22.0cm wide plastic sheet and wire, totaling thirty cavities. Trap-nests were set up in three vegetation types in restinga, viz. (1) open areas - dominance of grasses as *Paspalum maritimum* Trind., weeds, cactus (*Melocactus zehntneri,* Britton & Rose) and some sparsely distributed trees, direct sunlight; (2) shrubby vegetations - dominance of shrubs and few tree species as *Anacardium occidentale* L., *Byrsonima crassifolia* L. Kunth, *Myrciaria tenella* D.C. Berg, some grasses, partial shading with high luminosity; and (3) secondary vegetations – dominance of medium to large tree species as *A. occidentale, Hancornia speciosa* Gomes, *Tapira guianensis* Aublet and *Inga* sp., dense vegetation, soil covered by a thick litter layer, shaded with low luminosity. Four replicates for each vegetation type were chosen, totaling twelve sampling areas. Study sites were usually clustered in groups of three vegetation types to avoid spatial autocorrelation (Teodoro et al. 2011). At each study site, four trap-nests were hung by a wire and attached to a tree branch at 1.5m above the ground and distanced 1.0m from each other. Entomological glue was monthly applied to the wire to avoid crawling arthropods. Trap-nests were monthly inspected throughout two years (from July 2016 to June 2018) and nested bamboo canes were removed and replaced with empty ones with similar internal diameter.

Nested bamboo canes were individualized in a plastic cage and kept indoors at 27°C ± 2°C until the emergence of *C. tarsata* adults and their cleptoparasites, also known as cuckoo bees or cuckoo wasps that loot brood cells storage (Ebeling et al. 2012) and parasitic flies. Emerging adults were killed, sexed and the morphometry was performed. Nest architecture features such as the count of brood cells and measures of total nest length (from the first to last cell built), nest width, and thickness of the brood cell partition and entrance wall were also evaluated with a caliper ruler. Brood cell volume was calculated by the formula: $\pi.r^2.h$, where r is the width and h the length of the cell. Wings of three adults of each sex were measured with a scale-magnifier model MG13100, totaling 12 adults (females and males) from each vegetation type, except for secondary vegetation where in one of the sampling areas, no adults emerged. Identification of nest building material and counting of dead immatures (no emerging individuals of *C. tarsata*, cleptoparasites or offspring who died in early stages) were performed three months after the nests were taken to the laboratory.

2.3. - Nesting stratification

An additional nesting stratification preference study was performed by lining up two trap-nests tied together with a wire and attached to a rope at 1.5, 3.5 and 5.5m height in open areas and secondary vegetations, with four replicates. The rope was attached to a pulley at the tip of a 7.0m high bamboo pole. Entomological glue was applied to bamboo pole base to prevent crawling arthropods. Evaluations were monthly conducted for one year, beginning in September 2016, and the nested bamboo canes were taken to the laboratory and replaced by empty ones with similar internal diameters. Nested cavities were kept indoors as explained above.

2.4 - Statistical analyses

Data were nested and analyzed using generalized linear mixed-effects models (GLMEs) with Poisson (discrete variables) or Gaussian (continuous variables) error distributions (Crawley 2007). The models were subjected to analysis of variance (ANOVA), and *a posteriori contrasts* were performed to assess differences among treatments (Crawley 2007). Spearman correlations were performed between the number of nests built and temperature, rainfall and tree abundance using ISwR package. Pearson's chi square test (χ^2) was performed to compare *C. tarsata* sex ratios among vegetation types. All analyses were performed with R software version 3.3.1 (R Development Core Team 2016) and subjected to residual analyses in order to assess the suitability of the models and error distributions (Crawley 2007).

A classification and regression tree analysis was further performed for a better understanding of how climatic conditions influenced *C. tarsata* nest building on different vegetation types. Evaluation period (month), temperature (°C), rainfall (mm) and vegetation types were considered as explanatory variables, while the number of nests built by *C. tarsata* was treated as response variable. The root node represents total sampling, which further divides into two or more sets called decision nodes and into sub-nodes and/or terminal nodes. Differences among sub-nodes and parent node were accessed through the Chi-Squared Automatic Interact Detection (CHAID) method (Kass 1980). The analysis was performed in XLSTAT 2014.5.3 and adjusted by Bonferroni correction, at 5% significance level.

3 - RESULTS

3.1 – *Centris tarsata* nesting according to vegetation type

A total of 162 nests of *C. tarsata* were collected, the majority in open areas (52.47%), 37.03% in shrubby and only 10.50% in secondary vegetations. Altogether, 585 adults of *C. tarsata* emerged from the nests, most of them from open areas (59.6%), followed by 32.14% from shrubby vegetations and 8.20% from secondary vegetations. The cuckoo bee *Mesocheira bicolor* Fabricius (54.05%) was the main *C. tarsata* natural enemy emerging from nests, followed by an Anthidiini species

(37.84%) and *Coelioxys* sp. (1.8%) (Megachilidae). Other natural enemies emerging from nests were the dipterans *Anthrax* sp1 (4.5%) and *Anthrax* sp2 (1.8%) (Bombyliidae).

Centris tarsata nesting period lasted from October 2016 to February 2017, peaking in November and December during the dry season. A new nesting cycle was recorded from September 2017 until January 2018, peaking in November and in January (Fig. 1). Nesting was negatively correlated with rainfall (*rho* = -0.581, *P* <0.01) and abundance of tree species (*rho* = -0.755, *P* <0.01), but not with temperature (*rho* = 0.2047, *P*>0.05).

Classification and regression tree analysis yielded five levels of depth as shown in Figure 2. In higher temperatures, the mean number of nests was 0.81 in 36% of samples (*P*<0.001) contrasting with a lower number (0.28) in 64% of samples in lower temperatures (*P*<0.05). In shrubby and secondary vegetations, nesting mostly occurred when temperatures were high and associated to a low rainfall (*P*<0.001). Also, there was no nesting in 16% of samples in shrubby and secondary vegetations with increasing rainfall (*P*<0.001). In open areas, the main explanatory factor was the sampling period, being the mean number of nests (1.25) higher in December in 1.3% of samples (*P*<0.001) followed by September and October. Moreover, the mean number of nests was higher (4.0) in 1.3% of samples (*P*<0.001) when the temperature increased in June, July, August and November. In those months, there was a decrease in cumulative rainfall in relation to the previous period (Fig. 1).

3.2 Nest architecture and bionomical characteristics

Nests were constructed with a mixture of sand and vegetal oil which covered the outer wall of the entrance, hardening after dry. Brood cells were arranged according to cavity width, linear in smaller sized cavities, perpendicular in medium sized and in some cases, overlapping each other in larger cavities. The inner brood cell was smooth and hard in appearance, covered by a cellophane-like film. Brood cells contained a dark yellow to brown mixture of pollen and nectar as food supply for larvae.

The number of brood cells built per nest differed among vegetation types: open areas had the highest numbers, followed by shrubby and secondary vegetations. There was no difference in nest width, wall thickness, and brood cell volume among vegetation types. The partition wall thickness of the brood cells was higher in secondary vegetations compared to open areas and shrubby vegetations (Table I).

After field collection, emergence of adults from nests ranged from 2.0 to 49.0 days for males and from 4.33 to 40.6 days for females. The total number of emerged adults and males of *C. tarsata* was influenced by vegetation types ($\chi^2 = 4.84$, d.f.=1, $P<0.001$; $\chi^2 = 7.75$, d.f. = 1, $P<0.01$, respectively), being highest in shrubby vegetations, followed by open areas and secondary vegetations. The mean number of females, cleptoparasites and dead immatures were also influenced by vegetation types ($\chi^2 = 15.67$ d.f. = 1, $P<0.001$; $\chi^2 = 6.62$, d.f. = 1, $P<0.01$; $\chi^2 = 31.67$, d.f. = 1, $P<0.01$, respectively), with higher values for open areas, followed by shrubby and secondary vegetations. There was no difference in the size of male or female wings ($\chi^2 = 0.48$, d.f. = 2, $P>0.05$; $\chi^2 = 0.08$, d.f. = 2, $P>0.05$, respectively) (Table I) among vegetation types. Sex ratio was significantly male biased in secondary vegetations (sr= 1:0.37, $\chi^2 = 13.13$, d.f. = 5, $P< 0.05$), but not in open areas (sr = 1:0.35, $\chi^2 = 19.33$, d.f. = 19, $P>0.05$) and shrubby vegetations (sr = 1:0.27, $\chi^2 =17.42$, d.f. = 13, $P>0.05$).

3.3 – Nesting stratification

A total of 31 nests founded by *C. tarsata* were collected, roughly half of which (14 nests) in open areas and closer to the soil (1.5m height), followed by 9 and 3 nests at 3.5m and 5.5m height, respectively. We observed considerable fewer nests in secondary vegetations (16.13%; 1 nest at 1.5m, and 2 nests at 3.5m and 5.5.m height). The cuckoo bee *M. bicolor* was the only cleptoparasite that emerged from the nests and it was found only in open areas.

The highest number of brood cells and dead immatures ($P<0.001$) was recorded at 1.5m height and the lowest at 5.5m in open areas. The total of individuals was lower in nests closer to the canopy (at 5.5m height) when compared to those nearer to the soil (1.5m height). Neither vegetation nor trap-nest height influenced the total number of males and females (Table II).

4 - DISCUSSION

Rainfall was the main climate condition explaining *C. tarsata* nesting patterns over the 2-year sampling period, and it was negatively correlated with nesting. In contrast, temperature had no influence on nesting, possibly owing to its low variation throughout the year, which contrasts with well-defined rainy and drought periods in the study region. However, when temperature and rainfall were analyzed in relation to the type of vegetation and throughout the sampling period, new results emerged. The classification and regression tree shows two distinct groups of *C. tarsata* (Fig. 2): one influenced directly by rainfall and temperature and another influenced by the sampling period. Nesting in shrubby and secondary vegetations was favored at low rainfall and high temperature, increasing rainfall ceases nesting, possibly because high humidity is unfavorable for nesting. In open areas, *C. tarsata* nesting was also generally concentrated during the dry season, in months of low rainfall and higher temperatures. Either drought or rainfall periods beyond normal may disturb floral resources availability, and consequently bee frequency. The frequent annual population fluctuations appear to be a regular feature for bee species that nest in pre-existing cavities (Frankie et al. 1998).

This nesting pattern in the dry season is consistent with results from other Brazilian vegetations such as eucalyptus, riparian and mesophytic forests in Maranhão State, semideciduous seasonal forest and open savanna in Paraíba State, and swamps and pastures in the southern region (Aguiar & Martins 2002; Buschini & Wolff 2006; Mendes & Rêgo 2007). However, Aguiar and Garófalo (2004) observed more *C. tarsata* nests during the rainy season in semi-deciduous and semiarid caatinga vegetations. Sunny habitats can provide more resources for the construction and provision of nests, such as floral resources, when compared to shaded habitats, as observed in open areas. Concerning floral resources, we frequently observed *C. tarsata* foraging on *Byrsonima crassifolia* (Malpighiaceae) mainly in shrubby vegetations, which is in line with other studies that recorded bees foraging for oil and pollen on *Byrsonima* spp. (Mendes & Rêgo 2007; Mello et al. 2013).

Our results show that *C. tarsata*, in restinga vegetation, act as a bivoltine species with two generations per year, each generation lasting approximately two months. Nests were found for only five months per year, in both years. Similar results were found by Buschini & Wolff (2006) for *C. tarsata* and by Martins et al (2014) for *C. flavifrons*. Aguiar & Garófalo (2004) studying *C. tarsata* nesting behavior in caatinga and semi-deciduous vegetation observed some nests diapausing after being established in mid rainy season (caatinga vegetation) or in mid dry season (semi-deciduous vegetation), both stressful periods. These authors suggested that *C. tarsata* possibly spends stressful periods either as adults or as prepupae in diapause to withstand harsh environmental conditions. In fact, evidence indicates that diapause is the primary mechanism through which the annual rhythm of insect life-history phases are appropriately synchronized to seasonal conditions, and it is subjected to both genetic and environmental influence (Tauber & Tauber, 1981; Faria & Gonçalves, 2013). Another strategy may be taking shelter in unknown places, as suggested by Pereira et al (1999) and Ramos et al (2010). Adults of *C. tarsata* might diapause in restinga vegetation during stressful periods, but this remains yet to be investigated.

Regarding nest architecture, *C. tarsata* females built thicker brood cells partition wall in secondary vegetations compared to open areas and shrubby vegetations. This could be related to the smaller amount of resources for nest building (sand) in secondary vegetations, since its ground is covered by a large amount of litter. However, vegetation type did not influence the thickness of entrance plug wall and we observed a layer of oil outside of all nests entrance plug, which may be a characteristic from subgenus *Hemisiella* to protect the nest (Pereira et al. 1999; Buschini & Wolff, 2006).

Sex ratio was male biased in secondary vegetation, but not in open areas and shrubby vegetations. Aguiar & Martins (2002) and Aguiar & Garófalo (2004) also reported a male-biased sex ratio for *C. tarsata*. However, Silva et al. (2001), Buschini & Wolff (2006) and Mendes & Rêgo (2007) found a female-biased sex ratio. According to Silva et al. (2001), sex ratio is often variable, and it is associated to the abundance of resources available in the environment for females. Also, a lower number of emerging females might be caused by parasitism, as parasites and cleptoparasites prefer female brood cells, possibly due to higher nutritional quality of food stored (Aguiar & Martins 2002; Buschini & Wolff 2006).

Cleptoparasites observed in *C. tarsata* nests were the cuckoo bees *M. bicolor*, *Coelioxys* sp. and Anthidiini, and the dipterans *Anthrax* sp1, *Anthrax* sp2, which were also recorded in other Brazilian biomes (Aguiar & Martins 2002; Aguiar & Garófalo 2004; Buschini & Wolff 2006). According to a study carried out in small secondary forest remnants in Costa Rica, parasitism rates tend to be high in the understory due to the dominance of *Centris*, which was observed nesting at 2.0m height (Stangler et al. 2015). Here, the low parasitism rate recorded in the understory may possibly be due to the low number of nests founded. Therefore, further studies are needed to elucidate the parasitism of *C. tarsata* in restinga, mainly in the understory and canopy.

The number of dead immatures was higher in open areas, possibly due to a related high number of nests and brood cells built. Moreover, climate conditions, especially temperature, can reach extreme values in open areas, potentially increasing larvae and juvenile bee mortalities (Jesus & Garófalo 2000; Aguiar & Garófalo 2004; Buschini & Wolff 2006).

In open areas, *C. tarsata* preferred to nest in trap-nests near to the ground unlike in secondary vegetations, where only one nest was built at this height. This preference for lower heights in restinga may be favored by proximity from nest building resources such as sand, and floral source such as oil, nectar and pollen. On the other hand, for denser habitats such as secondary forests, microclimatic conditions may be more favorable for nesting at higher strata, which may explain our results for secondary vegetation. Also, Mendes & Rêgo (2007) observed that *C. tarsata* built more nests in the canopy of eucalyptus (5 to 12m height) and mesophytic forest (12.0m height) compared to nests at 1.5m heigh.

In restinga, rainfall is a determining factor in *C. tarsata* nesting which was concentrated in the dry season, mainly in open areas, where we also recorded the greatest amount of brood cells and highest nest length. In shrubby and secondary vegetations, nesting seems to be favored by specific climatic conditions present in the understory and canopies especially in the harsh dry season. *Centris tarsata* preferred to nest in the understory in secondary vegetations and open areas, however, further studies on nesting behavior and exploitation of floral resources in restinga are needed in order to improve the management and maintenance of related ecosystem functions and services.

ACKNOWLEDGMENTS

We are thankful to Dr. Felipe Vivallo from Museu Nacional do Rio de Janeiro for the collaboration in the identification of *C. tarsata*. We also thank both reviewers for helpful comments and suggestions, and to the Coordenação de Aperfeiçoamento de Pessoal (CAPES) for granting the scholarship for the first author and to Embrapa

Tabuleiros Costeiros for permission to assess the study area and for providing logistical support.

AUTHORS CONTRIBUTIONS DMC and AVT conceived this research and designed experiments; MCB participated in the design, analysis and interpretation of the data; ASB participated in the design; IB performed analysis and interpretation of the data. All authors read and approved the final manuscript.

CONFLICT OF INTEREST

"The authors declare that they have no potential conflict of interest in relation to the study in this paper".

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Table I - Nest architecture and bionomical characteristics of *C. tarsata* individuals in relation to restinga vegetation types

	Open areas		**Shrubby vegetations**		**Secondary vegetations**				
	X ± SD	N	*X* ± SD	N	*X* ± SD	N	χ^2	d.f.	*P*
Total brood cells	12.87 ± 23.96	515	7.32 ± 12.73	293	2.30 ± 4.45	92	214.6	1	<0.001
Nest lenght (cm)	5.95 ± 1.33	85	5.43 ± 1.54	60	4.48 ± 1.05	17	6.69	1	<0.05
Cavity width (cm)	1.45 ± 1.59	85	1.66 ± 2.30	60	1.07 ± 0.27	17	0.61	2	>0.05
Thickness of partition walls (mm)	0.77 ± 0.004	85	0.78 ± 0.01	60	0.79 ± 0.017	17	5.66	1	<0.05
Thickness of the entrance walls (mm)	0.82 ± 0.063	85	0.79 ± 0.026	60	0.82 ± 0.024	17	0.11	2	>0.05
Volume of cells (cm^3)	2.06 ± 0.56	85	1.89 ± 0.43	60	2.06 ± 0.70	17	0.43	2	>0.05
Total of individuals	13.04 ± 16.46	349	14.35 ± 19.13	188	3.31 ± 5.10	48	4.84	1	<0.001
Total of males	8.27 ± 11.18	224	9.47 ± 11.58	138	2.31 ± 3.56	30	7.75	1	<0.01
Total of females	4.77 ± 6.17	125	4.11 ± 5.36	50	1.5 ± 2.15	18	15.67	1	<0.001
Total of Cleptoparasites	1.32 ± 2.64	52	1.92 ± 3.99	29	0.22 ± 0.61	5	6.62	1	<0.01
Total of dead immatures	2.82 ± 7.0	114	1.9 ± 3.87	76	0.95 ± 2.09	39	31.67	1	<0.001
Male wing lenght (mm)	9.71 ± 0.75	12	9.61 ± 0.72	12	9.83 ± 0.86	9	0.48	2	>0.05
Female wing lenght (mm)	9.94 ± 0.53	12	9.94 ± 0.60	12	10.0 ± 0.68	8	0.08	2	>0.05

N = total number, *X* ± SD = mean ± standard deviation

Table II - Influence of vegetation and height on nesting features by *C. tarsata* in restinga open areas, shrubby and secondary vegetations.

Response variable	**Explanatory variable**	χ^2	**d.f**	***P***
Brood cells	Vegetation	34.503	1	<0.001
	Height	66.109	2	<0.05
	Vegetation x height	87.237	2	<0.001
Dead immatures	Vegetation	46.145	1	<0.05
	Height	36.669	2	<0.001
	Vegetation x height	82.519	2	<0.05
Total individuals	Vegetation	0.191	1	> 0.05
	Height	42.019	2	>0.05
	Vegetation x height	6.224	2	<0.05
Total males	Vegetation	0.411	1	>0.05
	Height	2.598	1	>0.05
	Vegetation x height	0.2507	2	>0.05
Total females	Vegetation	1.901	1	>0.05
	Height	1.626	1	>0.05
	Vegetation x height	2.313	2	>0.05

ANEXO

ANEXO – A

Types of Papers

Paper (up to 5,000 words): studies that will advance our understanding of evolutionary, ecological, or conservation theory in tropical systems. The data used to test hypotheses can be collected using any rigorous approach (e.g., experimental, observational, genetic, etc.).

Manuscript Format

Submit the entire manuscript, including figures and tables, as a single Microsoft Word document (*.doc or .*docx), or equivalent
for **Do NOT submit papers as pdf files**.

Use 8.5" x 11" page size (letter size) with a 1" margin on all sides. Align left and do not justify the right margin. Number all pages starting with the title page and include continuous line numbers.

Double space throughout the manuscript, including tables, figures and tittle legends, abstract, and literature cited

Use Times New Roman 12-point font throughout except in figures, for which Arial is preferred.

Use the abbreviations provided in Section D (below) throughout the text.

Assemble manuscripts in this order:

1. **Title page**
2. **Abstract (s)**
3. **Data Archiving Policy**
4. **Keywords**
5. **Text**
6. **Tables**
7. **Figure legends**
8. **Figures**
9. **Acknowledgments**
10. **Disclosure Statements**
11. **References**
12. **Supplementary Information (to be supplied as separate files)**

1. TITLE PAGE

Running Heads: The authors' family name should be included as left and right running heads. It is set in small caps. The format is as follows:

LRH and RRH: YAZ and PEIGH

(may not exceed 50 characters, two or more authors use YAZ et al.)

Title: No more than 12 words (usually), flush left, near the middle of the page. Use Bold Type.

Where species names are given in the title, it should be clear to general readers what type(s) of organism(s) are being referred to, either by using Family appellation or common name:

'Invasion of African savanna woodlands by the Jellyfish tree *Medusagyne oppositifolia*', **OR** 'Invasion of African savanna woodlands by *Medusagyne oppositifolia* (Medusagynaceae)'

Titles that include a **geographic locality** should make sure that this is clear to the general reader:

'Effect of habitat fragmentation on pollination networks on Flores, Indonesia', **NOT**

'Effect of habitat fragmentation and pollination networks on Flores'.

Authors: Below title, include the author(s) full name(s), affiliation(s), and unabbreviated complete address(es). Use superscript number(s) following author(s) name(s) to indicate current location(s) if different than above. In multi-authored papers, additional footnote superscripts may be used to indicate the corresponding author and e-mail address. Although geographical place names should use the English spelling in the text (e.g., Zurich, Florence, Brazil), authors may use their preferred spelling when listing their affiliation (e.g., Zürich, Firenze, Brasil).

Submission and Acceptance Dates: At the bottom of the title page every article must include: Received: ______; Revised:____(optional); Accepted:______. (*Biotropica* will fill in the dates.)

2. ABSTRACT PAGE

Abstracts have maximum of 250 words for papers and reviews and 50 words for Insights. There is no abstract for Commentary papers.

The Abstract should include brief statements about the intent or purpose, materials and methods, results, and significance of findings. Abstract can be given as multiple paragraphs (with subheadings such as Aim, Methods, Results, and Conclusion) or as a single paragraph. Do not use abbreviations in the abstract.

Authors are strongly encouraged to provide a second abstract in the language relevant to the country in which the research was conducted. The second abstract will be published in the online versions of the article. This second abstract should follow the first abstract.

3. KEYWORDS

Provide up to eight keywords after the abstract, separated by a comma (,). Keywords should be in English (with the exception of taxonomic information) and listed alphabetically.

Include the location of the study as a key word if it is not already mentioned in the title (see example below). Key words should *not* repeat words used in the title. Avoid words that are too broad or too specific. (e.g., keywords: Melastomataceae, *Miconia argentea*, Panama, seed dispersal, tropical wet forest).

4. TEXT

Headings

Main headings are 1. INTRODUCTION, 2. METHODS, 3. RESULTS, and 4. DISCUSSION in bold, capital letters, numbered, and flush left.

Indent all but the first paragraph of each section.

Leave one blank between main heading and text.

Second level headings should be in Initial caps, bold, numbered, and flush left. (e.g., **2. Inventory technique.**)

First three headings are numbered and fourth and fifth order headings are unnumbered.

Insights submissions do not use any subject headings.

When using previously published data in analyses please cite both the data archive(s) and the original manuscript(s) for which they were collected in the text: "We used previously archived data (Bruna et al., 2011a,b) in our simulations.", where a is the data archive and b is the publication. Be sure both citations are included in the literature cited.

Do not use footnotes in the main text.

Refer to figures as 'Figure 1', and tables as 'Table 1'. Reference to online Supporting Information is referred to as 'Figure S1' or 'Table S1'.**Units, Abbreviations, and style**

Abbreviations: year(s), month(s), week(s), day(s), hr, min, s, km, cm, mm, ha, kg, g, L, g/m2

Units: Use solidus style for simple units (e.g., m/s) and follow negative indices style for compound units (e.g., $\text{nmol} \cdot \text{hr}^{-1} \cdot \text{mg}^{-1}$)

Write out other abbreviations the first time they are used in the text and abbreviate thereafter: "El Niño Southern Oscillation (ENSO) . . ."

Numbers: Write out one to 9 unless a measurement or in combination with other numbers: four trees, 6 mm, 35 sites, 7 year, 10 × 5 m, 7 m, ± *SE,* 5 bees and 12 wasps).

Use a comma as a separator in numbers with four or more digits: 1,000 vs. 10,000

Decimals: 0.13 (leading zero and points, never commas)

Temperature: 21°C (no space after the degree symbol)

Use dashes to indicate a set location of a given size (*e.g.,* 1-ha plot).

Spell out 'percent' when used at the beginning of a sentence and use symbols when used in number combinations (e.g., "there was a 5% increase…", "plants were grown at high light levels (20%)…", 95% CI.)

Statistical abbreviations:

- Use italics for *P, N, t, F, R2, r, G, U, N,* χ^2 (italics, superscripts non-italics)
- Use italic for: *df, SD, SE, SEM*
- Use roman for CI, two-way ANOVA, ns

Dates: 10 December 1997

Times: 0930 h, 2130 h

Latitude and Longitude: 10°34′21″ N, 14°26′12″

Above sea level: a.s.l.

Regions: SE Asia, UK, USA (no periods

Geographical place names should use the English spelling in the text (Zurich, Florence, Brazil), but authors may use their preferred spelling when listing their affiliation (Zürich, Firenze, Brasil).

Lists: Follow the style**...** (a)... ; (b)...; and (c)...: "The aims of the study were to: (a) evaluate pollination success in *Medusagyne oppositifolia*; (b) quantify gene flow between populations; and (c) score seed set."

5. TABLES (Continue page numbering)

While Biotropica does have word limits that differ by manuscript category, there are not have strict limits on the number of tables and/or figures. However, printed manuscripts rarely exceed 32 pages in length, and we encourage authors to submit only necessary tables and figures. Additional information, figures, and tables should appear in the Supporting Information."

Each table must start on a separate page

Number tables with Arabic numerals followed by a period. Capitalize 'Table' (e.g., Table 1, Table 2, etc.).

Indicate footnotes by lowercase superscript letters

Do not use vertical lines in tables.

6. FIGURE LEGENDS (Continue page numbering)

Type figure legends in paragraph form, starting with 'Figure' and number.

Do not include symbols (lines, dots, triangles, etc.) in figure legends; either label them in the figure or refer to them by name in the legend

Label multiple plots/images within one figure as a, b, c etc., and please ensure the panels of each plot include these labels and are referred to in the legend (e.g., Figure 1 Fitness of *Medusagyne oppositifolia* as indicated by (a) seed set and (b) seed viability', making sure to include the labels in the relevant plot.)

7. FIGURES

ATBC members can publish graphs and other figures of results in color at no additional charge. Please make sure these figures are accessible by following our **Figures Guidelines.**

Please consult Wiley Author Services' **figures and illustrations guide** (PDF) for more detailed information about submitting electronic artwork. Authors are encouraged to utilize online Supporting Information for tables and figures that do not have central importance to the manuscript.

All figures and photographs are referred to as 'Figures' in the text.

If it is not possible to submit figures embedded within the text file, then submission as *.pdf, *.tif or *.eps files is permissible.

Native file formats (Excel, DeltaGraph, SigmaPlot, etc.) cannot be used in production. When your manuscript is accepted for publication, for production purposes authors will be asked upon acceptance of their papers to submit.

Line artwork (vector graphics) as *.eps, with a resolution of > 300 dpi at final print size

- Bitmap files (halftones or photographs) as *.tif or *.eps, with a resolution of >300 dpi at final sizeFinal figures will be reduced.
- To ensure all text will be legible when reduced to the appropriate size use large legends and font sizes. We recommend using Arial for labels within figures without bolding text.

Do not use negative exponents in figures, including axis labels.

Each plot/image grouped in a figure or plate requires a label (*e.g.*, a, b). Use lower case letters on grouped figures, and in text references.

8. ACKNOWLEDGEMENTS

Authors are encouraged to acknowledge funding, general supervision of the research group, or general support, in addition to any writing assistance, technical editing, language editing, and proofreading provided outside of the typical production process.

Author Contribution Statement

Authors are required to follow this taxonomy to identify each contributor's role. Please visit **https://www.casrai.org/credit.html** to learn more about the initiative and see the contributor roles to use when creating your statement.

9. DISCLOSURE STATEMENTS

Authors must provide the following disclosures where relevant, in the body of their manuscript (after acknowledgements, before references). If any of the following are not relevant to their research, a null statement is required. If no statement is given, we will may publish the article with statements indicating as such.

Conflict of Interest

Authors must disclose interests that might affect, or appear to affect, their ability to present or review work objectively. These might include relevant financial interests (for example, patent ownership, stock ownership, consultancies, or speaker's fees), or personal, political, or religious interests.

During submission, the corresponding author will be responsible for identifying potential conflicts of interest.

10. REFERENCES (follow APA Style Manual, 6th Edition)

We strongly recommend using reference management software such as Zotero or Endnote to simplify building the literature cited and to minimize mistakes.

- Citations of manuscripts as 'in ' or 'submitted' or 'in progress' are acceptable – similar to articles published, 'in press', or that have been deposited in pre-print archives (include DOI). Articles or book chapters cited as 'In press' must be accepted for publication; please include the journal or publisher.
- Verify all entries against original sources, especially journal titles, accents, diacritical marks, and spelling in languages other than English.

- When using data archives in the paper, cite both the data archive and the original manuscript using the following format

Bruna, E. M., Izzo, T. J., Inouye, B. D., Uriarte, M., & Vasconcelos, H. L. (2011a). Data from: Asymmetric dispersal and colonization success of Amazonian plant-ants queens. Dryad Digital Repository. **http://dx.doi.org/10.5061/dryad.h6t7g**

Bruna, E. M., Izzo, T. J., Inouye, B. D., Uriarte, M., & Vasconcelos, H. L. (2011b). Asymmetric dispersal and colonization success of Amazonian plant-ants queens. PLoS ONE 6, e22937.

When using datasets, use:

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The term [Dataset] will be removed before publication.

Cite references in alphabetical order by first author's surname. References by a single author precede multi-authored works by the same senior author, regardless of date.

List works by the same author chronologically, beginning with the earliest date of publication.

Insert a period and space after each initial of an author's name; example: Yaz, A. B., & Azy, B. (1980).

Authors Names should be in Title Case and every reference should spell out author names.

Use journal name in expanded form. To find a journal, please search the NIH's **list**.

Double-space all citations with a hanging indent of 0.5 inch.

Leave a space between the volume number and page numbers and include issue numbers (if available). 27, 3–12

Article in books: Azy, A. B. (1982). Title of book chapter. In: G. Yaz (Ed.). *Book title* (pp. 24–36). Boca Raton, FL: CRC Press.

For theses and dissertations: 'PhD Dissertation' and 'MSc Dissertation'. Author, A. A. (2003). *Title of doctoral dissertation or master's thesis* (Doctoral dissertation or master's thesis). Retrieved from Name of database. (Accession or Order No.)

11. SUPPLEMENTARY INFORMATION (to be supplied as separate files)

Supporting Information (SI) accompanies the online version of a manuscript and will be fully accessible to everyone with electronic access to *Biotropica.* We urge authors to make use of the SI section to add context or additional information that do not have central relevance to the manuscript. **All such material must be cited in the text of the printed manuscript.**

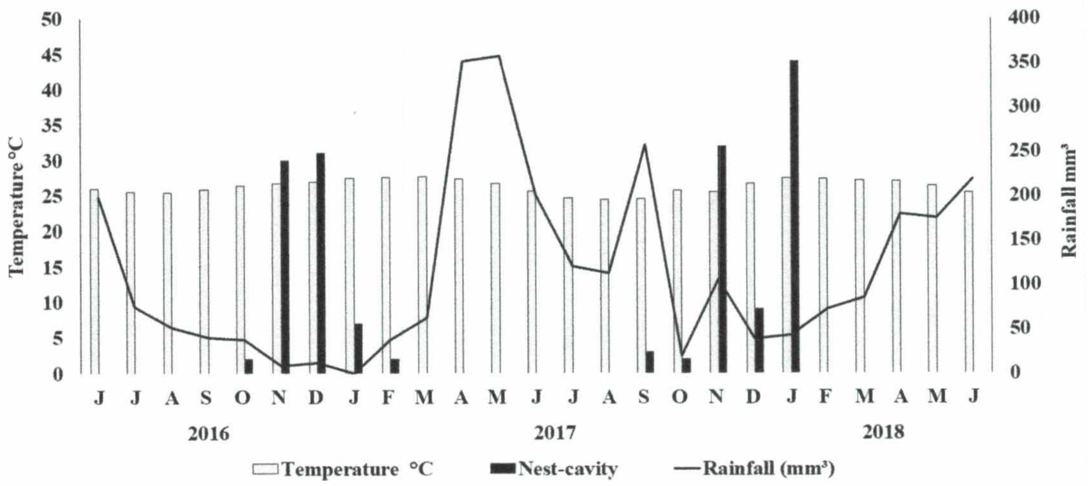

Figure 1 - Temperature (°C), rainfall (mm) and number of nests built by *C. tarsata* in restinga open areas, shrubby and secondary vegetations from July 2016 to June 2018

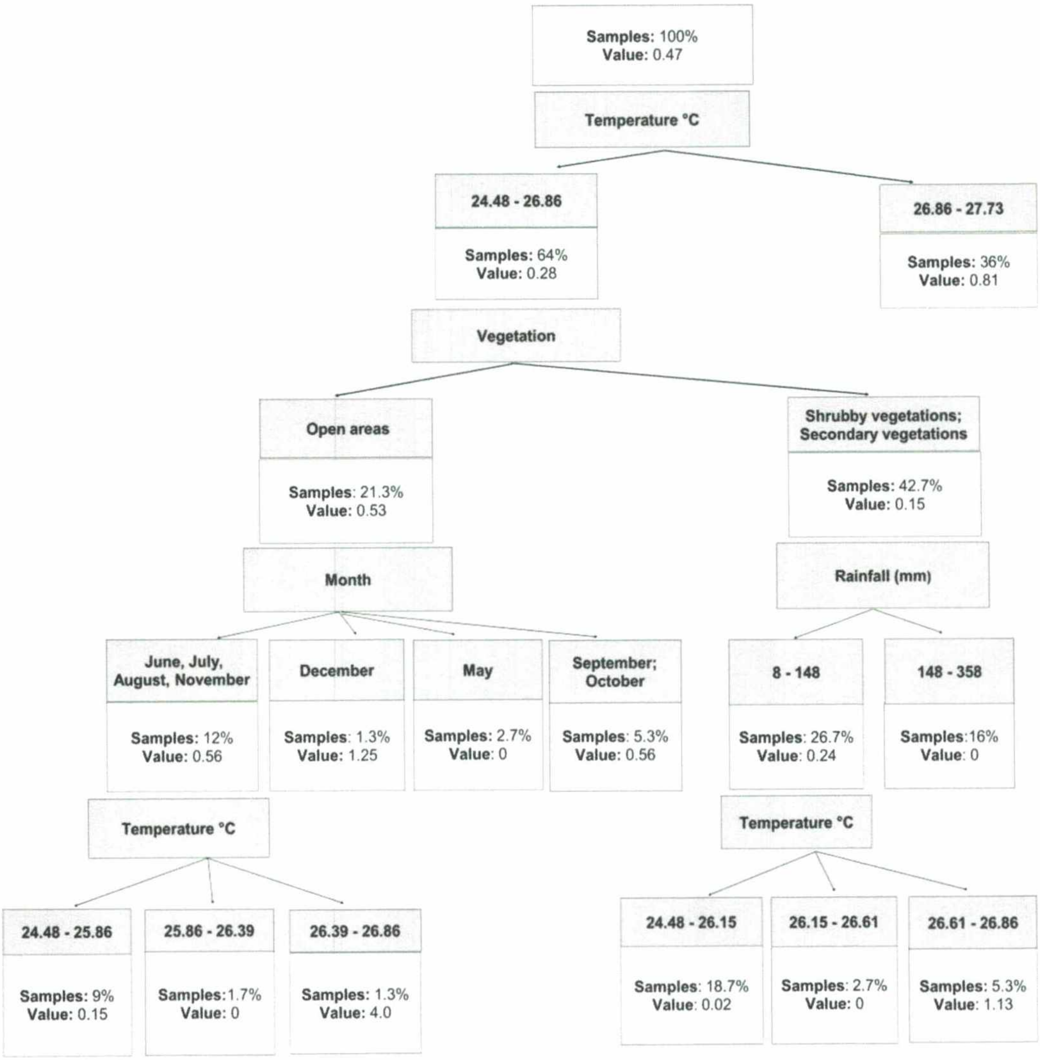

Figure 2 - Regression tree showing the influence of climatic conditions and sampling period on nesting by *C. tarsata* in restinga open areas, shrubby and secondary vegetations

CONSIDERAÇÕES FINAIS

Abelhas e vespas solitárias respondem fortemente às condições climáticas e ao tipo de vegetação em restinga, com preferência por nidificação em áreas abertas e vegetação secundária. A composição de espécies varia ao longo dos níveis de complexidade de habitat, e os padrões que direcionam a distribuição de espécies difere entre os tipos de vegetação e condições climáticas.

Na restinga, a precipitação é um fator determinante na nidificação de *C. tarsata*, que ficou concentrada na estação seca, principalmente em áreas abertas. Por outro lado, em vegetação arbustiva e secundária a nidificação foi favorecida por condições climáticas específicas, além de ser maior no sub-bosque. No entanto, são necessários mais estudos sobre o comportamento de nidificação e exploração de recursos florais na restinga.

Portanto, compreender a composição da comunidade de espécies de abelhas e vespas solitárias é crucial para o manejo e conservação dessas espécies que fornecem serviços ambientais essenciais ao funcionamento dos ecossistemas.