



THALINE DE FREITAS BRITO

**Abelhas das orquídeas (Apidae: Euglossini) e as plantações de palma de óleo (*Elaeis guineensis* Jacq.) na Amazônia Oriental: mudanças na composição de espécies, tamanho corporal e diversidade funcional.**

Belém,  
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Tese apresentada ao Programa de Pós-Graduação em Zoologia, do convênio da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do título de Doutor em Zoologia.

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**Orientador(a): Prof. Dr. Felipe Andrés León Contrera**  
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THALINE DE FREITAS BRITO

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**Orchid bees (Apidae: Euglossini) and oil palm plantations (*Elaeis guineensis* Jacq.) in eastern Amazon: changes in species composition, body size and functional diversity.**

***ABSTRACT***

In this study, we evaluated the role of legal reserves (LR) and areas of permanent protection (APP) in the maintenance of orchid bee species, and we tested the influence of abiotic and habitat parameters on taxonomic and functional diversity of this group. In addition, we investigated the occurrence of phenotypic variations (body and wing size, and fluctuating asymmetry) in response to environmental stress caused by oil palm plantations. Orchid bee males were sampled in nine areas (3 RL, 3 APP, and 3 oil palm plantations) in the municipality of Tailândia, southeast of the state of Pará. In each area, we installed six separate sampling stations, 500 m apart, each one with six scent traps; totaling 36 traps per area, and 108 per habitat type. We compared differences in observed abundance and richness using a One-Way ANOVA, we evaluated species composition patterns with a PCoA, and we also used a species indicator analysis. A partial RDA was applied to evaluate the influence of habitat attributes, space and habitat type on taxonomic and functional parameters of bees. In addition, we compared body and wing size variations of the individuals through the types of habitat. Our results indicate that oil palm areas are characterized by the presence of few individuals and species, low functional diversity, and by larger bees. Despite this, we recorded four species associated to LR, which can be useful indicators of orchid bee's communities in the Amazon rainforest. The habitat structure was not a good predictor of both functional and taxonomic composition, and no levels of fluctuating asymmetry were detected, but bees from oil palm showed larger wings compared to forest areas. Our research highlights that APPs play an important role in maintaining both taxonomic and functional composition of orchid bees, which could reinforce the fact that bees use these areas as displacement corridors in a matrix formed by oil palm plantation. Thus, both LRs and PPAs areas fulfill their purpose of protecting the biodiversity of orchid bees.

**Keywords:** areas of permanent protection; oil palm; functional diversity; fragmentation; legal reserve.

# **Abelhas das orquídeas (Apidae: Euglossini) e as plantações de palma de óleo (*Elaeis guineensis* Jacq.) na Amazônia Oriental: mudanças na composição de espécies, tamanho corporal e diversidade funcional.**

## **RESUMO**

Neste trabalho, foi avaliado o papel das reservas legais (RL) e das áreas de preservação permanente (APP) na manutenção das espécies de abelhas das orquídeas, e testada a influência de parâmetros abióticos e estruturais do hábitat sobre a diversidade taxonômica e funcional desse grupo. Além disso, foi investigada a ocorrência de variações fenotípicas (tamanho corporal e de asas e assimetria flutuante) como resposta ao estresse ambiental provocado por plantações de palma de óleo. Os machos de abelhas das orquídeas foram coletados em nove áreas (3 RL, 3 APP e 3 plantios de palma de óleo) no município de Tailândia, sudeste do estado do Pará. Em cada área foram instaladas seis estações de coleta separadas 500 m entre si, contendo seis armadilhas odoríferas; totalizando 36 armadilhas por área e 108 por tipo de hábitat. Foram comparadas as diferenças na abundância e riqueza observadas usando uma ANOVA One-Way, os padrões de composição de espécies foram avaliados através de uma PCoA, e também por uma análise de indicador de espécies. Uma RDA parcial foi aplicada para avaliar a influência de atributos do hábitat, do espaço e do tipo de hábitat sobre parâmetros taxonômicos e funcionais das abelhas. Adicionalmente, foram comparadas as variações de tamanho corporal e de asas dos indivíduos em função do tipo de hábitat. Os resultados deste trabalho indicam que os plantios de palma de óleo são caracterizados pela presença de poucos indivíduos e espécies, baixa diversidade funcional e por abelhas de maior tamanho corporal. Apesar disso, foram registradas quatro espécies associadas às RL, que podem ser indicadores úteis de comunidades de abelhas de orquídeas da floresta Amazônica. A estrutura do hábitat não foi um bom preditor da composição funcional e taxonômica, e não foram detectados níveis de assimetria flutuante, mas as abelhas dos plantios apresentaram asas maiores comparadas com as das áreas de floresta. Esta pesquisa destaca que as APPs desempenham um papel importante na manutenção da composição taxonômica e funcional das abelhas das orquídeas, o que poderia reforçar o fato de que as abelhas utilizam essas áreas como corredores de deslocamento em uma matriz formada por plantação de palma de óleo. Assim, tanto as RLs quanto as PPA's cumprem seu propósito de proteger a biodiversidade das abelhas das orquídeas.

**Palavras-chave:** áreas de preservação permanente; palma de óleo; diversidade funcional; fragmentação; reserva legal.

## INTRODUÇÃO GERAL

A polinização é um serviço ecossistêmico dependente da biodiversidade, sendo uma atividade essencial para a segurança alimentar e a perpetuação de diversas plantas nativas, além de sua elevada contribuição para a produtividade de espécies cultivadas (Klein et al. 2007, Ollerton et al. 2011). Nas últimas décadas, as ações antrópicas decorrentes das mudanças no uso da terra e a perda de hábitat, com consequente redução dos recursos florais e dos locais para nidificação (Kremen et al. 2007, Hernandez et al. 2009, Steffan-Dewenter et al. 2005, Klein et al. 2007, De Palma et al. 2015, Giannini et al. 2015, Oliveira et al. 2016), aliado ao uso indiscriminado de pesticidas (Henry et al. 2012), tem acarretado o preocupante cenário de declínio das populações de diversos grupos de polinizadores em todo o mundo. Como resultado, os locais mais impactados são caracterizados pela ocorrência de espécies generalistas e com dispersão elevada, cuja composição são subconjuntos das espécies que ocorrem nos ambientes mais conservados (Vellend et al. 2007, Karp et al. 2012).

Contudo, essas pressões ambientais nem sempre afetam todas as espécies de forma idêntica, e acredita-se que elas sejam mediadas por características inerentes à cada espécie (Kassen 2002). As respostas dos polinizadores frente às diferentes formas de uso da terra são frequentemente avaliadas utilizando métricas de riqueza e/ou abundância das espécies, e mais recentemente têm sido enfatizadas e cada vez mais tem sido utilizadas abordagens conjuntas dessas características com atributos morfológicos (ex. tamanho corporal e comprimento da glossa) e comportamentais (ex. estratégias reprodutivas, socialidade e amplitude de nicho) dos polinizadores (Williams et al. 2010, Benjamin et al. 2014, De Palma et al. 2015). Em geral, as espécies que apresentam maior sensibilidade aos processos resultantes da intensificação da agricultura e isolamento de habitats são aquelas que possuem nicho mais limitado (especialistas) e um nível organizacional mais complexo (como as abelhas sociais), quando comparadas com as espécies generalistas e de hábito solitário (Williams et al. 2010, Kassen 2002).

As mudanças na paisagem podem também afetar a estabilidade do desenvolvimento dos indivíduos, reduzindo a energia que seria empregada para crescimento e reprodução, provocando alterações no seu arranjo corpóreo (Leung et al. 2000, Koehn e Bayne 1989). Nesse caso, as populações de áreas alteradas tendem a apresentar indivíduos com menor tamanho corporal, ou ainda, com modificações no seu plano simétrico, como a ausência de simetria (Del Lama et al. 2002, Sanseverino e Nessimian 2008). Essa instabilidade do desenvolvimento pode ser expressada pelo aumento nos níveis de assimetria flutuante (AF) em alguns caracteres morfológicos dos organismos. Para alguns autores, a AF é definida como um desvio aleatório e não direcional da

simetria bilateral, sendo sua intensidade associada à estresses ambientais sofridos pelo indivíduo ainda durante o seu desenvolvimento (Palmer e Strobeck 1986). Essas alterações podem ser provocadas por variações de temperatura (Bjorksten et al. 2011), sazonalidade (Silva et al. 2009), ou ainda pela contaminação por pesticidas e poluição (Hardersen e Frampton 1999, Abaga et al. 2011).

Em abelhas, o arranjo simétrico e o tamanho corporal (este último comumente estimado através da medida da distância intertegular) constituem importantes atributos relacionados diretamente com a distância de voo e capacidade de dispersão dos indivíduos (Cane 1987). Alguns trabalhos demonstraram a relação existente entre o tamanho dos polinizadores e as mudanças no uso da terra, indicando que as respostas do tamanho de corpo de abelhas (maior ou menor) dependem tanto da proporção de hábitat natural disponível, quanto da escala espacial considerada (ex. paisagem ou local; Steffan-Dewenter et al. 2002, Bommarco et al. 2010, Benjamin et al. 2014). Além disso, a ocorrência de altos níveis de AF nas asas pode afetar o forrageamento, a fuga de predadores e os comportamentos de acasalamento (Córdoba-Aguilar 1995, Stewart e Vodopich 2013).

Uma das principais atividades modificadoras da paisagem na região Amazônica nos últimos anos tem sido a expansão das áreas cultivadas com a palma de óleo *Elaeis guineensis* Jacq. (Arecaceae), também conhecida como dendê. No Brasil, mais de 90% dos plantios implementados encontram-se na porção nordeste do estado do Pará, que se apresenta como o maior produtor de óleo de palma do país (Nahum e Santos 2016, Alves et al. 2013). Contudo, diferentemente dos plantios situados na Malásia e Indonésia, por exemplo, o estabelecimento de novas áreas plantadas tem ocorrido principalmente pela conversão de pastagens, e uma fração muito pequena é resultante da remoção de florestas naturais intactas (Benami et al. 2018). Esse cenário tem se concretizado a partir da implementação do Programa de Produção Sustentável de Óleo de Palma (PSOP), iniciado em 2010, submetendo a expansão do cultivo de palma de óleo exclusivamente à áreas já antropizadas, obedecendo as regras de recuperação de áreas degradadas, conservação da biodiversidade e uso racional dos recursos naturais (Carvalho et al. 2015; Brasil PLC N° 119/2013)

Apesar disso, as áreas de plantios de palma de óleo na Amazônia são caracterizadas por um número reduzido de indivíduos e espécies de alguns grupos de insetos aquáticos (ex. Heteroptera e Ephemeroptera; Cunha et al. 2015, e imaturos de Plecoptera e Trichoptera; Paiva et al. 2017), devido principalmente ao comprometimento da qualidade dos cursos d'água situados em meio aos plantios, em função de mudanças nas características físico-químicas da água e devido à redução da vegetação ripária (Bleich et al. 2014, Juen et al. 2016). Ainda assim, apesar do baixo valor de conservação apresentado pelos plantios de palma de óleo quando comparados com áreas de floresta

(Lucey e Hill 2011, Livingston et al. 2013), há evidências de que essas áreas cultivadas representem certa permeabilidade à organismos terrestres, como pássaros, borboletas e formigas (Koh 2008, Lucey e Hill 2011), e mesmo para algumas espécies de abelhas (Rosa et al. 2015).

Como a demanda por óleo de palma tem crescido exponencialmente, é urgente a necessidade de estabelecer estratégias que minimizem os impactos ambientais provocados pelas plantações (Butler et al. 2009, Fitzherbert et al. 2008). A manutenção de áreas de florestas naturais protegidas nas formas de Reserva Legal (RL) e Áreas de Preservação Permanente (APP), por exemplo, configuram alguns dos principais mecanismos de proteção dos serviços ambientais em áreas agrícolas no país (Brasil Lei Nº 12.651/2012; Marques e Ranieri 2012). A presença dessas áreas naturais favorece a ocorrência de diversas espécies de polinizadores ao proporcionar habitat disponível, contribuindo para o equilíbrio dos serviços ecossistêmicos, e podendo inclusive aumentar a produtividade de culturas agrícolas que dependem da polinização, situadas em áreas adjacentes aos plantios (De Marco Jr e Coelho 2004, Greenleaf e Kremen 2006, Pywell et al. 2015).

As abelhas das orquídeas (Apidae, Euglossini) constituem um importante grupo de polinizadores endêmicos da região Neotropical (Nemésio e Rasmussen 2011). Com aproximadamente 250 espécies distribuídas em cinco gêneros (*Aglae* Lepeletier & Serville, 1825, *Eufriesea* Cockerell, 1908, *Euglossa* Latreille, 1802, *Eulaema* Lepeletier, 1841 e *Exaerete* Hoffmannsegg, 1817), essas abelhas são caracterizadas pelo tegumento metálico e por apresentam uma forte relação com as flores de orquídeas, onde os machos ao realizarem coleta de fragrâncias, acabam polinizando-as (Dressler 1982). Além disso, tanto os machos quanto as fêmeas são responsáveis pela polinização de diversas plantas nativas (Maués et al. 2002, Ramírez et al. 2002, Cavalcante et al. 2012, Rocha-Filho et al. 2012).

Alguns estudos têm demonstrado que áreas bem preservadas e com cobertura vegetal contínua favorecem a ocorrência de um maior número de indivíduos e espécies de abelhas das orquídeas, e que as áreas desmatadas podem representar barreiras ao movimento de algumas espécies (Tonhasca Jr et al. 2003, Brosi 2009), sendo muitas consideradas especialistas do interior de florestas e sensíveis à fragmentação florestal (Milet-Pinheiro e Schindwein 2005). Por essas razões e, aliado ao fato de serem facilmente amostradas, os Euglossini têm sido considerados um grupo chave nas avaliações de indicadores de perturbações ecológicas provocadas por mudanças no uso da terra (Solar et al. 2015, 2016).

Os resultados encontrados por Livingston et al. (2013) e Rosa et al. (2015), que avaliaram as respostas de abelhas das orquídeas em plantios de palma cultivados na Costa Rica e em um corredor de Floresta Atlântica no estado da Bahia, respectivamente, revelam que essas abelhas possuem respostas espécie-específicas, com diferentes níveis de tolerância e sensibilidade. Além disso, os



Euglossini apresentam certa mobilidade entre os ambientes de floresta e os plantios, mas essas mudanças estão possivelmente relacionadas à bases filogenética e funcional (Livingston et al 2013, Rosa et al 2015). Assim, a incorporação de abordagens complementares, como métricas de diversidade funcional, identificando quais atributos (morfológicos e/ou comportamentais) tornam as espécies mais vulneráveis às ações antrópicas, podem ser ferramentas úteis para uma melhor compreensão da relação entre os impactos das plantações de palma de óleo e a diversidade de polinizadores naturais, como as abelhas das orquídeas, além de servirem de base para o direcionamento de prioridades de conservação (Rader et al. 2014, Luiza-Andrade et al. 2017).

Diante do exposto, neste trabalho foram exploradas as variações de atributos populacionais (abundância e riqueza), da composição de espécies, assim como dos aspectos morfométricos e funcionais de assembleias das abelhas das orquídeas, comparando indivíduos amostrados em áreas de florestas naturais protegidas (as Reservas Legais e as Áreas de Preservação Permanente, aqui também referidas como “reservas florestais” e “corredores ripários”, respectivamente) e em plantios de palma de óleo (*Elaeis guineensis* Jacq.) no município de Tailândia, nordeste do estado do Pará.

A presente tese é composta por três artigos, cada um correspondente à um capítulo, cujo dois primeiros estão publicados e o último encontra-se submetido. No Capítulo 1, foi avaliado o papel das reservas florestais e dos corredores ripários na conservação e manutenção da biodiversidade de abelhas das orquídeas, em uma matriz formada por plantios de palma de óleo. Esse trabalho foi publicado na Revista *Apidologie* (Qualis A2-Biodiversidade) com o título “*Forest reserves and riparian corridors help maintain orchid bee (Hymenoptera: Euglossini) communities in oil palm plantations in Brazil*”, no qual foram testadas as hipóteses de que (a) a riqueza e abundância de abelhas das orquídeas são maiores nas reservas florestais e menores no plantio de palma de óleo, e as APPs (Áreas de Preservação Permanente) apresentam níveis intermediários de riqueza e abundância, e (b) que existe diferença nos padrões de composição de espécies dessas abelhas entre os três tipos de usos da terra avaliados.

No Capítulo 2, foram avaliadas a influência de características do hábitat e a resposta da diversidade funcional das abelhas das orquídeas à diferentes tipos de hábitat (os mesmos utilizados no capítulo anterior). Para tal, foram testadas as seguintes hipóteses: (a) tanto a variação de tamanho de corpo das abelhas quanto a diversidade funcional são maiores nas reservas legais (RL) do que nos demais tipos hábitats, (b) indivíduos de maior tamanho de corpo ocorrem nas áreas de plantio de palma de óleo comparados com aqueles encontrados nas áreas de floresta (RLs e APPs), e (c) que parâmetros abióticos e variáveis da estrutura do hábitat afetam a abundância e características funcionais das espécies de abelhas das orquídeas. Esse capítulo resultou no manuscrito intitulado “*Effects of habitat type change on taxonomic and functional composition of orchid bees (Apidae:*

*Euglossini) in the Brazilian Amazon*”, o qual está publicado na revista *Journal of Insect Conservation* (Qualis B1- Biodiversidade).

Por fim, no Capítulo 3, foi investigada a presença de variações fenotípicas (assimetria flutuante e tamanho das asas) em abelhas das orquídeas como respostas ao estresse ambiental provocado pelo plantio de palma de óleo. Para tal, foram utilizados exemplares das espécies *Eulaema (Eulaema) meriana* (Olivier, 1789) e *Euglossa (Glossura) ignita* Smith, 1874 coletados nos três tipos de hábitat. Neste trabalho, intitulado “*The wings of two orchid bee species are larger but not asymmetrical in oil palm plantations of eastern Amazon*”, foi testada a hipótese de que os indivíduos de ambas as espécies coletados nas áreas de plantio apresentam maiores níveis de AF e também asas maiores, quando comparados com indivíduos das áreas de floresta (RL e APPs). O manuscrito resultante desde capítulo foi submetido para a revista *Insectes Sociaux* (Qualis B1- Biodiversidade).

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# Capítulo 1

**Forest reserves and riparian corridors help maintain orchid bee (Hymenoptera: Euglossini) communities in oil palm plantations in Brazil**

O capítulo I desta Tese foi elaborado e formatado conforme as normas da publicação científica *Apidologie*, as quais se encontram em anexo (Anexo 1).

# Forest reserves and riparian corridors help maintain orchid bee (Hymenoptera: Euglossini) communities in oil palm plantations in Brazil

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**Abstract** – Orchid bees (Apidae, Euglossini) are important pollinators in the Amazon forest. In eastern Brazilian Amazon, secondary forest and pastures are being replaced by oil palm plantations. Here, we tested the role of forest reserves and riparian corridors in maintaining orchid bees. We sampled bees in three different soil-type uses, comparing richness, abundance, and assemblage composition. Estimated richness was lowest in palm plantations than in forest reserves and riparian corridors on diversity of orchid bees. Riparian corridors had the highest abundance, followed by reserves, and oil palm plantations. Bee assemblage also varied with land cover, with the reserves having the most distinct composition. We also identified indicator bees for primary forest. Our results demonstrate riparian corridors and forest reserves can maintain orchid bees in oil palm landscapes.

Amazon / Euglossini / fragmentation / land use / permanent protection areas

## 1. INTRODUCTION

One of the greatest challenges facing conservation biologists in an age of rapid agricultural

expansion for food, fiber, and fuel is understanding how to retain biodiversity and associated ecosystem services within sustainable production landscapes (MEA 2005; Tomich et al. 2011; Laurance et al. 2014). Pollination is a critical biodiversity-dependent ecosystem service in both natural and human landscapes that can be negatively impacted by land-use changes (Steffan-Dewenter et al. 2005; Klein et al. 2007; Giannini et al. 2015). In tropical plantations, such as coffee and cacao, proximity to natural areas and forests can boost farmers' yields by providing habitat to

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wild pollinators that pollinate farmers' crops (De Marco Jr and Coelho 2004; Greenleaf and Kremen 2006). However, despite their ecological and economic importance, pollinators are declining worldwide due to habitat loss, land-use changes, and the pervasive use of pesticides (Henry et al. 2012; Burkle et al. 2013; Oliveira et al. 2016).

In the Neotropics, orchid bees (Apidae, Euglossini) compose an important group of endemic pollinators containing nearly 250 species (Nemésio and Rasmussen 2011). They are known for their striking metallic colors and males' scent-collecting behaviors from blooming orchids and other flowers, which is allegedly used to attract females (Dressler 1982a). This behavior makes orchid bees ecologically critical as long-distance pollinators (Dressler 1982a), where individual plants are often widely spaced at low densities (Janzen 1971). Orchid bees pollinate more than 600 species of plants and are frequent visitors to hundreds more (Dressler 1982a; Ramírez et al. 2002; Rocha-Filho et al. 2012), including economically important species like Brazil nuts (Maués 2002). Orchid bees are more diverse in rainforests (Nemésio and Silveira 2007), and many species are forest-interior specialists and are sensitive to forest fragmentation (Milet-Pinheiro and Schlindwein 2005), in contrary to most bee groups that are usually more diverse in xeric and temperate zones (Michener 2007). Consequently, habitat loss, conversion, and degradation negatively impact orchid bee assemblages (Brosi 2009).

In the tropics, oil palm (*Elaeis guineensis* Jacq.) is one of the of the most important commodity plantations, as the oil has multiple uses from food to cosmetics to biofuel (Fitzherbert et al. 2008). Oil palm plantations now cover more than 14.5 million hectares worldwide, and continue to rapidly expand (Foster et al. 2011; Livingston et al. 2013). Most oil palm is in Southeast Asia, but Neotropical oil palm plantations are expanding, particularly in Brazil where oil palm production doubled from 46,000 ha in 2001 to 109,000 ha in 2009 (FAO 2013). The great majority of oil palm plantations in Brazil are located in the State of Pará, within the Belém Endemism

Center biodiversity hotspot (Gascon et al. 2001; Brandão and Schoneveld 2015). In general, conventional oil palm plantations have low conservation value due to the loss of biodiversity and simplification of habitats compared to native forests (Turner and Foster 2009; Foster et al. 2011). Further, oil palm plantation insect assemblages are typically dominated by a few abundant generalists, non-forest species, and pests (Chey 2006; Fitzherbert et al. 2008).

Some studies in the Neotropics found that orchid bee communities are sensitive to oil palm plantations and increasing isolation from forest habitat, as well as other landscape changes (Livingston et al. 2013; Powell and Powell 1987, respectively). To mitigate some of these effects, Brazilian law requires land owners to preserve forest reserves and riparian corridors (permanent protection areas or "*Áreas de Preservação Permanente*" in Portuguese, henceforth APPs), believing that these refuges may maintain biodiversity and corridors can connect fragmented populations (Brazilian Law nº 12.651 2012; Marques and Ranieri 2012).

In this study, we examined the role of forest reserves and riparian corridors in conserving and maintaining orchid bee biodiversity in the oil palm landscape in the Brazilian State of Pará, the most important agricultural frontier for oil palm in the region (Fitzherbert et al. 2008; Butler and Laurance 2009). Since some orchid bees species are very sensitive to fragmentation and do not use the matrix environment surrounding forest fragments to disperse throughout their habitats (Milet-Pinheiro and Schlindwein 2005; Rosa et al. 2015), we hypothesized that orchid bee richness and abundance would be greatest in the forest reserves and lowest in the palm plantation, with the APPs containing intermediate levels of richness and abundance.

## 2. MATERIALS AND METHODS

### 2.1. Study site

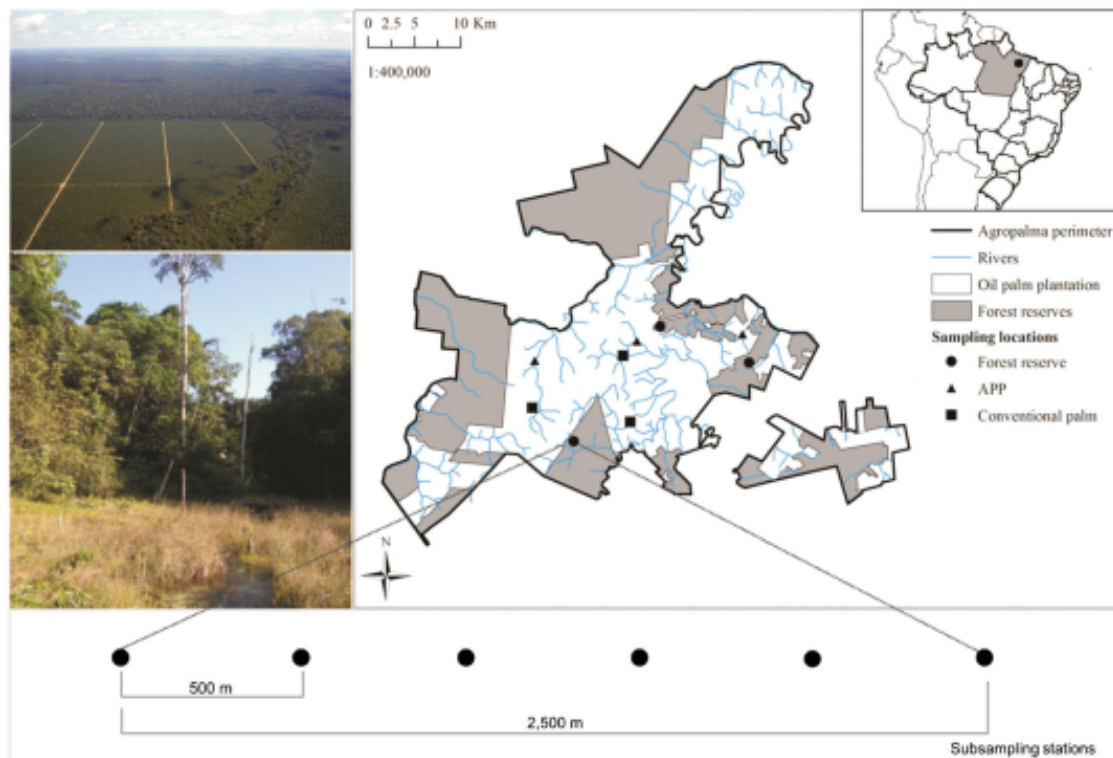
The study was carried out in oil palm plantations, forest reserves, and APPs at the Agropalma Industrial Complex, near the



municipality of Tailândia, in the southeast of the state of Pará, Brazil (Figure 1), approximately 02°20' and 02°40'S by 48°30' and 49°0'W. Agropalma consists of 107,000 ha where 64,000 ha are preserved as forest reserves and the other 40,000 ha are conventional palm plantation (the remainder being company infrastructure). The region's climate is hot and humid, with two well-defined seasons, a dry season between June and November, when orchid bee sampling took place, and a rainy season, between December and May. Mean annual precipitation is 2451 mm, mean temperature approximately 26 °C, and relative humidity around 88.5% (Albuquerque et al. 2010) and according to the Köppen classification is defined Af and Am (Peel et al. 2007; Alvares et al. 2014). Agropalma has eight large forest reserves in the region and forested APPs connecting them.

## 2.2. Orchid bee sampling

We sampled male orchid bees from 12 July to 28 July 2015 in three areas (sites) of each land-use type (3 forest reserves, 3 APPs, and 3 oil palm plantations) (Figure 1), totaling nine sampling days. This rapid survey approach is appropriate for this group of bees, and short sampling periods have been demonstrated to be nearly as effective in revealing community patterns as year-long surveys (Roubik 2004; Livingston et al. 2013). We sampled one site per day using 36 scent traps, displaced in groups of six, constituting a subsampling station, similarly to what has been previously done by Silva and De Marco Jr (2014) in Cerrado areas. The six subsampling stations within the same site were separated from one another by 500 m (Figure 1). The distance between palm plantation sites ranged from 5 to 10 km; APPs



**Figure 1.** Map of study region near Tailândia in State of Pará, Brazil, and image of forest reserves, oil palm plantation and APPs, the dominant land uses in the region sampled. The aerial landscape photo shows the oil palm plantations, APPs (“Áreas de Preservação Permanente” or permanent protection areas), and forest reserves. The second photo shows an example of an APP with a wide, meandering stream. *Points* on map represent the sampled sites; each point on the map was further subsampled with 6 subsampling stations (below), each with 6 scents. (Photo credit: Agropalma Industrial Complex, upper left; C. Phifer, lower left.)

sites were separated from 10 to 11 km apart from each other, and the distance between forest sites ranged from 10 to 19 km. Though proximity between different land-use types was often 1–2 km and maximum distance was approximately 20 km. Traps were built from empty 2-L PET plastic bottles with three openings as conceived by Campos et al. (1989). At each subsampling station, six scent traps were used and each trap contained a cotton swab dipped in one of six scents: vanillin, eucalyptol, methyl cinnamate, methyl salicylate, benzyl acetate, and eugenol (Nemésio 2009).

Each land-use type site was sampled three times, with the sampling location haphazardly selected based upon existing trails and roads. All oil palm plantation sites were  $\geq 2$  km from the edge of the nearest forest reserve. For the forest sites, we walked along established trails in three large forest reserves (the smallest 4200 ha; the largest 16,700 ha, Figure S1), setting one sampling station near the edge, and then every 500 m along the trail, penetrating approximately 2.5 km into the forest reserves. Weather was warm with no rain during the sampling period and palm flowering was universally low. Traps were hung for 24 h (sampling effort of 2592 trap h<sup>-1</sup>) and then, bees were sampled, pinned, and identified to species level using taxonomic keys (Dressler 1982b; Roubik and Hanson 2004; Moure 2000; Nemésio 2009; Oliveira 2006). All bees were compared with specimens previously confirmed by Dr. André Nemésio and Dr. Márcio Oliveira, deposited in Entomology Museum of the Embrapa Amazônia Oriental and Museu Paraense Emílio Goeldi. Specimens were deposited at the Entomology Museum of the Embrapa Amazônia Oriental.

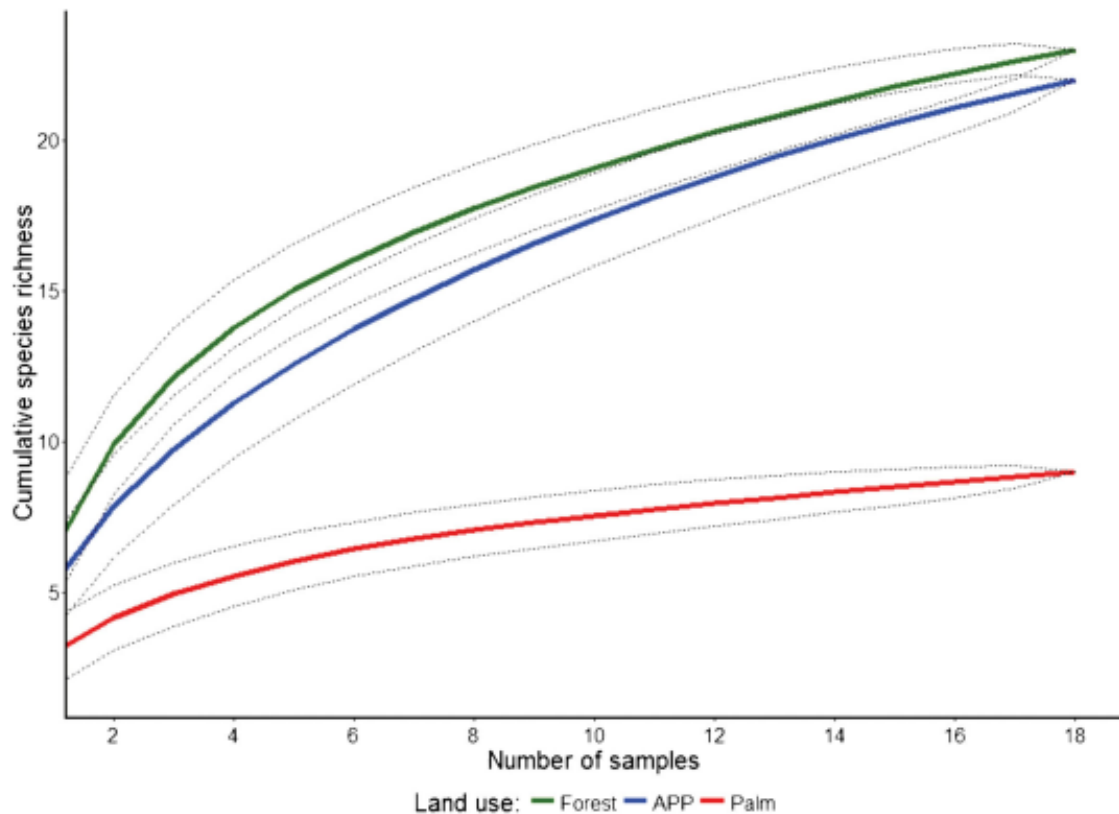
### 2.3. Statistical analysis

We calculated estimators of species richness based on first-order Jackknife using EstimateS Win9.10 software (Colwell 2013) for each site, and we compared the differences between land uses (APP, forest reserve, and palm plantations) by performing a Kruskal-Wallis test due to the non-normality nature of our data. We also performed accumulation curves of species to each

land-use types, considering the random method with 9999 permutations. Differences in observed species abundance and richness among sites were compared using a one-way ANOVA, with abundance from each subsampling station log<sub>10</sub> transformed. We performed post hoc comparisons of significant ANOVA results by Tukey test.

To assess the distance dependence among subsampling stations on bee assemblage composition, richness, and abundance, we performed a Mantel test. The Mantel test provides a correlation coefficient value ( $r$ ) of comparisons between the attributes of the orchid bees and the distance of each subsampling station. Patterns of species composition were evaluated with a principal coordinates analysis (PCoA), an ordination technique where species abundances of each site (subsampling station) were log( $x + 1$ ) transformed to balance values, and applied the Bray–Curtis index. To test for differences in species composition between land uses, we used a permutational multivariate analysis of variance (PERMANOVA) and to compare differences within groups and determine the effect of heterogeneity (dispersion) on significant PERMANOVA results, we performed pairwise comparisons of dispersion using Primer 6 software (PERMDISP; Anderson 2006). We also performed a nonmetric multidimensional scaling (NMDS) only as a complementary analysis, since contrary to PCoA, this ordination method does not provide explanation values of each ordination axis. We complemented our PCoA analysis with a species indicator analysis (IndVal; Dufrêne and Legendre 1997; Cáceres and Legendre 2009) to evaluate potential land-use associations for each species with the three land uses at our study site. A perfect indicator species should occur only in sampling units from a given category (specificity) and in all sampling units of that given category (fidelity).

Lastly, we evaluated the patterns of scent sampling efficiency with a Kruskal-Wallis test, and these are detailed in the supplementary material (Figure S1 and Table S2). We followed the assumptions for all statistical tests, transforming the data when necessary. We also assumed an  $\alpha$  value of 0.05 in all analyses. We performed all analyses using R (2016).



**Figure 2.** Cumulative curves of species (*solid lines*) with standard deviation (*dashed lines*), of orchid bees sampled at Agropalma, Tailândia municipality, State of Pará, Brazil. Land-use codes: *APP* “Áreas de Preservação Permanente” (permanent protection areas), *Palm* oil palm plantations, *Forest* forest reserves.

### 3. RESULTS

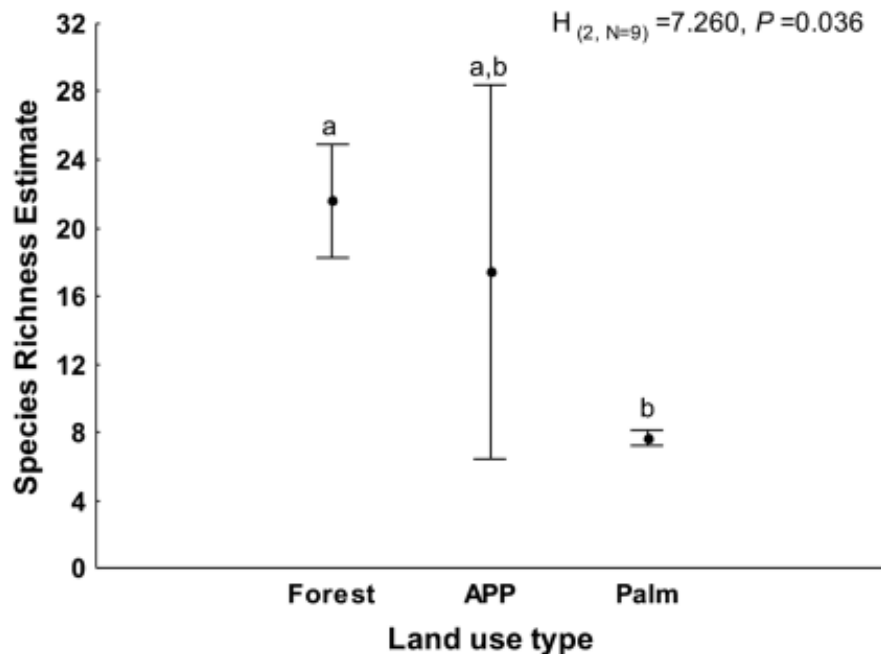
During our sampling period, we collected 867 male euglossine bees from 25 species belonging to four genera *Eulaema* (*El.*), *Eufriesea* (*Ef.*), *Euglossa* (*Eg.*), and *Exaerete* (*Ex.*) (Table S1), respectively, abbreviated for clarity and brevity throughout the text. In all three land uses, *El. cingulata* and *El. meriana* accounted together for >60% of all bees collected. These two species were the dominant species in APPs and palm plantation. In contrast, *Eg. chalybeata* was the most abundant species in forest reserves.

Observed species richness was greatest in the forest reserves and APPs, and lowest in palm plantations ( $F_{(2, 51)} = 22.577$ ,  $P < 0.001$ ). Oil palm plantations had about 14 species less than forest reserves ( $P_{\text{Tukey}} < 0.001$ ) and an amount of 13 species less when compared to APPs ( $P_{\text{Tukey}} < 0.001$ ). Jackknife species richness estimates

in forest reserves averaged  $21.61 \pm 1.34$  (mean  $\pm$  standard deviation),  $17.44 \pm 4.43$  in APPs, and  $7.67 \pm 0.16$  in palm plantations. Accumulation curves of species sampled in forest fragments and APPs were similar, while oil palm areas showed low values (Figure 2). Species richness estimated of forest reserves and APP areas were not different from one another ( $H_{(2, N=9)} = 7.260$ ,  $P = 0.036$ ) (Figure 3). Observed abundance patterns were different from species richness patterns for each land use. Surprisingly, total abundance of orchid bees was highest in APPs (382 individuals), followed by forests (244 individuals) and palm (241 individuals) (Online Resource: Table S1), even though these differences were not significant ( $F_{(2, 51)} = 1.303$ ;  $P = 0.280$ ).

The composition of the orchid bee assemblage varied with land use. Both PCoA and NMDS tests revealed a clear difference between forest sites and two other land uses based on the

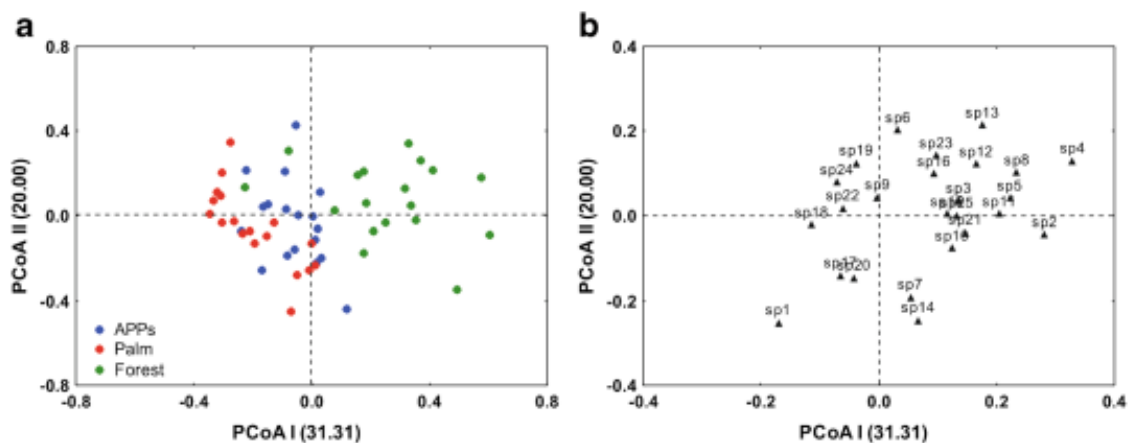




**Figure 3.** Comparison of the estimated species richness of euglossine bees by land use in Tailândia municipality, State of Pará, Brazil, based on first-order jackknife method. *Center* represents the mean and the *bars* represent 95% confidence intervals. Land-use codes: *APP* “Áreas de Preservação Permanente” (permanent protection areas), *Palm* oil palm plantations, *Forest* forest reserves.

sample composition (Figure 4a and Figure S2), with the formation of two distinct species groups within these areas (Figure 4b). Additionally,

results from PERMANOVA and PERMDISP tests showed significant differences in the community composition between land uses, except



**Figure 4.** The principal coordinates analysis (PCoA) for data ordered by samples (a) and euglossine species (b). Land-use codes: *APP* “Áreas de Preservação Permanente” (permanent protection areas), *Palm* oil palm plantations, *Forest* forest reserves. Species codes: *sp1*, *Eufriesea ornata*; *sp2*, *Euglossa amazonica*; *sp3*, *E. augaspis*; *sp4*, *E. bidentata*; *sp5*, *E. chalybeata*; *sp6*, *E. crassipunctata*; *sp7*, *E. ignita*; *sp8*, *E. imperialis*; *sp9*, *E. intersecta*; *sp10*, *E. modestior*; *sp11*, *E. orellana*; *sp12*, *E. parvula*; *sp13*, *E. securigera*; *sp14*, *Euglossa* sp.1; *sp15*, *E. townsendi*; *sp16*, *Eulaema bombiformis*; *sp17*, *E. cingulata*; *sp18*, *E. meriana*; *sp19*, *E. mocsaryi*; *sp20*, *E. nigrita*; *sp21*, *E. polyzona*; *sp22*, *E. pseudocingulata*; *sp23*, *Exaerete frontalis*; *sp24*, *E. lepeletieri*; *sp25*, *E. smaragdina*.



between APP and palm plantation (pairwise Monte Carlo test; Table I; Figure 4). Finally, the species indicator analysis revealed five species as potential environmental bioindicators (Table II). Although *Eg. bidentata*, *Eg. securigera*, and *Eg. imperialis* were unique to forest (Table S1), other four species were indicated as potential indicators of forest reserves (*Eg. amazonica*, *Eg. augaspis*, *Eg. bidentata*, and *Eg. imperialis*). *Euglossa chalybeata* was considered indicator of preserved areas (APP and Forest), despite it has been recorded in all land-use types (Table II, see also Table S1). *Euglossa modestior*, *Eg. chalybeata*, *Eg. ignita*, *Eg. augaspis*, *El. bombiformis*, *El. cingulata*, *El. meriana*, *El. mocsaryi*, and *El. nigrita* were found in all three land uses, and oil palm plantation was the only land use with none unique bee species (Figure 5).

We observed an effect of subsampling distances on bee abundance (Mantel  $r = 0.12$ ,  $P = 0.006$ ), observed richness (Mantel  $r = 0.10$ ,  $P = 0.015$ ) and on the variation on assemblage similarity (Mantel  $r = 0.11$ ,  $P = 0.013$ ). However, as the explanation of the geographic space on the attributes evaluated was low (Mantel  $r$  values <15%),

in subsequent analyses, we assumed that sites represented independent samples.

#### 4. DISCUSSION

In this study, we found significant differences in the orchid bee assemblages present in forest reserves, APPs, and oil palm plantations. Contrary to our hypothesis, APPs did not show intermediate levels of richness and abundance of orchid bees, but had an approximately equally diverse assemblage to forest reserves. The Amazon basin contains an estimated 127 species of euglossine bees (Nemésio and Silveira 2007), and we sampled more than 20% of this species pool in a short time during the dry season when catch rates are about 38 species (Mateus et al. 2015). Overall, the community we sampled was dominated by a few species, with *El. cingulata* and *El. meriana* accounting for >60% of the total orchid bee abundance. Nevertheless, in both forest and APP areas the species accumulation curves never plateaued, indicating that the communities are under-sampled in land-use type, while sampling in the oil palm plantation seemed to have reached its peak richness.

The sampled APPs maintained high levels of euglossine bee richness and abundance, and we sampled 20 of the 23 forest species within the APPs, as well as all the species sampled within the palm plantations. This suggests that these corridors are being effectively used by the orchid bees as dispersal routes, and that they are potentially connecting all the large forest reserves. In the Atlantic rain forest, riparian strips and small forest patches were also found to be effective stepping-stones or corridors for orchid bees (Rosa et al. 2015), and APPs are believed to explain the presence of some Amazonian orchid bees within the Brazilian savanna (Silva et al. 2013; Martins et al. 2016). Similar results were also found in northeastern Brazilian humid tropical forests, where riparian forests of the São Francisco River function as biocorridors, providing refuge areas and maintaining orchid bee species (Moura and Schlindwein, 2009). Edge-dominated forests, like the APPs, in Costa Rica also supported diverse orchid bee communities (Brosi 2009). Throughout the plantation, the APPs' width varied from 50 to 250 m, depending on the size of the stream, habitat

**Table I.** Results of PERMANOVA and PERMDISP tests based on Bray–Curtis dissimilarities (25 species; 9999 permutations). The analysis did not provide values for the missing cells in the table

	df	MS	Pseudo-F
Source <sup>a</sup>			
Habitat	2	11,547	7.568 ***
Residuals	51	1525.8	
Total	53		
Groups <sup>b</sup>			<i>T</i>
APP vs palm	34		1.495 <sup>ns</sup>
APP vs forest	34		2.494 ***
Palm vs forest	34		3.632 ***

<sup>ns</sup> not significant

\*\*\* $P=0.001$

<sup>a</sup> Main tests

<sup>b</sup> Pairwise comparisons

**Table II.** Indicator values (IndVal) for euglossine species collected at different land uses in the municipality of Tailândia (State of Pará, Brazil)

Species	IndVal	<i>P</i>	Association
<i>Eufriesea ornata</i>	0.236	1.000	
<i>Euglossa (Euglossa) amazonica</i>	0.488	0.035	Forest
<i>Euglossa (Euglossa) bidentata</i>	0.707	0.005	Forest
<i>Euglossa (Euglossa) modestior</i>	0.236	NA	
<i>Euglossa (Euglossa) securigera</i>	0.236	1.000	
<i>Euglossa (Euglossa) sp. 1</i>	0.333	0.345	
<i>Euglossa (Euglossa) townsendi</i>	0.408	0.200	
<i>Euglossa (Glossura) chalybeata</i>	0.808	0.005	APP + forest
<i>Euglossa (Glossura) ignita</i>	0.707	NA	
<i>Euglossa (Glossura) imperialis</i>	0.707	0.005	Forest
<i>Euglossa (Glossura) orellana</i>	0.333	0.570	
<i>Euglossa (Glossurela) augaspis</i>	0.555	0.035	Forest
<i>Euglossa (Glossurella) crassipunctata</i>	0.236	1.000	
<i>Euglossa (Glossurella) parvula</i>	0.481	0.060	
<i>Euglossa (Glossuropoda) intersecta</i>	0.333	0.545	
<i>Eulaema (Apeulaema) cingulata</i>	0.933	NA	
<i>Eulaema (Apeulaema) mocsaryi</i>	0.304	NA	
<i>Eulaema (Apeulaema) nigrita</i>	0.512	0.110	
<i>Eulaema (Apeulaema) pseudocingulata</i>	0.298	0.610	
<i>Eulaema (Eulaema) bombiformis</i>	0.606	0.090	
<i>Eulaema (Eulaema) meriana</i>	0.892	NA	
<i>Eulaema (Eulaema) polyzona</i>	0.289	0.750	
<i>Exaerete frontalis</i>	0.527	0.075	
<i>Exaerete lepeletieri</i>	0.236	1.000	
<i>Exaerete smaragdina</i>	0.236	1.000	

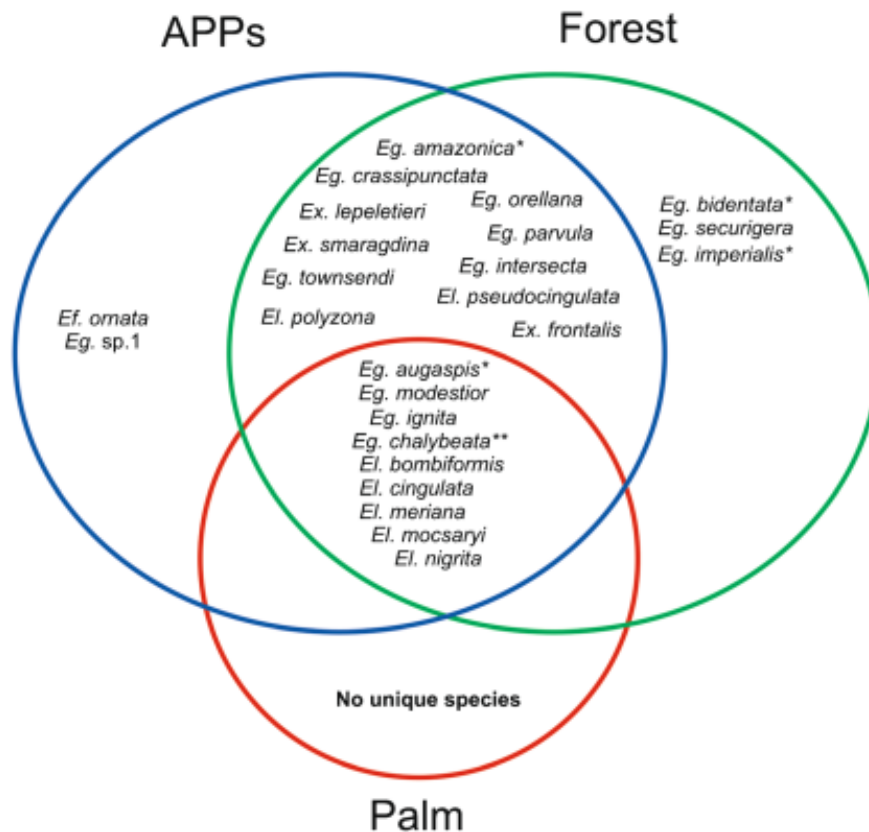
Ital values indicate species as potential environmental bioindicators

NA non-significant values

complexity and intactness, and habitat heterogeneity, habitat features that may also explain the wider standard deviation for observed species richness in this land-use type in our study area. Other invertebrate-riparian corridor studies have shown that these forest corridors can benefit biodiversity, even if spill-over into palm matrix is low, and forest maintains greater diversity (Gray et al. 2016).

Forest fragments have been shown to be important landscape components for some euglossine bees, and it has been suggested that some of these species indeed do not leave the fragments to use the surrounding matrix (Milet-Pinheiro and Schlindwein 2005). Individual male euglossine

bees routinely travel widely, especially outside of small fragments that are unlikely to provide all the life-history requirements needed for stable populations of several species of large, fast-flying bees (Tonhasca Jr et al. 2003; Brosi 2009). Additionally, orchid bees are known to fly long distances (~30 km in a single day), especially the larger ones (Janzen 1971; Raw 1989; Becker et al. 1991; Wikelski et al. 2010; Pokorny et al. 2015). Thus, some *Eulaema* species (i.e., *El. cingulata*, *El. mocsaryi*, *El. meriana*, and *El. bombiformis*) should be more capable of leaving forest fragments than smaller bees, as was observed for other large body size species (e.g., *El. nigrita*) (Raw 1989;



**Figure 5.** Venn diagram of species composition in the three land uses in Tailândia municipality, State of Pará, Brazil. Asterisks refer to species identified as indicators of forest reserves (\*), indicators of preserved areas (forest reserves + APPs) (\*\*) by the indicator analysis IndVal. No unique species was identified as being part of the oil palm plantation.

Wikelski et al. 2010; Pokorny et al. 2015). The remarkably simple orchid bee assemblages found in oil palm plantations, regarding species richness, abundance, and composition, seems to confirm the importance of forest patches to populations of these bees in the area.

Our species indicator analysis identified four euglossine bee species associated with forest reserves and one species occurred in both forested areas (forests and APPs), suggesting they are not tolerant to disturbance. Therefore, these species may be useful indicators of intact Amazonian forest orchid bee communities. *Euglossa analis* and *Eg. sapphirina* are known to be associated with forest interiors, while other species may not be affected by habitat loss (Tonhasca Jr et al. 2002; Nemésio and Silveira 2006). Contrary to what we expected, based on other studies, *El. nigrita* was not identified as an indicator of

disturbed areas, such as the plantations we sampled. Given the ability of this species to occur in disturbed landscapes and its high flight capacity, habitat loss is not expected to cause populational decreases of this species (Silva and De Marco Jr 2014). Nonetheless, this species is expected to benefit in future scenarios of climate change and deforestation in this biome, what may facilitate its expansion to Central Amazonia (Silva et al. 2015).

Overall, our results should still be carefully interpreted. This is one of the first studies of its kind in Amazonian oil palm plantations (e.g., Shimano and Juen 2016), and we considered only three coarse land-use types. Future studies should also consider how land use affects dispersal patterns of orchid bees in the region, including fine-scale habitat features that may also influence bee communities, as well as temporal variations. We



believe that previous radio-tracking studies involving bees in general (Wikelski et al. 2010; Hagen et al. 2011) may improve our understanding on how these species disperse in oil palm plantation embedded within landscapes with natural vegetation.

We also report some low-level of spatial correlation. There is no consensus on the appropriate spatial design of sampling euglossine bees, with evidence that both local and landscape features influence species (Giangarelli et al. 2015; Nemésio et al. 2016). The similarity of the orchid bee assemblage, richness, and abundance had some relatedness to the proximity of the sampled sites, but the percentage of explanation was low (<15%). This result suggests that the differences we found are caused by the evaluated land-use types rather than sampling sites' distances. Moreover, our community results also suggest a true divergence between forest and non-forest bees. Only one study explicitly addressed the effects of spatial autocorrelation upon orchid bee diversity, with similar low levels of correlation (Brosi 2009). Considering the flight capabilities of these bees described above, ideally, all sampling points should be long-distanced from one another. Still, field logistics and site availability usually do not allow an optimal distribution of collecting sites, particularly when working in agricultural landscapes such as ours. Since we found a certain degree of space-dependence between sites, new studies that address this issue must be performed, although selecting optimal sites in crop areas, which are delimited primarily by economic reasons, is a challenging task.

Our results support the hypothesis that orchid bee species diversity would be greatest in the forest reserves and lowest in the palm, but, surprisingly, orchid bee abundance was equal in forest and APPs. Despite the worldwide negative reputation of oil palm plantations for biodiversity (e.g., Lees et al. 2015), landowners are interested in mitigating biodiversity loss. It is, therefore, critical to provide research results on the efficacy of different plantation management strategies for retaining biodiversity. Our research highlights that large-scale oil palm plantations with forest reserves and connecting APPs can be managed to protect orchid bee biodiversity.

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**Authors' contributions** TFB, CCP, JLK, FALC, MMM and DPS wrote the manuscript. TFB, CCP, JLK, CMF, NMB, and FCB collected data. TFB and CCP analyzed the data. LJ and LFAM reviewed the manuscript. CRW, DJF, JLK, LJ, LFAM and MPDS provided logistic/financial support.

**Les zones forestières mises en réserve et les corridors riverains aident à maintenir les communautés d'abeilles à orchidée (Hymenoptera: Euglossini) dans les plantations de palmiers à huile au Brésil**

**Amazone / fragmentation / utilisation des terres / aires de protection permanente**

**Waldschutzgebiete und Uferwaldkorridore tragen zur Erhaltung von Prachtbienenengemeinschaften (Hymenoptera: Euglossini) in Ölpalmenplantagen in Brasilien bei**

**Amazonas / Euglossini / Fragmentation / Landnutzung / Permanente Schutzgebiete**

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## Supplementary material

**Table S1.** Complete species name and total abundance of orchid bees collected with scent traps at the Agropalma Industrial Complex study areas, municipality of Tailândia, Pará State, Brazil in July 2015. APP: “Áreas de Preservação Permanente” (Permanent Protection Areas).

Species	Conventional oil palm	APP	Forest reserve
<i>Eufriesea ornata</i> Mocsáry, 1896	0	1	0
<i>Euglossa (Euglossa) amazonica</i> Dressler, 1982	0	1	6
<i>Euglossa (Euglossa) bidentata</i> Dressler, 1982	0	0	15
<i>Euglossa (Euglossa) modestior</i> Dressler, 1982	1	1	3
<i>Euglossa (Euglossa) securigera</i> Dressler, 1982	0	0	1
<i>Euglossa (Euglossa) sp. 1</i>	0	2	0
<i>Euglossa (Euglossa) townsendi</i> Cockerell, 1904	0	3	3
<i>Euglossa (Glossura) chalybeata</i> Friese, 1925	4	16	46
<i>Euglossa (Glossura) ignita</i> Smith, 1874	15	52	25
<i>Euglossa (Glossura) imperialis</i> Cockerell, 1922	0	0	15
<i>Euglossa (Glossura) orellana</i> Roubik 2004	0	2	4
<i>Euglossa (Glossurela) augaspis</i> Dressler, 1982	1	4	19
<i>Euglossa (Glossurella) crassipunctata</i> Moure, 1968	0	1	1
<i>Euglossa (Glossurella) parvula</i> Dressler, 1982	0	1	5

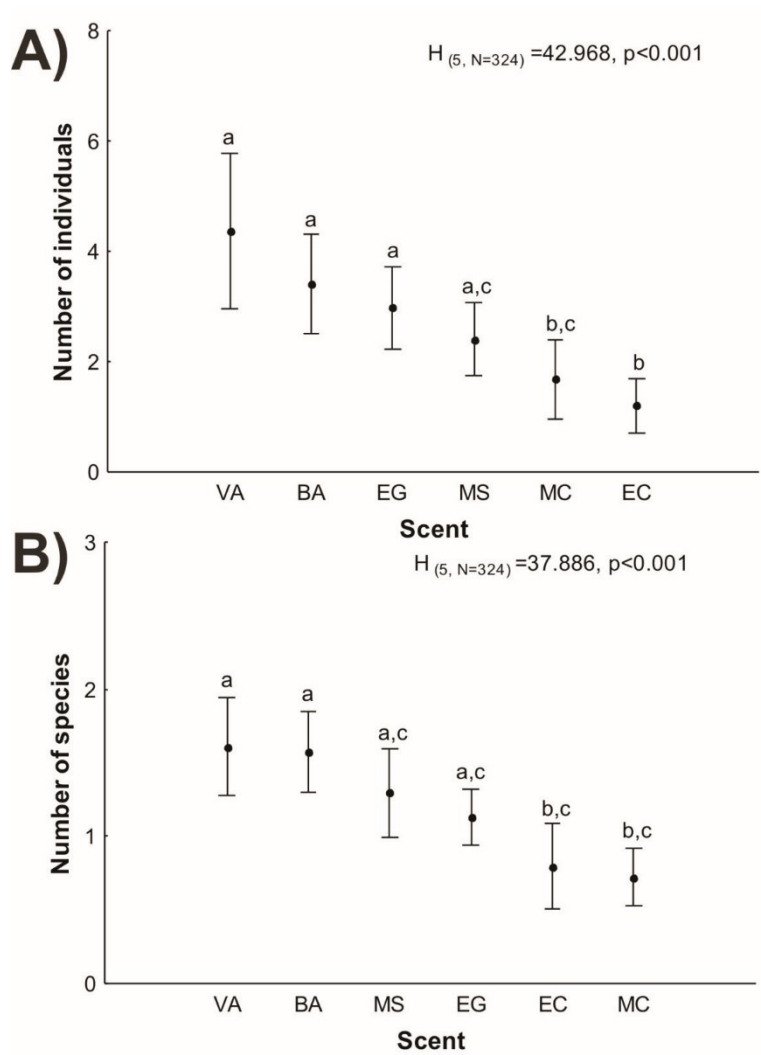


<i>Euglossa (Glossuropoda) intersecta</i> Latreille, 1817	0	4	2
<i>Eulaema (Apeulaema) cingulata</i> Fabricius, 1804	137	157	33
<i>Eulaema (Apeulaema) mocsaryi</i> Friese, 1899	1	2	2
<i>Eulaema (Apeulaema) nigrita</i> Lepeletier, 1841	5	7	2
<i>Eulaema (Apeulaema) pseudocingulata</i> Oliveira, 2006	0	4	1
<i>Eulaema (Eulaema) bombiformis</i> Packard, 1869	3	9	13
<i>Eulaema (Eulaema) meriana</i> Olivier, 1789	74	108	35
<i>Eulaema (Eulaema) polyzona</i> Mocsáry, 1897	0	1	2
<i>Exaerete frontalis</i> Guérin, 1844	0	4	7
<i>Exaerete lepeletieri</i> Oliveira & Nemésio, 2003	0	1	1
<i>Exaerete smaragdina</i> Guérin, 1844	0	1	3
<b>Total individuals</b>	<b>241</b>	<b>382</b>	<b>244</b>
<b>Total species</b>	<b>9</b>	<b>22</b>	<b>23</b>

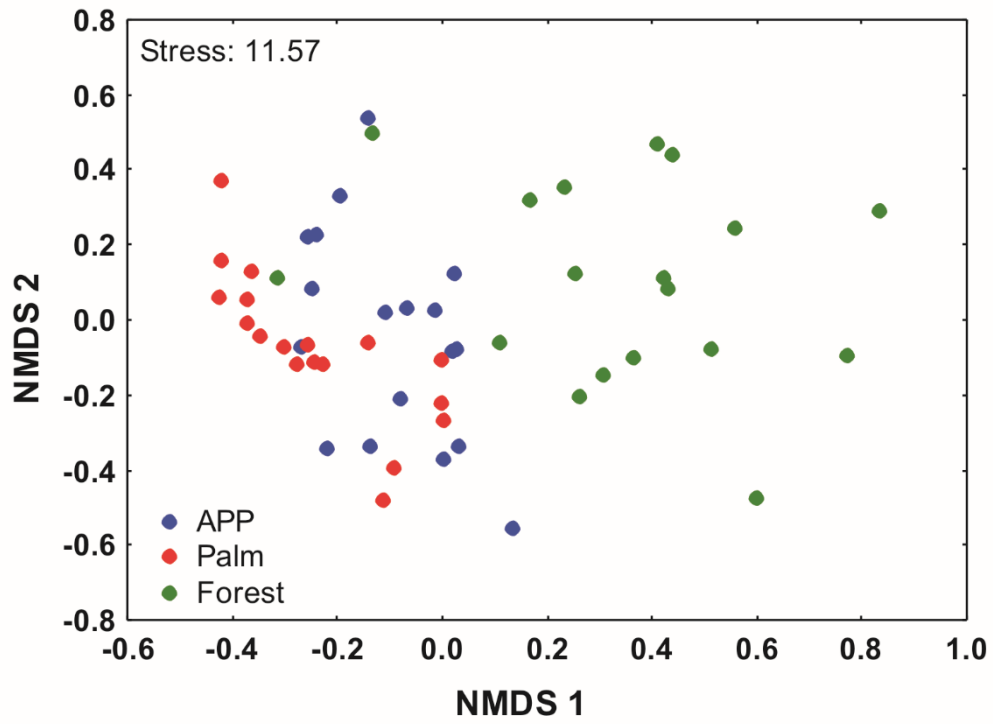
**Table S2.** Euglossine bee species attracted to bait scents in Tailândia, Pará State, Brazil (BA = benzyl acetate, EC = eucalyptol, EG = eugenol, MC = methyl cinnamate, MS = methyl salicylate, VA = vanilin).

	<b>BA</b>	<b>EC</b>	<b>EG</b>	<b>MC</b>	<b>MS</b>	<b>VA</b>
<i>Eufriesea ornata</i>	0	0	1	0	0	0
<i>Euglossa amazonica</i>	1	2	4	0	0	0
<i>Euglossa augaspis</i>	0	0	5	0	0	19
<i>Euglossa bidentata</i>	0	0	4	0	6	5
<i>Euglossa chalybeata</i>	3	32	5	2	19	5
<i>Euglossa crassipunctata</i>	0	0	2	0	0	0
<i>Euglossa ignita</i>	67	4	1	17	3	0
<i>Euglossa imperialis</i>	0	0	0	0	15	0
<i>Euglossa intersecta</i>	0	6	0	0	0	0
<i>Euglossa modestior</i>	0	4	0	1	0	0
<i>Euglossa orellana</i>	0	0	1	3	1	1
<i>Euglossa parvula</i>	0	0	0	0	0	6
<i>Euglossa securigera</i>	0	0	0	0	1	0
<i>Euglossa</i> sp. 1	0	1	0	1	0	0
<i>Euglossa townsendi</i>	0	0	0	0	0	6
<i>Eulaema bombiformis</i>	10	0	0	2	13	0
<i>Eulaema cingulata</i>	19	0	135	0	0	173
<i>Eulaema meriana</i>	79	2	0	59	69	8
<i>Eulaema mocsaryi</i>	4	0	0	0	0	1
<i>Eulaema nigrita</i>	0	4	0	0	1	9

<i>Eulaema polyzona</i>	1	0	0	0	2	0
<i>Eulaema pseudocingulata</i>	0	0	3	0	0	2
<i>Exaerete frontalis</i>	0	6	0	5	0	0
<i>Exaerete lepeletieri</i>	0	2	0	0	0	0
<i>Exaerete smaragdina</i>	0	2	0	1	0	1
<b>Total individuals</b>	<b>184</b>	<b>65</b>	<b>161</b>	<b>91</b>	<b>130</b>	<b>236</b>
<b>Total species</b>	<b>8</b>	<b>11</b>	<b>10</b>	<b>9</b>	<b>10</b>	<b>12</b>
<b>Exclusive species</b>	<b>0</b>	<b>2</b>	<b>2</b>	<b>0</b>	<b>2</b>	<b>2</b>



**Figure S1.** Kruskal-Wallis results of abundance (A) and richness (B) of orchid bees collected using different scent baits in Tailândia municipality, State of Pará, Brazil. Center represents the mean and the bars represent 95% confidence intervals. Scent codes: BA=benzyl acetate, EC=eucalyptol, EG=eugenol, MC=methyl cinnamate, MS=methyl salicylate, VA=vanillin.



**Figure S2.** Nonmetric Multidimensional Scaling (NMDS) for data ordered by subsamples. Land use codes: APP = “Áreas de Preservação Permanente” (Permanent Protection Areas), Palm= Oil palm plantations, Forest=Forest reserves.

# Capítulo 2

## **Effects of habitat type change on taxonomic and functional composition of orchid bees (Apidae: Euglossini) in the Brazilian Amazon**

O capítulo II desta Tese foi elaborado e formatado conforme as normas da publicação científica *Journal of Insect Conservation*, as quais se encontram em anexo (Anexo 2).



# Effects of habitat type change on taxonomic and functional composition of orchid bees (Apidae: Euglossini) in the Brazilian Amazon

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## Abstract

Land use change impact species richness and functional diversity (FD). In the Brazilian Amazon, we examined the impacts of oil palm plantations on orchid bee (Apidae: Euglossini) species using abundance and FD. We collected male orchid bees in oil palm plantation (PALM), legal reserves (LR), and riparian corridors (APP), and then we used morphological and life-history traits to characterize each species. We evaluated differences in bee body size by comparing intertegular span values. We tested the influence of habitat on taxonomic and functional parameters of orchid bees by applying a partial redundancy analysis (pRDA). We contrasted FD by calculating species richness, functional richness, and functional dispersion. We sampled 1176 bees from 30 species in 18 sampling days across 2015 and 2016. Males from PALM were 13.6% bigger than those in LR areas, and bees from APP showed a similar pattern compared to LR and PALM. Less than 15% of the variation in species composition was related to the distance among sampling sites, and 8% was due to habitat structure. In our pRDA, the spatial difference explained 6% of the variation in orchid bee traits, but there were no effects of habitat parameters upon FD. FD was reduced with land use change caused by oil palm plantations. Our findings support the belief that many bees are impacted by cultivated lands. Nevertheless, the functional similarity between LRs and APPs reflects common structural elements between them, although we did not find significant relationship between functional composition and habitat structure that we evaluated.

**Keywords** Body size · Functional dispersion · Functional diversity · Habitat structure · Oil palm

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## Introduction

The conversion of natural areas for agricultural activities caused the need to monitor and predict how plant and animal communities vary over these landscape gradients (Williams et al. 2010). Considering this, life history and ecological attribute approaches have shown a different perspective of

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the species' vulnerability to land-use changes, demonstrating how human-modified landscapes affects the taxonomic and functional diversity (FD) of communities (Flynn et al. 2009; Laliberté et al. 2010; De Palma et al. 2015). Although there is evidence of loss of taxonomic and FD in amphibians (Correa et al. 2015), birds (Almeida et al. 2016), and some aquatic organisms (Luiza-Andrade et al. 2017), there is little consensus on the actual effects of land-use changes on terrestrial invertebrate communities. Still, compelling studies recently published show that human effects upon insects may be many times greater than previously reported (Hallmann et al. 2017).

Bees are one of the main terrestrial insect groups that provides essential pollination services, promoting food security and contributing to the persistence of many native plants and domesticated crops (Klein et al. 2007; Ollerton et al. 2011). However, in recent decades, marked changes in most terrestrial ecosystems, primarily caused by human activities, have contributed to widespread biodiversity loss, changes in the structure of ecological communities, and a decrease of ecosystem services (Mitchell et al. 2015; Newbold et al. 2015). As a result, the most disturbed sites are characterized by depopulated species pools and homogenous communities, with only a subset of original bee species present dominated by generalist species, with high dispersal abilities compared to pristine bee communities (Vellend et al. 2007; Karp et al. 2012; Solar et al. 2015).

Land-use changes and the conversion of natural habitats to other habitat types can impact bee communities by reducing floral and nesting resources (Kremen et al. 2007; Burkle et al. 2013; Brito et al. 2017). The response of bee species to different forms of habitats are usually determined using metrics related to species richness and/or abundance of bees (Winfree et al. 2011; Benjamin et al. 2014; De Palma et al. 2015). In general, species with more specialized niches (space, time, phenotype, and/or interspecific interactions) are more sensitive to the effects of agricultural intensification compared to generalist species (Kassen 2002).

Studies have shown that reduction of vegetation cover influences the distribution pattern of the local bee fauna and exerts a selective pressure upon the communities (Steffan-Dewenter and Tscharrntke 1999; Silva and Rebêlo 2002; Brito et al. 2017; Campbell et al. 2018). Despite the fact that more complex environments are usually characterized by a higher number of species and diversity of niches, which are related to the availability of feeding resources (Tews et al. 2004), differences in bee communities among habitat types may provide a better understanding of species patterns in mosaic landscapes, allowing us to identify more vulnerable and intolerant species to certain physical factors (Lovejoy et al. 1986). For insects, habitat structure and abiotic parameters are important factors influencing community taxonomic composition (Viana et al. 2006;

Mendes et al. 2017). In addition, in a more refined way, it is necessary to identify which environmental conditions are filtering species with certain traits, in order to know the mechanisms related to FD changes in communities as a result of environmental changes (Tilman et al. 1997).

Groups of eusocial and semi-social bees have been strongly affected by the isolation of natural habitats and the use of pesticides, compared to solitary bees (Williams et al. 2010; Milet-Pinheiro and Schlindwein 2005; Brosi et al. 2008), because of their smaller foraging range (Greenleaf et al. 2007). In addition, measures of morphological characters reveal that certain traits can specifically influence the vulnerability of bees to habitat type, i.e. species with a wide foraging area may cover a larger area in fragmented landscapes, but this could increase the probability of contamination by pesticides in agricultural landscapes (Carvalho et al. 2011; Whitehorn et al. 2012; Rader et al. 2014). Castilla et al. (2016) highlight the importance of pollinator body size when evaluating the relationship between biodiversity and ecosystem function, where even small-bodied pollinators play an important role in the maintenance of genetic connectivity in plant populations. Even so, increased bee body size is often translated into an improved ability to manipulate complex floral structures, as seen in many buzz-pollinated plant species (Solís-Montero et al. 2015).

Orchid bees (Apidae, Euglossini) are a Neotropical group of bees with a strong relationship with orchid flowers, but most species also pollinate many other plant species (Dressler 1982a; Ramírez et al. 2002; Rocha-Filho et al. 2012; Cavalcante et al. 2012). Comprising about 250 species (Nemésio and Rasmussen 2011), these bees are sensitive to environmental changes, habitat isolation, and fragmentation (Powell and Powell 1987; Nemésio and Vasconcelos 2013; Brito et al. 2017; Storck-Tonon and Peres 2017). They can also be easily sampled by using inexpensive scent traps, making them an ideal proxy for evaluating effects of habitat disturbances (Solar et al. 2015). In recent studies conducted in Eastern Amazon, orchid bees showed the highest species diversity in secondary forests, intermediate levels in primary forests, and only a few species in agricultural areas (Solar et al. 2016). However, species composition in forested and non-forested areas is highly differentiated, with apparently smaller and more specialist species occurring within forests, while non-forested areas are dominated by larger generalist species that have a greater flying capability (Milet-Pinheiro and Schlindwein 2005; Brito et al. 2017). This pattern of species occurrence throughout the landscape is not surprising, considering that large orchid bees have a higher dispersal capacity (Janzen 1971; Raw 1989; Wikelski et al. 2010; Pokorny et al. 2015) and, thus, have a greater ability to forage in and colonize new areas, even cross open expanses (Nemésio and Silveira 2007).



In Brazilian Amazon, oil palm (*Elaeis* sp. Jacq, Arecaceae) is becoming in one of the most important commercial crops, by producing several products derived from palm oil (Müller et al. 2006a; Alves et al. 2013). Results obtained by previous studies have shown that orchid bee community of forest habitats may be replaced by non-forest species, as the distance from forest patches increases (e.g. Livingston et al. 2013; Storck-Tonon and Peres 2017). However, to promote forest conservation, the Brazilian government has a program for the sustainable production of palm oil, promoting oil palm plantations only in the indicated areas that exclude native vegetation (i.e. forests) (Brazilian Decree, no 7.172/2010; Embrapa 2010). Thus, current areas used for oil palm plantations in the eastern Amazon, are characterized by the presence of already deforested areas, differing from the usual scenario found in Asian plantations, for example (Bicalho et al. 2016).

Although some orchid bee species show some degree of permeability through oil palm, particular characteristics, such as the altered abiotic environment and the rarity of orchids, made this land-use a low-quality matrix compared to agroforestry systems (Livingston et al. 2012, 2013). Further, even though bee species did not show clear variation in functional traits in forest and oil palm (Livingston et al. 2013), the study of functional responses to land-use change and identifying which morphological traits make species more or less vulnerable to human impacts may be useful to guide conservation priorities (Rader et al. 2014).

In Brazil, to allow for economic development of land and ensure the maintenance of ecosystem services in the Amazon Biome, rural landowners are required to maintain 50–80% of their properties as natural areas. These protected areas can be large blocks of contiguous forest, called legal reserves (LR), devoted to the conserve and rehabilitate of ecological processes, and promote biodiversity conservation. The second, include forest patches or native vegetation aside riparian corridors, called the areas of permanent protection (APPs). These APPs promote geological stability, water filtration, and also act as corridors connecting populations between forest fragments (Brazilian Law, no 12.651/2012). These mandatory protected natural habitats are considered one of the main mechanisms for the protection of environmental services in the country (Marques and Ranieri 2012).

In this study, we evaluated the influence of habitat characteristics and the response of FD of orchid bees to different habitat types. We selected eight morphological traits that relate to ecological filtering from 26 species that we collected from LR, oil palm plantations (PALM), and APP in the Brazilian Eastern Amazon. If large orchid bees have a greater flight capacity than smaller ones, and habitat structure may influence community composition of insects, we hypothesized that the variation of orchid bee body sizes and FD would be greater in RLs than in other habitats.

Additionally, we expected that abiotic parameters and habitat variables structuring habitat type conditions would affect abundance and traits of orchid bee species.

## Materials and methods

### Study site and sampling

We sampled orchid bees in the southeastern portion of the state of Pará, Brazil, at a large-scale oil palm plantation (Agropalma Industrial Complex), near the municipality of Tailândia (approximately 02°20' and 02°40'S by 48°30' and 49°0'W), between 12 and 28-July-2015 and 17 and 30-August-2016. We attracted and collected the male orchid bees with six separate sampling stations with six scent traps each in nine sampling sites (three LR, three APP, and three PALM; see Fig. 1 in Brito et al. 2017), for a total of 36 traps per site and 108 per habitat type. To attract bees, we hung six scent traps spaced 2 m apart, at each sampling station with the following unique scents: benzyl acetate, eucalyptol, eugenol, methyl cinnamate, methyl salicylate, and vanillin. The sampling stations within each site were 500 m apart, and we sampled one site per day.

The proximity between LRs ranged from 10 to 19 km; APPs were 10–11 km apart, while PALM areas were separated from 5 to 10 km. Sites from different habitat type were at a minimum distance of 1–2 km, and at a maximum distance of, approximately, 20 km. In LR sites, we established the first sampling station near to the edge and the subsequent along every 500 m in established trails inside forest (in a previously established trail), while in APP sites, the set of traps were arranged in the middle of the vegetation that followed the streams.

We made the scent traps with 2 L PET plastic bottles containing an internal swab cotton, and three equidistant holes in the medium portion, with landing platforms for entrance of bees. We hung the sets of these traps for 48 h in each sampling site (equal amounts of sampling effort during 2015 and 2016; 216 h). Then we removed, pinned, and identified the captured (males) bees based on taxonomic keys (Dressler 1982b; Moure 2000; Oliveira 2006; Nemésio 2009), and using reference entomological collection from Embrapa Amazônia Oriental and Museu Paraense Emílio Goeldi. We deposited the sampled specimens at the Entomological Collection of the Embrapa Amazônia Oriental. Additional information on methodology can be found in Brito et al. (2017).

### Orchid bee traits

We measured five morphological traits for each captured orchid bee species (the pinned specimens): intertegular span (ITS) (as a measure of body size), wing length (WL),

wing width (WW), interocular distance (ID), and head width (HW) (Online Resource 1). We selected all species with total abundance greater than or equal to two specimens, and no more than 10 individuals per species were measured. For species with more than 10 individuals sampled, we made sure to include representative specimens captured in each one of the habitat type. We obtained individual pictures for each specimen with a Motic Cam 5.0 coupled to stereomicroscope (Motic SMZ 168, 0.75X), and then we analyzed the pictures in Motic Images Plus 2.0 software. Additionally, we compiled data from published literature of three life-history traits known to be affected by habitat changes: dietary specialization (pollen-specificity), nest construction behavior (nest type), and sociality (Table 1). When there was no such data for one species, we used the life-story traits reported to the nearest phylogenetic related species (Ramírez et al. 2010; Cameron 2004; Online Resource 2).

We based the choice of morphological traits on evidence that they directly link organism's performance with environmental conditions or ecosystem processes. For example, body and wing size are related to flight distance capability and susceptibility to environmental changes, and variations on these morphological traits will certainly influence the amount and composition of resources used by bees (Winfree et al. 2009; Moretti et al. 2016). ITS is a common body size measurement obtained in bee studies that is correlated to the specimen's body mass and wing muscles (Cane 1987), and also relates to flight distance capacity and foraging behavior (Greenleaf et al. 2007; Garibaldi et al. 2011). Finally, eye morphology may be filtered by environmental conditions

that can reflect prey and/or predator recognition (Moretti et al. 2016).

### Habitat characterization

To describe physical habitat conditions within each site, we established one 5 × 5 m plot in each sampling station, resulting in 150 m<sup>2</sup> of sampling area for each LR, APP, and PALM site. This protocol was based on Magalhães et al. (2014) with some adaptations (Online Resource 3). Within each plot, we measured 16 habitat characteristics (variables): (1) number of large trees [Diameter at Breast Height (DBH onwards) > 15 cm], (2) small trees (DBH < 15 cm), and percent cover of (3) epiphytes, (4) palm trees, (5) shrubs, (6) grasses, (7) lianas, (8) and soil plant cover, (9) litter height, (10) canopy opening, (11) canopy height, (12) number of clearings, (13) dead trees, (14) fallen trunks, and (15) flowering trees, and (16) temperature.

We measured variables 1–8 by visual estimation and we assessed the canopy opening using non-hemispherical digital photos analyzed on Gap Light Analyzer 2.0 (Frazer and Canham 1999), defined as the average from three randomly locations in each plot (see details on Online Resource 3). For variables 12–15, we counted the amount of each variable inside our 5 × 5 plot, and we estimated canopy height based on the highest tree found in the plots. We assessed the mean daily temperature of each of our sampling days from the Agropalma's Weather Station database. We used the same mean value of temperature for all sampling stations of the

**Table 1** Traits of orchid bees used in the analysis

Trait	Type	Description
Intertegular span	Continuous	The distance between the nearest edges of the tegulae, the plates covering the bee's wing bases, in mm. ITS is a proxy for body size and foraging distance in bees
Wing length	Continuous	Measurement from the beginning of the wing (border of the tegulae) to the distal end, in mm. Only the left anterior wing was measured
Wing width	Continuous	Larger wing width, in mm. Only the left anterior wing was measured. Wing size is a functionally essential trait for flight performance, foraging and dispersal abilities (Wootton 1992)
Interocular distance	Continuous	Measure of the distance between the two inner edges of the eye, aligned by the insertion of the antennae, in mm
Head width	Continuous	Measure of the distance between the two outer edges of the eye, aligned by the insertion of the antennae, in mm. Head parameters are proxy to environmental perception and recognition (Srinivasan et al. 1991)
Sociality	Semi-social Solitary	Social structure, based on the descriptions for each genus of orchid bee (Michener 2007; Zucchi et al. 1969)
Pollen-specificity	Oligolectic Polylectic	Trophic specialization defined by the range of pollen species collected by females and males. Oligolectic is a pollen specialist species that forages on plants from less than one plant family. Polylectic species are generalist foragers, collecting pollen from two or more plant families (Ramírez et al. 2002; 2010; Cameron 2004)
Nest type	Excavator Renter Cleptoparasitic	Excavators build the nest on stems or twigs in the open or dig the chamber within existing substrate. Renters construct nests within existing cavities, or tunnels regardless of nest location (under buildings, preexisting burrows, termite nests). Cleptoparasitic bees parasitizes the nest or brood of other species (Michener 2007; Ramírez et al. 2002; Augusto and Garófalo 2004; Zucchi et al. 1969)



same sampling site, since samples belonging to the same site were performed in a single day.

### Statistical analysis

To test the hypothesis that LRs harbor the greatest variation of orchid bee body sizes, we compared differences in body size of orchid bees among sites using ITS values with a One-Way ANOVA. Significant ANOVA results were compared with post hoc Tukey tests with  $\alpha=0.05$ . We also performed One-Way ANOVA for the other four morphometric measures (WL, WW, ID and HW) only as a complementary analysis. In all analyses, we tested the data for the assumptions of normality and homoscedasticity.

We evaluated the influence of habitat characteristics of habitat types on taxonomy and functional parameters of orchid bee assemblages by applying a partial redundancy analysis (*p*RDA), a multivariate technique that allows the ordination of a dependent matrix data and its association with explanatory variables, controlling the covariate effects (Borcard et al. 2011). We tested the influence of environmental characteristics (habitat), distance among sampling stations (space), and habitat types (system) on the variation of taxonomic (species matrix with abundance values) and functional composition (traits) (Fig. 1). We obtained the community-weighted trait means (CWM onwards) using all continuous traits for each site (Garnier et al. 2004) as measures of functional composition, using the function “functcomp” from the FD package (Laliberté and Legendre 2010; Laliberté et al. 2014). This method consists of a post-multiplication of species per site values by traits per species values, resulting in a matrix of mean traits per site weighted by species abundances (“traits matrix”; Fig. 1a).

We used three sets of predictors to understand the patterns of taxonomic and functional composition of orchid bee assemblages: habitat matrix (i), space matrix (ii), and system matrix (iii). First, we initially made a previous choice of habitat variables using three selection criteria: (a) the parameters that did not vary among sampling stations were excluded from the analyses once they contributed little to the characterization of habitat types analyzed, (b) variables with > 60% of zeros values in the original data, and (c) correlated parameters ( $r$  Pearson > 0.60). Thus, among the 16 original habitat variables, a set of nine variables followed the selection criteria that we established (see details on Online Resource 4). Because temperature is an important predictor for bees, we choose to maintain this variable. Therefore, ten predictors of habitat variables remained, constituting the “habitat matrix” (Fig. 1b).

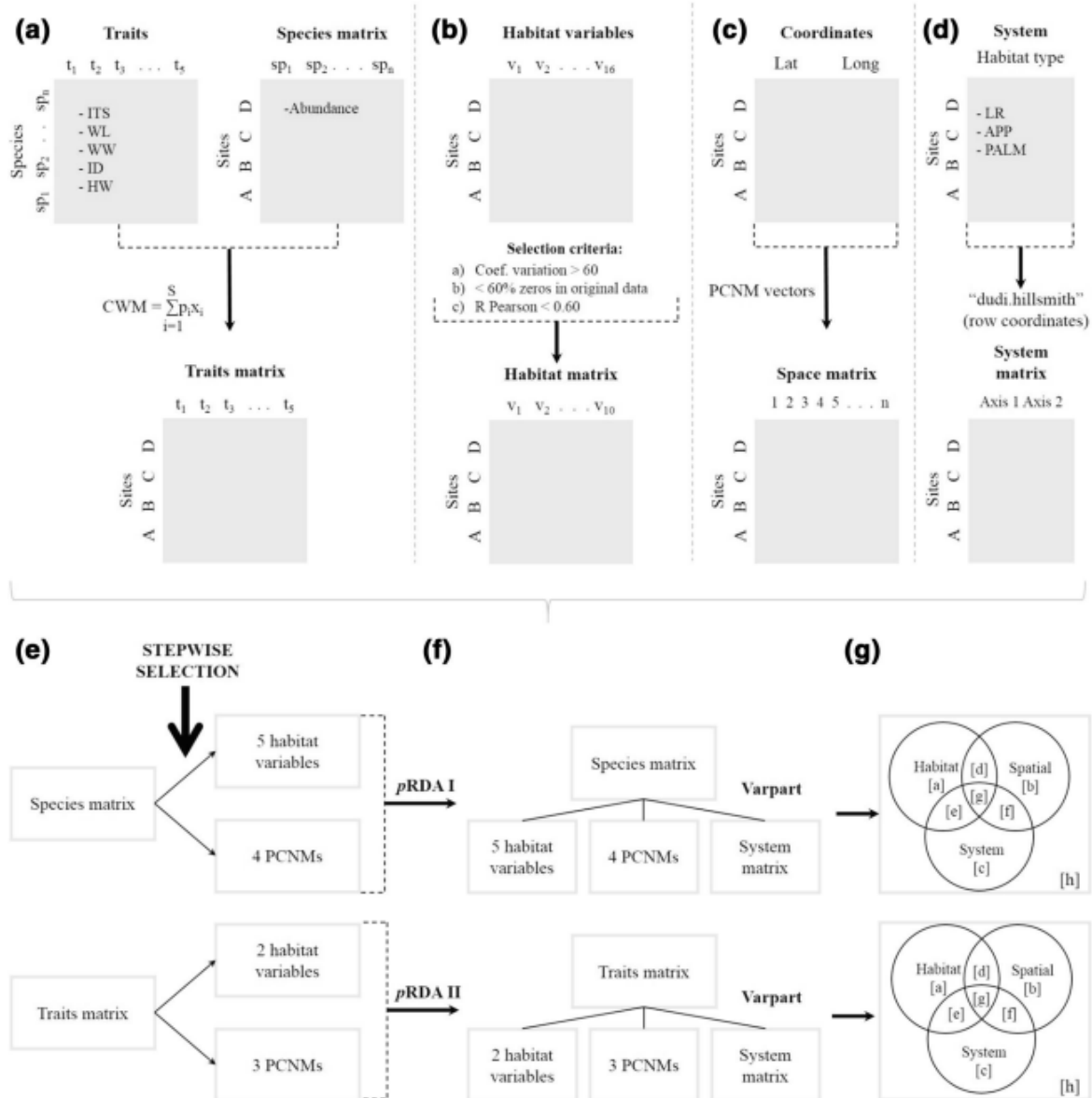
Second, to spatially represent the sites, we generated continuous spatial variables from latitude and longitude data of each sampling station by calculating principal coordinates of neighbor matrices (PCNM; Borcard and Legendre 2002; Dray

et al. 2006). The resulting axes orders (“space matrix”) were used to quantify the influence of space on the variation of bee assemblages (Fig. 1c). This spatial predictor is necessary to understand the fraction of the results that could be explained only by the spatial distribution among the collection sites. This is because it is expected that nearby sites may have similar species composition, and when this is not verified the spatial autocorrelation could bias the hypothesis tests (Dormann et al. 2007).

In order to include habitat as a predictor, we transformed the vector of habitat types (LRs, APPs, and PALM) into continuous numerical axes. We created the new numerical variable by applying the “dudi.hillsmith” function of the ade4 package (Dray and Dufour 2007) on the data of habitat type per sample (“system matrix”) (Fig. 1d).

Then, we used stepwise regression models to select habitat parameters (using the habitat matrix) and space (using PCNM matrix) related to functional and taxonomic composition of orchid bees to be used in *p*RDA (Fig. 1e). In these selection models, we applied the function “adonis” of the vegan package, using the matrix of species composition per site and for traits matrix, the CWM matrix. Finally, we performed two *p*RDA analyses. In the first *p*RDA, we tested the associations between orchid bee taxonomic composition as a dependent variable, and the explanatory variables habitat, space, and system as the predictor variables. In the second *p*RDA, we used orchid bee functional composition (CWM) as a dependent variable (Fig. 1f) against the same predictor variables used before. This analysis considers the dependence among all three dataset, expressing the individual fraction of variation explained by habitat parameters [a], spatial distribution [b], habitat type [c], the interaction between them [d, e, f, g] and the unexplained variation [h] (Fig. 1g). The percentages of explanation of each explanatory variable and the interaction between them were obtained with adjusted- $R^2$  values, by applying the “varpart” function of the vegan package (Oksanen et al. 2017).

FD was calculated in terms of species richness (richness), functional richness (FRic) and functional dispersion (FDis) with Gower distance matrices and using the “dbFD” function of the FD package (Laliberté and Legendre 2010; Laliberté et al. 2014). We used all traits as response variables and habitat type as a potential predictor variable. We performed a One-Way ANOVA followed by a post hoc Tukey test (if ANOVA differences among the habitat types showed differences) to test for differences in richness, FRic, and FDis among habitat types. We performed all analyses using R 3.4 (R Development Core Team 2017).



**Fig. 1** General summary of the analysis employed in our study. **a** Obtaining the community-weighted trait (CWM) using all continuous traits for each site pondered by species abundance; **b** habitat variables selection based on three criteria, forming the "habitat matrix"; **c** calculating principal coordinates of neighbor matrices (PCNM) using spatial variables of each sampling station; **d** creation of the new numerical variable using the data of habitat type per sample ("system matrix"); **e** stepwise regression models to select habitat and space

parameters related to taxonomic ("species matrix") and functional composition ("traits matrix") of orchid bees; **f** applying a partial redundancy analysis (pRDA) to test the influence of selected habitat and space variables, and habitat types ("system matrix") on the variation of both taxonomic and functional composition; **g** partition of the variance of each explanatory variable and the interaction between them

## Results

In 18 sampling days across both years, we collected a total of 1176 male euglossine bees from 30 species (Online

Resource 5). *Eulaema cingulata* Fabricius, 1804 and *E. meriana* Olivier, 1789 were the most common species both in APP and PALM sites, representing 51.2% of all bees sampled. In LR, *E. meriana* and *Euglossa chalybeata* Friese,

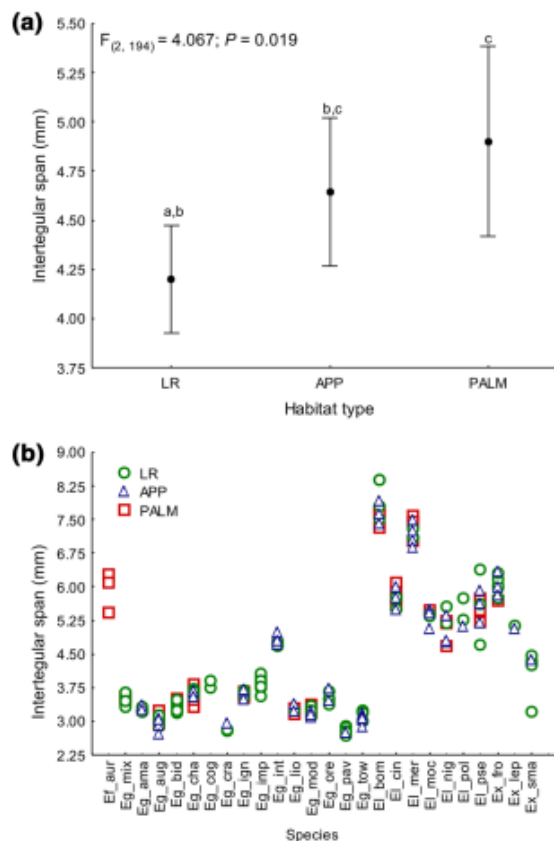
1925 were the most abundant, accounting for 30% of total bees. Complete species name and total abundance are available in Online Resource 5.

Orchid bee body size varied among habitat types ( $F_{(2,194)} = 4.067, P = 0.019$ ), with males sampled in PALM being 13.6% bigger than those in LR (Tukey's HSD,  $P = 0.037$ ). Individuals from APPs showed a similar pattern in size compared both to LR (Tukey's HSD,  $P = 0.111$ ) and PALM (Tukey's HSD,  $P = 0.797$ ). In PALM, there was a greater variation in bee body size (Fig. 2a), which can be verified also when observing the species individually (Fig. 2b). Also, males from PALM showed heads about 10.2% wider ( $F_{(2,194)} = 4.788, P = 0.009$ ; Tukey's HSD,  $P = 0.013$ ), and a difference of 8.7% in distance between eyes when compared to individuals from LR ( $F_{(2,194)} = 4.029, P = 0.019$ ; Tukey's HSD,  $P = 0.013$ ) (Online Resource 6). The comparisons of both wing measures (WL and WW) between habitats were non-significant (Online Resource 6).

Stepwise regression models selected five habitat parameters (large and small trees, shrubs, lianas, and fallen trunks) and four spatial variables (PCNM 1, PCNM 2, PCNM 3, and PCNM 13) related to the taxonomic composition of orchid bee. Additionally, using functional traits as a response variable in stepwise regression models, we found a significant relationship with two habitat parameters (large trees and small trees) and three related to space (PCNM 1, PCNM 2 and PCNM 13).

Although we found significant effects, the taxonomic composition of orchid bees exhibited a weak relationship with habitat variables (large trees:  $R^2 = 0.067, P < 0.001$ ; small trees:  $R^2 = 0.090, P < 0.001$ ; shrubs:  $R^2 = 0.038, P = 0.016$ ; lianas:  $R^2 = 0.030, P = 0.047$ ; fallen trunks:  $R^2 = 0.035, P = 0.025$ ) and with spatial parameters (Online Resource 7). However, when we used orchid bee functional traits as a response, an intermediate explanatory value was recorded for large trees ( $R^2 = 0.186, P = 0.001$ ) and small trees ( $R^2 = 0.188, P < 0.001$ ), and one spatial variable (PCNM 2:  $R^2 = 0.364, P < 0.001$ ) (Online Resource 8). The other variables showed low explanatory power of the variation in orchid bee traits (PCNM 1:  $R^2 = 0.088, P = 0.003$ ; PCNM 13:  $R^2 = 0.115, P = 0.001$ ) (Online Resource 8).

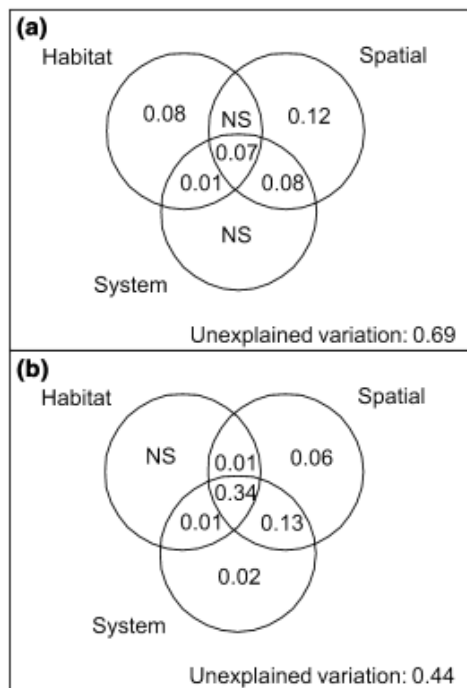
The results of *p*RDAs showed that < 15% of the variation in orchid bee species composition was related to geographic distance among sampling sites ( $F_{5,44} = 3.046; P = 0.001$ ), only 8% of this variation occurred due to habitat structure variation ( $F_{2,44} = 2.032; P = 0.020$ ), and most of the variation (about 69%) may be occurring because of unmeasured factors (residual) (Fig. 3a). Further, there was no effect of habitat types (system) on orchid bee assemblages ( $F_{2,44} = 0.817; P = 0.564$ ). When we analyzed functional composition as a response parameter, the three parameters together (habitat, system, and space) explained 34% of the variation in orchid bee traits, and the space alone responded for only



**Fig. 2** One-way ANOVA results of body size comparison of orchid bees by habitat type based on **a** ITS and **b** ITS size variation of male orchid bees by species sampled in the three habitat types ( $n = 196$ ) in Tailândia municipality, State of Pará, Brazil. The center represents the mean and the bars represent 95% confidence intervals. Habitat type codes: LR=legal reserves, APP=areas of permanent protection, PALM=oil palm plantations. Species codes: Ef\_aur=*Eufriesea auripes*, Eg\_mix=*Euglossa* aff. *mixta*, Eg\_ama=*E. amazonica*, Eg\_aug=*E. augaspis*, Eg\_bid=*E. bidentata*, Eg\_cha=*E. chalybeata*, Eg\_cog=*E. cognata*, Eg\_cra=*E. crassipunctata*, Eg\_ign=*E. ignita*, Eg\_imp=*E. imperialis*, Eg\_int=*E. intersecta*, Eg\_lio=*E. liopoda*, Eg\_mod=*E. modestior*, Eg\_ore=*E. orellana*, Eg\_par=*E. parvula*, Eg\_tow=*E. townsendi*, El\_bom=*Eulaema bombiformis*, El\_cin=*E. cingulata*, El\_mer=*E. meriana*, El\_moc=*E. mocsaryi*, El\_nig=*E. nigrita*, El\_pol=*E. polyzona*, El\_pse=*E. pseudocingulata*, Ex\_fro=*Exaerete frontalis*, Ex\_lep=*E. lepeletieri*, Ex\_sma=*E. smaragdina*

6% of the variation ( $F_{3,45} = 3.413; P = 0.027$ ) (Fig. 3b). The other parameters evaluated show no effect on bee functional composition (habitat:  $F_{3,45} = 0.347; P = 0.719$ ; system:  $F_{2,45} = 2.154; P = 0.125$ ) (Fig. 3b).

As expected, species richness, functional richness, and functional dispersion were significantly reduced with the differentiation of the habitats (ANOVA Richness:  $F_{2,51} = 10.212, P < 0.001$ ; FRic:  $F_{2,51} = 4.978, P = 0.010$ ;



**Fig. 3** Venn diagrams representing the partitioning of the variance in **a** orchid bee species, and **b** functional traits of orchid bees between sampling sites into fractions explained by habitat, spatial, system differences, and the interaction between them.  $R^2$  values (in %) obtained from  $p$ RDA are given for each fraction. *NS* non-significant values

FDIs:  $F_{2,51} = 11.980$ ,  $P < 0.001$ ) (Fig. 4). In PALM, there was a mean decrease of 40% of species compared to LR (Tukey's HSD,  $P < 0.001$ ), and of about 28% of species from APP sites (Tukey's HSD,  $P = 0.008$ ) (Fig. 4a). Functional richness of orchid bees tended to decline noticeably in PALM (LR vs.

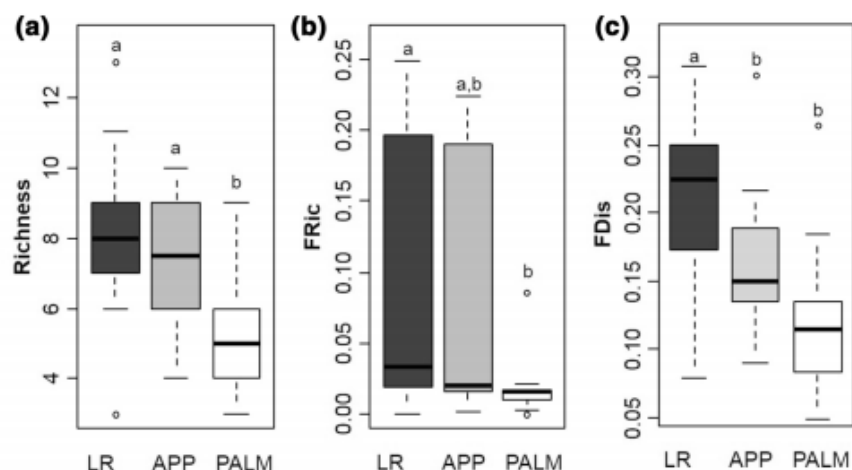
PALM: Tukey's HSD,  $P = 0.009$ ) (Fig. 4b). Functional dispersion, however, were higher in LR compared both to APP (LR vs. APP: Tukey's HSD,  $P = 0.032$ ) and PALM areas (LR vs. PALM: Tukey's HSD,  $P < 0.001$ ) (Fig. 4c).

## Discussion

In a previous study of the same sites, species composition and richness of orchid bees showed variation with habitat types, with individuals sampled in forest reserves significantly different compared to riparian corridors (APPs) and oil palm plantations (Brito et al. 2017). In our current study, we found additional information about orchid bees at individual and species level, with the largest orchid bees occurring in PALM sites, and the smallest individuals present inside LR areas. According to what we expected, the physical conditions of the different habitat types analyzed influence species composition, but the same was not true for FD of orchid bees in our study area. However, among the three parameters we analyzed (habitat structure, space, and type of habitat), the explanation of the variation in both species composition and functional traits was mainly attributed to the distance between the sampling sites.

In bees, body size affects characteristics associated with flight ability and the adaptive value of individuals (Cane 1987; Greenleaf et al. 2007), and some data suggest that environmental factors, such as rainfall variations, climate changes, and food availability, may influence body size heterogeneity in orchid bee populations (Peruquetti 2003; Silva et al. 2009). This is an important attribute because it determines the way the organisms perceive the environment, considering different habitats, environmental gradients or between distinct regions (Mason et al. 2007). Previous studies have shown that bees respond in different ways to

**Fig. 4** Box plots of FD metrics of orchid bees across different habitat types in Tailândia municipality, State of Pará, Brazil. Boxes show medians and interquartile ranges; whiskers extend to values within  $1.5 \times$  the interquartile range of the upper and lower quartiles. **a** Species richness, **b** functional richness, **c** functional dispersion. Significant differences are indicated by different letters based on Tukey's HSD tests. Habitat type codes: *LR* legal reserves, *APP* areas of permanent protection, *PALM* oil palm plantations





habitat and landscape changes, depending on the mean body size and the proportion of suitable habitat (Steffan-Dewenter et al. 2002; Silva et al. 2017). For solitary wild bees, for example, the species' perception of the landscape structure is more affected at local or field spatial scale, and this is related to their dispersal abilities or foraging ranges (Steffan-Dewenter et al. 2002).

The large-bodied orchid bees, such as *Eulaema* (*Eulaema*) and *Exaerete* species, often use large rainforest areas and are able to fly across deforested areas (Raw 1989; Tonhasca et al. 2003; Wikelski et al. 2010) and open-water, with a range flight of about 5–20 km (Janzen 1971; Wikelski et al. 2010; Storck-Tonon and Peres 2017). This could be related to the capacity to withstand high temperatures that the larger euglossine bees produce, compared to the small ones (May and Casey 1983), and because many small-bodied species are not able to fly over deforested or degraded areas (Milet-Pinheiro and Schlindwein 2005). Moreover, these restrictions on orchid bee movements may depend on the size and scale of the habitat change or dispersal barrier, but also on the presence of high-quality habitat for orchid bees in the landscape, which could favor dispersal of bees and other pollinators along them (Pokorny et al. 2015).

There is evidence that isolation of Atlantic Forest islands and a mainland forest in 7–11 km represents a significant dispersal barrier for *Euglossa cordata* Linnaeus, 1758, for example, leading individuals to genetic differentiation (Boff et al. 2014). Additionally, for *Euglossa imperialis* Cockerell, 1922, it has been shown that male individuals were recaptured at a maximum of 810 m far from the released site (Pokorny et al. 2015; Opedal et al. 2016). In our study, some small-bodied species occurred in greater number inside the forests (although they were also recorded in lower abundances the oil palm areas, see Brito et al. 2017), while most of them were restricted to forested areas (LR and APPs), reinforcing the fact that some orchid bee species, mainly the small bodied ones, seem to be more closely bound to forest habitats (Milet-Pinheiro and Schlindwein 2005).

Differences in species composition, abundances, and richness of orchid bees may be associated with small changes in local abiotic factors (e.g., temperature, humidity and rainfall; Andrade-Silva et al. 2012; Giangarelli et al. 2014), habitat characteristics, such as forest canopy, density of understory and sunlight exposition (Viana et al. 2006), but also with other unmeasured variables, such as the number and dispersal of scents used (Nemésio and Silveira 2006), and the variation on natural fragrance resources (Armbruster 1993). Our results demonstrate that, despite a great effort and number of variables measured, the habitat structure alone is not a good predictor of the taxonomic and functional composition of orchid bees. On the other hand, the exclusive presence of some species we collect in preserved areas (see Online Resource 5), suggests that even homogeneous plantations of

medium-sized trees, such as the oil palm, may act as barriers for some Euglossini species, at least for the local fauna of these bees. Other environmental variables—not measured in our study—likely related to observed patterns of orchid bees that we documented. The challenge in identifying habitat structure features that relate to orchid bee communities is partially because these bees are able to fly long-distances and just how the bees perceive landscape quality and scale remains under studied.

Previous research conducted in the same study area found some low-level of spatial correlation (Mantel  $r$  values < 15%) on abundance, richness, and species composition of orchid bees (Brito et al. 2017). Brosi (2009) showed that both abundance and community similarity of bees were significantly spatially autocorrelated, in forest fragments situated in a matrix of primarily cattle pasture. One potential explanation is that that landscape variables, such as size and shape of forest fragments and connectivity between them, are the most important in determining at least abundance of orchid bees (Brosi 2009; Winfree et al. 2007), while richness and diversity show negative relationship with increasing edge index (Storck-Tonon et al. 2013). And given the variety of resources used by all bees during their life cycle (e.g., pollen, nectar, and nest-construction materials) found in different habitats (Müller et al. 2006b), habitat structure may not have altered bee communities because adjacent and nearby forest patches may be able to supplement resources for plantation dwelling bee species (Roberts et al. 2017).

Our findings that land-use change negatively affected both orchid bee species richness and FD supports the widely held belief that many bees are significantly impacted by cultivated, human-altered habitats (Livingston et al. 2013; Forrest et al. 2015). Planting and agricultural land-use provide changes not only in the species richness and abundance, but also species and trait compositions of pollinator communities (Rader et al. 2014). Changes in pollinator communities occurs because these land uses share some attributes, such as loss of native plant species and soil compaction, that may impact distinct functional groups (Forrest et al. 2015). Evidence suggest that in other taxa, areas with intensive agriculture leads to a reduced functional-trait diversity (Flynn et al. 2009; Laliberté et al. 2010). In a study conducted in the same area of our study, Luiza-Andrade et al. (2017) demonstrated that both taxonomic and functional richness of aquatic insect communities (i.e. ephemeropteran, plecoperan, and trichopteran) were affected by oil palm plantation, and the authors emphasize the need of active conservation measures in order to conserve the diversity of these groups in streams associated with oil palm plantations. Differences in heteropteran (Cunha et al. 2015) and bird (Lees et al. 2015; Almeida et al. 2016) communities were also recorded in oil palm plantations in eastern Amazonia compared to the other available land uses.

In general, species richness as the sole measure of biodiversity may not be sufficient to describe the species communities, other parameters that reflect the variation in species composition are recommended, as we have presented here (Wilsey 2005). Using species traits is a complementary and refined way of describing biodiversity and to document at how communities of interacting species can be affected by land-use change (Cernansky 2017). For example, Braaker et al. (2017) demonstrated a positive relationship between species traits and environment variables, where social bees were positively associated with green roofs and with flower abundance.

Although we sampled bees using scent traps in a short period of time, our sampling was sufficient and comparable with other studies, which the expected catch rates is of < 40 species (Mateus et al. 2015; Storck-Tonon et al. 2009). These rapid, targeted sampling has been demonstrated to be almost as effective in revealing community patterns of orchid bees as long-term surveys (Roubik 2004; Livingston et al. 2013). The use of passive scent traps remains the standard for landscape-level sampling like ours, because of the difficult logistics in sampling large areas at the same time, and because it removes bias inherent in hand netting (as reported by Ferreira et al. 2011). Nonetheless, additional sampling techniques like hand-netting may capture additional species not collected with scent traps (Nemésio and Morato 2004; Nemésio 2012). In our related work (Brito et al. 2017), we found that the community-wide sampling to reveal distinct orchid bee communities with robust statistical results, and we are confident the current work reveals true ecological communities.

Our results support the idea of including morphological attributes to describe insect communities in ecological studies. The long-distance flight capacity of the orchid bees suggests that the large-bodied species could travel farther into oil palm, while smaller bees are more restricted to forest reserves. Nevertheless, the APPs seem to play an important role in the maintenance of both taxonomic and functional composition of orchid bee communities, since the APPs showed similar patterns to forest reserves and oil palm plantations. These results suggest that forest patches and semi-natural habitats connected with the APPs are being used by the bees as corridors of displacement between the forest fragments, in a matrix formed by oil palm. The functional similarity between LRs and APPs reflects the structural elements common to them, although relations between the taxonomic and functional compositions have not been verified with the physical structure of the habitat of the land uses that we evaluated. Future studies evaluating these questions regarding bee species, habitat structure and dispersal need to be replicated elsewhere to check whether our results are also found in other geographic locations.

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## Compliance with ethical standards

**Conflict of interest** All authors declare that they have no conflict of interest.

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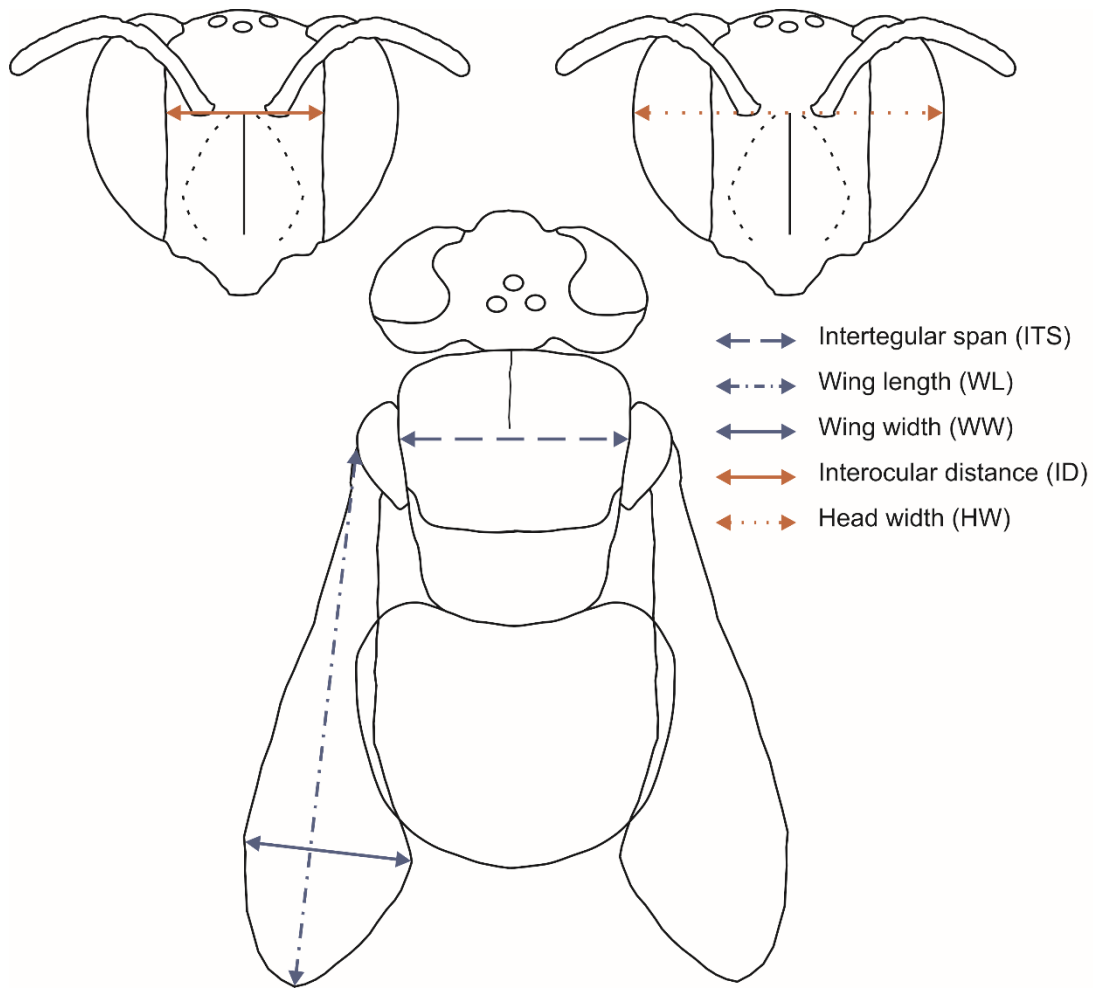
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**Online Resource 1** Morphological traits measured in orchid bee species sampled in this study



**Online Resource 2** Mean size of morphological traits (in mm) and life-history traits of each orchid bee species collected in legal reserves, permanent protection areas and oil palm plantations, in Agropalma Industrial Complex, municipality of Tailândia, state of Pará, Brazil. In this table are included the references of previous works used to classify the orchid bee species into two categories of social behavior (solitary or semi social), two categories of dietary specialization (oligoletic or polyletic), and three categories of nest construction behavior (renter, excavator or cleptoparasitic). Traits codes: ITS = intertegular span, WL = wing length, WW = wing width, ID = interocular distance, HW = head width

Species	ITS	WL	WW	ID	HW	sociality	pollen specificity	nest type	Reference
<i>Ef. auripes</i>	5.933	15.900	5.303	3.720	6.887	solitary	polyletic	renter	Pollen-specificity: Ramírez et al. 2002 (based on phylogeny Cameron et al. 2004). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. aff. mixta</i>	3.504	8.095	2.365	2.526	4.498	semi social	polyletic	excavator	Pollen-specificity: Mori and Boeke 1987; Dressler (obs. pers.) (In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. amazonica</i>	3.251	8.136	2.408	2.358	4.420	semi social	polyletic	excavator	Pollen-specificity: Ramírez et al. 2002 (based on phylogeny Ramírez et al. 2010). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. bidentata</i>	3.363	8.756	2.692	2.544	4.543	semi social	polyletic	excavator	Pollen-specificity: Ramírez et al. 2002 (based on phylogeny Ramírez et al. 2010). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. cognata</i>	3.830	9.800	2.855	2.785	4.985	semi social	polyletic	excavator	Pollen-specificity: Ackerman 1983b, Mori and Boeke 1987 (In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. liopoda</i>	3.233	8.059	2.446	2.356	4.318	semi social	polyletic	excavator	Pollen-specificity: Dressler 1982c (In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. modestior</i>	3.221	7.901	2.351	2.416	4.455	semi social	polyletic	excavator	Pollen-specificity: Dressler 1982c (In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.

Cont.

Species	ITS	WL	WW	ID	HW	sociality	pollen specificity	nest type	Reference
<i>Eg. townsendi</i>	3.090	7.114	2.163	2.257	4.157	semi social	polyletic	excavator	Pollen-specificity: Ackerman 1985, Dressler (obs. pers.) (In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969; Augusto and Garófalo 2004; Garófalo et al. 1993.
<i>Eg. chalybeata</i>	3.618	10.168	3.094	2.610	5.085	semi social	oligoletic	excavator	Pollen-specificity: Mori and Boeke 1987 (In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. ignita</i>	3.609	10.297	3.113	2.614	4.922	semi social	polyletic	excavator	Pollen-specificity: Ducke 1901, 1902a, 1906 (In Zucchi et al. 1969); Singer and Sazima 2001, Dodson 1966a, Dressler 1968b (In Ramírez et al. 2002). Sociality and Nest type: Roberts and Dodson 1967 (In Ramírez et al. 2002); Michener 2007; Zucchi et al. 1969.
<i>Eg. imperialis</i>	3.840	10.665	3.274	2.741	5.184	semi social	polyletic	excavator	Pollen-specificity: Ackerman 1983, 1985, Ackerman et al. 1982, Kymsey 1984, Zimmerman and Madriñan 1988 (In Ramírez et al. 2002). Sociality and Nest type: Roberts and Dodson 1967 (In Ramírez et al. 2002); Michener 2007; Zucchi et al. 1969.
<i>Eg. orellana</i>	3.530	10.343	3.177	2.697	5.072	semi social	oligoletic	excavator	Pollen-specificity: based on phylogeny (Ramírez et al. 2010). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. augaspis</i>	2.993	8.457	2.467	2.250	4.127	semi social	oligoletic	excavator	Pollen-specificity: Dressler (obs. pers.; In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. crassipunctata</i>	2.847	6.908	2.096	2.025	3.696	semi social	oligoletic	excavator	Pollen-specificity: Dressler (obs. pers.; In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Eg. parvula</i>	2.792	7.116	2.176	1.678	2.954	semi social	oligoletic	excavator	Pollen-specificity: based on phylogeny (Ramírez et al. 2010). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.

Cont.

Species	ITS	WL	WW	ID	HW	sociality	pollen specificity	nest type	Reference
<i>Eg. intersecta</i>	4.794	12.377	3.981	3.034	5.984	semi social	polyletic	renter	Pollen-specificity: Ducke 1901, 1902a (In Zucchi et al. 1969b); Dodson 1966a (In Ramirez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>El. cingulata</i>	5.753	17.355	5.586	3.342	6.504	semi social	polyletic	renter	Pollen-specificity: Friese 1930 (In Zucchi et al. 1969b); Dodson 1982, 1966a, Singer and Sazima 2001, Ackerman 1985, Ramirez (obs. pers.), Schemske and Horvitz 1984, Janzen 1971, Oliveira 2000, Lopes and Machado 1998, Vogel 1966, Armbruster 1993 (In Ramirez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>El. mocsaryi</i>	5.367	16.357	5.090	3.005	5.880	semi social	polyletic	renter	Pollen-specificity: Ducke 1901, 1902a (In Zucchi et al. 1969b); Dodson 1966a, Williams and Dodson 1972 (In Ramirez et al. 2002); Romer and Warford 1995 (In Oliveira 2000). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>El. nigrita</i>	5.147	16.078	5.383	3.021	5.840	semi social	polyletic	renter	Pollen-specificity: Ackerman 1983a, Ackerman et al. 1982, Oliveira 2000 (In Ramirez et al. 2002); Zucchi et al. 1969. Sociality and Nest type: Pereira-Martins and Kerr 1991 (In Ramirez et al. 2002); Michener 2007; Zucchi et al. 1969
<i>El. pseudocingulata</i>	5.555	17.003	5.534	3.228	6.401	semi social	polyletic	renter	Pollen-specificity: based on phylogeny (Ramirez et al. 2010). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>El. bombiformis</i>	7.770	22.688	7.857	3.886	7.564	semi social	polyletic	renter	Pollen-specificity: Dressler 1979b, Mori and Boeke 1979, Ackerman 1983a (In Ramirez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.



Cont.

Species	ITS	WL	WW	ID	HW	sociality	pollen specificity	nest type	Reference
<i>El. meriana</i>	7.219	21.876	7.572	3.785	7.031	semi social	polyletic	renter	Pollen-specificity: Dodson 1966a, Ackerman 1985, Armbruster 1988, Ackerman et al. 1982, Prance 1976, Janzen 1971 (In Ramírez et al. 2002); Dodson and Frymire 1961b, Vogel 1966 (In Zucchi et al. 1969). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>El. polyzona</i>	5.370	16.120	5.723	2.957	5.997	semi social	polyletic	renter	Pollen-specificity: Dressler (obs. pers.), Dodson 1966a (In Ramírez et al. 2002); Ducke 1902b (In Zucchi et al. 1969). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Ex. frontalis</i>	6.010	23.620	7.419	3.418	6.536	solitary	polyletic	cleptoparasitic	Pollen-specificity: Ackerman 1983, 1985, Ackerman et al. 1982, Kimsey 1979 (In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Ex. lepeletieri</i>	5.095	19.905	6.565	3.095	5.760	solitary	polyletic	cleptoparasitic	Pollen-specificity: based on phylogeny (Ramírez et al. 2010). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.
<i>Ex. smaragdina</i>	4.179	17.443	5.927	2.829	5.503	solitary	polyletic	cleptoparasitic	Pollen-specificity: Dressler (obs. pers.), Ducke 1901, Dodson 1966a, Ackerman 1985, Kimsey 1979 (In Ramírez et al. 2002). Sociality and Nest type: Michener 2007; Zucchi et al. 1969.

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**Online Resource 3** Habitat and abiotic variables and type of each data (States) evaluated on 5 x 5 m plots (54 plots), in legal reserves, areas of permanent protection, and oil palm plantations, in Agropalma Industrial Complex, municipality of Tailândia, state of Pará, Brazil

<b>Variable</b>	<b>States</b>	<b>Definition</b>
<b>large trees</b>	Rank <sup>1</sup>	Estimated number of trees with DAP >15cm.
<b>small trees</b>	Rank <sup>1</sup>	Estimated number of trees with DAP <15cm.
<b>epiphytes</b>	Rank <sup>1</sup>	Estimated number of epiphytes.
<b>palm trees</b>	Rank <sup>1</sup>	Estimated number of palm trees.
<b>shrubs</b>	Rank <sup>1</sup>	Estimated number of shrubs, with up to 3m in height.
<b>grasses</b>	Rank <sup>1</sup>	Estimated number of grasses.
<b>lianas</b>	Rank <sup>1</sup>	Estimated number of vines.
<b>soil cover</b>	Rank <sup>1</sup>	Visual estimate of vegetation cover/litter.
<b>litter height</b>	Continuous	Litter height (when present). Average value of the measurements taken with a ruler, at three different points in the plot.
<b>canopy opening</b>	Percentage	Canopy openness, obtained by the average of three photographs taken in 3 different points of the plot, at 1.30 m from the ground. Values in percentage.
<b>canopy height</b>	Continuous	Estimated value of canopy height, in meters.
<b>dead trees</b>	Presence/absence	Presence of dead standing trees.
<b>clearings</b>	Continuous	Number of clearings
<b>fallen trunks</b>	Continuous	Number of trunks in the ground.
<b>flowering trees</b>	Continuous	Number of flowering trees.
<b>temperature</b>	Continuous	Mean daily temperature, in °C.

Rank<sup>1</sup>: value ranges from 0 to 4, where 0 represents absence of the variable evaluated; 1 indicates its presence in <10% considering all the plot; 2, the variable occurred in 10 to 40%; 3, between 40 to 75%; and 4, it occurred in >75%.

**Online Resource 4** Results of the tree selection criteria of habitat and abiotic variables evaluated on 5 x 5 m plots (54 plots), in legal reserves, areas of permanent protection, and oil palm plantations, in Agropalma Industrial Complex, municipality of Tailândia, state of Pará, Brazil. Asterisks (\*) represent significative values of (a) low variation on the original data (<60), (b) high proportion of zeros values (>60%), and (c) correlated parameters (Pearson  $r>0.60$ ).

Habitat variable	Variation <sup>a</sup>	Zeros (%) <sup>b</sup>	Pearson Correlation <sup>c</sup>														
			large trees	small trees	canopy opening	canopy height	clearings	dead trees	epiphytes	palm trees	shrubs	grasses	liana	soil cover	litter	fallen trunks	flowering trees
large trees	78.70	14.81	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
small trees	112.31	44.44	0.53	X	-	-	-	-	-	-	-	-	-	-	-	-	-
canopy opening	98.50	0.00	-0.51	-0.33	X	-	-	-	-	-	-	-	-	-	-	-	-
canopy height	48.50*	0.00	0.80*	0.62*	-0.60	X	-	-	-	-	-	-	-	-	-	-	-
clearings	110.76	50.00	-0.52	-0.39	0.22	-0.42	X	-	-	-	-	-	-	-	-	-	-
dead trees	315.99	90.74*	0.08	0.18	-0.14	0.11	-0.18	X	-	-	-	-	-	-	-	-	-
epiphytes	126.27	48.15	0.14	-0.10	-0.19	0.25	0.02	-0.01	X	-	-	-	-	-	-	-	-
palm trees	56.73*	12.96	-0.30	-0.49	0.23	-0.34	0.27	-0.14	0.39	X	-	-	-	-	-	-	-
shrubs	119.15	44.44	0.28	0.47	-0.22	0.34	-0.09	0.15	-0.13	-0.40	X	-	-	-	-	-	-
grasses	182.42	68.52*	-0.42	-0.32	0.27	-0.37	0.40	-0.11	0.00	0.17	-0.35	X	-	-	-	-	-
liana	129.74	51.85	0.55	0.58	-0.40	0.49	-0.24	0.03	-0.21	-0.39	0.31	-0.33	X	-	-	-	-
soil cover	69.81	25.93	0.52	0.52	-0.48	0.51	-0.46	0.28	0.02	-0.51	0.19	-0.36	0.59	X	-	-	-
litter	147.74	53.70	0.35	0.39	-0.03	0.24	-0.43	0.19	-0.10	-0.35	0.07	-0.38	0.46	0.63*	X	-	-
fallen trunks	166.24	59.26	0.32	0.44	-0.17	0.32	-0.18	0.17	-0.12	-0.25	0.15	-0.24	0.38	0.34	0.43	X	-
flowering trees	379.29	92.59*	0.07	0.03	0.02	0.08	0.23	-0.09	-0.09	-0.12	-0.06	0.44	0.09	-0.02	0.14	-0.12	X
temperature	1.74*	0.00	-0.35	-0.17	0.17	-0.23	0.40	0.08	-0.10	0.11	-0.19	0.12	-0.32	-0.40	-0.13	0.14	-0.07

**Online Resource 5** Complete species name and total abundance of male orchid bees collected with scent traps at the Agropalma Industrial Complex study areas in July 2015 and August 2016, municipality of Tailândia, Pará State, Brazil. Forest: Habitat type codes: LR = legal reserves, APP = areas of permanent protection, PALM = oil palm plantations

Species	LR	APP	PALM	Total
<i>Eufriesea auripes</i> (Gribodo, 1882)			3	3
<i>Eufriesea ornata</i> Mocsáry, 1896		1		1
<i>Euglossa (Euglossa) aff. mixta</i> Friese, 1899	6		2	8
<i>Euglossa (Euglossa) amazonica</i> Dressler, 1982	6	2		8
<i>Euglossa (Euglossa) bidentata</i> Dressler, 1982	15		1	16
<i>Euglossa (Euglossa) cognata</i> Moure, 1970	2			2
<i>Euglossa (Euglossa) gaianii</i> Dressler, 1982	1			1
<i>Euglossa (Euglossa) liopoda</i> Dressler, 1982	1	2	2	5
<i>Euglossa (Euglossa) magnipes</i> Dressler, 1982	1			1
<i>Euglossa (Euglossa) modestior</i> Dressler, 1982	10	11	10	31
<i>Euglossa (Euglossa) sp.</i>	1		1	2
<i>Euglossa (Euglossa) townsendi</i> Cockerell, 1904	4	5		9
<i>Euglossa (Glossura) chalybeata</i> Friese, 1925	59	17	6	82
<i>Euglossa (Glossura) ignita</i> Smith, 1874	25	59	22	106
<i>Euglossa (Glossura) imperialis</i> Cockerell, 1922	17		1	18
<i>Euglossa (Glossura) orellana</i> Roubik 2004	4	2		6
<i>Euglossa (Glossurella) augaspis</i> Dressler, 1982	29	5	4	38
<i>Euglossa (Glossurella) crassipunctata</i> Moure, 1968	2	1		3
<i>Euglossa (Glossurella) parvula</i> Dressler, 1982	6	1		7
<i>Euglossa (Glossuropoda) intersecta</i> Latreille, 1817	3	6		9
<i>Eulaema (Apeulaema) cingulata</i> Fabricius, 1804	33	158	141	332
<i>Eulaema (Apeulaema) mocsaryi</i> Friese, 1899	2	3	1	6
<i>Eulaema (Apeulaema) nigrita</i> Lepeletier, 1841	2	10	10	22
<i>Eulaema (Apeulaema) pseudocingulata</i> Oliveira, 2006	16	71	46	133
<i>Eulaema (Eulaema) bombiformis</i> Packard, 1869	15	9	4	28
<i>Eulaema (Eulaema) meriana</i> Olivier, 1789	46	130	94	270
<i>Eulaema (Eulaema) polyzona</i> Mocsáry, 1897	2	1		3
<i>Exaerete frontalis</i> Guérin, 1844	12	5		17
<i>Exaerete lepeletieri</i> Oliveira & Nemésio, 2003	1	1		2
<i>Exaerete smaragdina</i> Guérin, 1844	6	1		7
<b>Total of individuals</b>	<b>327</b>	<b>501</b>	<b>348</b>	<b>1176</b>
<b>Total of species</b>	<b>28</b>	<b>22</b>	<b>16</b>	<b>30</b>

**Online Resource 6** Mean values of morphological traits used in this study and results of land use comparisons. The standard error is shown in parentheses. Levene’s test and One-Way ANOVA results of the comparisons of each trait among habitat types. Significant differences are indicated by different letters based on Tukey’s HSD tests. Habitat type codes: LR = legal reserves, APP = areas of permanent protection, PALM = oil palm plantations. Traits codes: ITS = intertegrular span, WL = wing length, WW = wing width, ID = interocular distance, HW = head width

Trait	Land use			Levene		One-Way ANOVA	
	Forest	PPA	Palm	F	P-value	F	P-value
Intertegular span	4.194 (0.138) <sup>a,b</sup>	4.644 (0.188) <sup>b,c</sup>	4.902 (0.239) <sup>c</sup>	1.670	0.191	4.067	0.019
Wing length	12.437 (0.539)	13.948 (0.727)	14.084 (0.826)	0.394	0.675	2.256	0.107
Wing width	3.919 (0.196)	4.527 (0.250)	4.533 (0.300)	0.495	0.610	2.475	0.087
Interocular distance	2.743 (0.051) <sup>a,b</sup>	2.897 (0.070) <sup>b,c</sup>	3.007 (0.087) <sup>c</sup>	1.596	0.205	4.029	0.019
Head width	5.148 (0.110) <sup>a,b</sup>	5.546 (0.149) <sup>b,c</sup>	5.736 (0.180) <sup>c</sup>	1.267	0.284	4.788	0.009
Amount of measured specimens	97	60	40				

**Online Resource 7** Results of analysis of variance of stepwise regressions models of habitat and spatial variables with influence on male orchid bee assemblages collected at the Agropalma Industrial Complex, municipality of Tailândia, Pará State, Brazil

Type of parameter	Variable	Df	Sum of squares	Mean squares	F model	R2	Pr (>F)	
Habitat	large trees	1	0.789	0.789	4.438	0.067	<0.001*	
	small trees	1	1.061	1.061	5.964	0.090	<0.001*	
	canopy opening	1	0.268	0.268	1.505	0.023	0.147	
	clearings	1	0.069	0.069	0.389	0.006	0.940	
	epiphytes	1	0.166	0.166	0.933	0.014	0.484	
	shrubs	1	0.445	0.445	2.505	0.038	0.016*	
	lianas	1	0.353	0.353	1.986	0.030	0.047*	
	soil cover	1	0.167	0.167	0.937	0.014	0.477	
	fallen trunks	1	0.412	0.412	2.316	0.035	0.025*	
	temperature	1	0.306	0.306	1.718	0.026	0.084	
	Residuals		42	7.469	0.178		0.636	
	Total		53	11.741			1.000	
	Spatial	PCNM1	1	0.544	0.544	2.983	0.046	0.007*
PCNM2		1	1.789	1.789	9.813	0.152	<0.001**	
PCNM3		1	0.431	0.431	2.366	0.037	0.020*	
PCNM4		1	0.362	0.362	1.986	0.031	0.050	
PCNM5		1	0.165	0.164	0.902	0.014	0.503	
PCNM6		1	0.167	0.167	0.918	0.014	0.491	
PCNM7		1	0.188	0.188	1.031	0.016	0.403	
PCNM8		1	0.101	0.101	0.553	0.009	0.828	
PCNM9		1	0.149	0.149	0.817	0.013	0.581	
PCNM10		1	0.137	0.137	0.752	0.012	0.642	
PCNM11		1	0.107	0.107	0.585	0.009	0.805	
PCNM12		1	0.083	0.083	0.457	0.007	0.899	
PCNM13		1	0.591	0.591	3.241	0.050	0.003*	
PCNM14		1	0.328	0.328	1.802	0.028	0.076	
PCNM15		1	0.057	0.056	0.310	0.005	0.949	
PCNM16		1	0.135	0.135	0.742	0.012	0.652	
PCNM17		1	0.025	0.025	0.139	0.002	0.992	
PCNM18		1	0.258	0.258	1.414	0.022	0.186	
PCNM19		1	0.123	0.123	0.675	0.010	0.714	
PCNM20		1	0.063	0.063	0.346	0.005	0.905	
PCNM21		1	0.105	0.105	0.579	0.009	0.803	
Residuals			32	5.833	0.182		0.497	
Total		53	11.741			1.000		

\*The test was significant ( $P < 0.05$ ), but with a very low power of explanation ( $R^2 < 0.10$ ).

\*\*The test was significant ( $P < 0.05$ ), with a medium power of explanation ( $R^2 > 0.10$ ).



**Online Resource 8** Results of analysis of variance of stepwise regressions models of habitat and spatial variables with influence on functional traits of male orchid bees collected at the Agropalma Industrial Complex, municipality of Tailândia, Pará State, Brazil

Type of parameter	Variable	Df	Sum of squares	Mean squares	F model	R2	Pr (>F)	
Habitat	large trees	1	11.309	11.309	15.952	0.186	0.001**	
	small trees	1	11.404	11.405	16.087	0.188	<0.001**	
	canopy opening	1	2.442	2.442	3.445	0.040	0.073	
	clearings	1	0.328	0.328	0.462	0.005	0.496	
	epiphytes	1	0.827	0.827	1.166	0.014	0.286	
	shrubs	1	1.265	1.265	1.784	0.021	0.193	
	lianas	1	0.080	0.080	0.113	0.001	0.748	
	soil cover	1	0.021	0.021	0.029	0.000	0.896	
	fallen trunks	1	0.008	0.008	0.012	0.000	0.952	
	temperature	1	2.239	2.239	3.159	0.037	0.081	
	Residuals		42	29.775	0.709		0.490	
	Total		53	60.816			1.000	
Spatial	PCNM1	1	5.366	5.366	10.755	0.088	0.003*	
	PCNM2	1	22.150	22.150	44.394	0.364	<0.001**	
	PCNM3	1	1.212	1.212	2.429	0.020	0.131	
	PCNM4	1	1.885	1.885	3.778	0.031	0.058	
	PCNM5	1	0.011	0.011	0.021	0.000	0.915	
	PCNM6	1	0.410	0.410	0.821	0.007	0.371	
	PCNM7	1	0.401	0.401	0.804	0.007	0.379	
	PCNM8	1	0.252	0.252	0.505	0.004	0.485	
	PCNM9	1	0.766	0.766	1.536	0.013	0.225	
	PCNM10	1	0.196	0.196	0.392	0.003	0.538	
	PCNM11	1	0.290	0.290	0.581	0.005	0.452	
	PCNM12	1	0.800	0.800	1.603	0.013	0.221	
	PCNM13	1	7.018	7.018	14.066	0.115	0.001**	
	PCNM14	1	0.297	0.297	0.595	0.005	0.444	
	PCNM15	1	0.269	0.269	0.540	0.004	0.460	
	PCNM16	1	0.986	0.986	1.977	0.016	0.169	
	PCNM17	1	0.173	0.173	0.346	0.003	0.552	
	PCNM18	1	1.956	1.956	3.920	0.032	0.056	
	PCNM19	1	0.302	0.302	0.606	0.005	0.433	
	PCNM20	1	0.046	0.046	0.092	0.001	0.729	
	PCNM21	1	0.066	0.066	0.131	0.001	0.735	
	Residuals		32	15.966	0.499		0.263	
Total		53	60.816			1.000		

\*The test was significant ( $P < 0.05$ ), but with a very low power of explanation ( $R^2 < 0.10$ ).

\*\*The test was significant ( $P < 0.05$ ), with a medium power of explanation ( $R^2 > 0.10$ ).

# Capítulo 3

**Orchid bees (Apidae, Euglossini) from oil palm plantations in eastern Amazon have larger but not asymmetrical wings**

O capítulo III desta Tese foi elaborado e formatado conforme as normas da publicação científica *Insectes Sociaux*, as quais se encontram em anexo (Anexo 3).

**Orchid bees (Apidae, Euglossini) from oil palm plantations in eastern Amazon have larger but not asymmetrical wings**

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## **Abstract**

Phenotypic variation in both morphology and symmetry of individuals may appear as a result of environmental stress caused by land-use changes. Fluctuating asymmetry (FA), a measure of individual's body sides, and it is considered as a useful indicator of environmentally induced stresses because it reflects developmental changes in the symmetry of specimens in altered habitats. Here, we evaluated FA and wing size variations of two orchid bee species, *Euglossa ignita* Smith, 1874 and *Eulaema meriana* (Olivier, 1789), a small- and a large-bodied species, respectively, comparing 11 wing traits of individuals from legal reserves (LR), areas of permanent protection (APP), and oil palm plantations (PALM) in Eastern Amazonia. We calculated FA as the absolute difference between 11 wing measurements made in right and left wings of specimens, and also the wing size of both species. We found no effect of FA between land-use types in any of the wing traits of orchid bee species considered in the analysis. However, we observed individuals of both *Euglossa. ignita* and *Eulaema. meriana* from PALM areas having larger wings compared to those from LR areas. Bees from APP areas had intermediary values of what was found in both LR and PALM areas. Our results demonstrate that at least for the two species analyzed, there seems to be a pressure exerted by land-use change associated with palm oil cultivation favoring individuals with larger wings, although both species had shown substantial permeability of oil palm.

**Keywords** Fluctuating asymmetry, land-use, measurement error, morphological trait, wing size.

## Introduction

Environmental changes may cause phenotypic changes in organisms, modifying their morphological, physiological, and behavioral characteristics. Many of these changes can be attributed to the ability of individuals to make changes without genetic variation, known as “phenotypic plasticity” (Leung et al. 2000; Silva et al. 2009), and it can be considered as an important tool for adaptation to heterogeneous and unstable environments (Parsons 1990). The way in which the environment can influence phenotypes is complex, and many traits can be altered by a single environmental factor, although not all of these changes can be recognized or studied (Agrawal 2005; Agarwala 2007). Consequently, it is difficult to ascertain whether or not altered phenotypes are beneficial (van Kleunen and Fischer 2005).

Phenotypic variation in morphological traits (e.g., body or wing size) or in the symmetry of the body axes may result from human-induced environmental stress and habitat loss (Delgado-Acevedo and Restrepo 2008). Consequently, individuals from populations of altered and impacted habitats could have smaller body sizes, greater body size variation, and the absence of perfect bilateral symmetry (Del Lama et al. 2002; Sanseverino and Nessimian 2008). There are at least three kinds of bilateral asymmetry, distinguished by differences in the distribution of left-right values of a trait among individuals. Directional asymmetry occurs when a trait has a higher value, usually, on one side of the body (e.g., the human heart in the left side of our thorax). When dealing with antisymmetry, as in the claws of male lobsters and fiddler crabs, whose individuals in a population are a random mixture of left- and right-handed (Graham et al. 2010), most individuals in a population are asymmetric, but the side showing greater development is not always the same for all individuals (Graham et al. 1993; Leary and Allendorf 1989). Finally, fluctuating asymmetry (FA) describes deviations between values of right and left traits of normally bilaterally symmetrical organisms, and without a trend for one side to have a higher value than the other side (Leary and Allendorf 1989; De Block et al. 2008).

Both directional and antisymmetry morphologies result from normal development, and only FA has been considered a useful indicator of environmentally induced stress, since this feature reflects developmental changes in the individual’s body resulting from altered environments (Leary and Allendorf 1989). It is hypothesized that individuals sampled in altered areas could have an increase in environmental stressors that are not related to evolutionary processes, showing a less stable development compared to individuals from conserved areas (Palmer and Strobeck 1986; Leung et al. 2000; Silva et al. 2009). The relationship between AF and developmental stress could be interpreted as a compensatory effect when the organism is submitted to a stressor, there is an increase in the amount of energy required for its development that could reduce the energy necessary for normal growth, reproduction, and developmental precision maintenance (Koehn and Bayne 1989; Sommer 1996). Thus, FA analyses may offer several advantages as bioindicators of environmental development stress (Clarke 1993).

For flying organisms, wing shape and size directly influence flight distance and dispersal ability, and it is expected that symmetric individuals would fly more efficiently and aerodynamically when compared to the asymmetric ones (De Block et al. 2008). The occurrence of high levels of FA in the wings may be caused by several factors, such as exposure to sun and rain, lack of food, and high temperatures during developmental stages (Lima et al. 2016; Kanegae and Lomônaco 2003). Thus, asymmetrical wings may affect the individual’s foraging activities, chances of escaping predators, and also mating behaviors (Stewart and Vodopich 2013).

Orchid bees (Apidae: Euglossini) are a diverse and charismatic group of bee endemic to the Neotropical region. These bees are sensitive to the effects of land-use change and environmental disturbances (Nemésio and Vasconcelos 2013; Brito et al. 2017; Storck-Tonon and Peres 2017), and can be readily sampled with scent traps, making them a useful model to study the effects of disturbance on FA and other biometric and geomorphic analysis (Peruquetti 2003; Silva et al. 2009; Pinto et al. 2015). In this group of bees, morphological trait changes have been

related to seasonality and consequent scarcity of food sources caused by deforestation (Peruquetti 2003), but also to different habitats and environments (Brito et al. 2018).

In the Brazilian Amazon, the expansion of cultivated areas with the oil palm (*Elaeis guineensis* Jacq., Areaceae) is one of the main modifying activities of the landscape (Alves et al. 2013). Despite historical links between deforestation and oil palm worldwide, recent studies show that in the Eastern Amazon about 90% of oil palm areas were mostly established from converting pastures, and less than 3% were from direct conversion of intact forests (Benami et al. 2018). In addition to public policies to reduce deforestation, the Brazilian environmental legislation requires the maintenance of 20-80% of natural areas in all rural properties, including oil palm plantations, in the form of two types of preserved areas: the Legal Reserves (LR) and Areas of Permanent Protection (APP) (Brasil 2012). The LR encompasses a percentage of the entire rural property (the value depends on the biome) where native vegetation has to be maintained, while the APPs preserve both the source and the banks of streams, protecting against erosion, and act as corridors for the local fauna, connecting forest fragments (Brasil 2012; Silva and Ranieri 2014). The width of the APPs varies from 30-500m, depending on the width of the watercourse (Brasil 2012).

Even though oil palm and other crops provide some level of permeability for the movement and the occurrence of organisms (Koh 2008; Livingston et al. 2013; Rosa et al. 2015), these land-uses have remarkable reduced richness, abundance, and diversity of invertebrate communities (Lucey and Hill 2011; Cunha et al. 2015; Shimano and Juen 2016; Brito et al. 2017), and have a more simplified species composition compared to forest areas (Livingston et al. 2013; Brito et al. 2017; Paiva et al. 2017). Thus, the habitat simplification caused by oil palm planted areas is expected to increase the stress on the individuals, because these areas are characterized by low habitat complexity and limited food resources compared with forest environments (Turner et al. 2011).

The orchid bees *Eulaema (Eulaema) meriana* (Olivier, 1789) and *Euglossa (Glossura) ignita* Smith, 1874 are among the most common species for most Brazilian biomes, especially in the Amazon (Storck-Tonon et al. 2009; 2013; Moure et al. 2012). Despite the extraordinary dispersal ability of the group (Raw 1989; Wikelski et al. 2010; Pokorny et al. 2015), *Eg. ignita* individuals seem to be more restricted to forest in some areas (Milet-Pinheiro and Schindwein 2005), while most *Eulaema* species can be found in different phytophysionomies (Costa and Francoy 2017), which suggests that these species may have different levels of tolerance to environmental modifications or have different dispersal capabilities.

The relative ease and low costs involved in taking wing size measurements and FA compared to other biomarkers (e.g. life history, direct fitness markers, or molecular biomarkers), is an advantage of using morphological traits as an estimator of how changes in environmental or habitat conditions are affecting bee species (Leung et al. 2003). Recently, it has also been shown that FA is a good predictor of environmental stress (Beasley et al. 2013). In this context, based on the assumption that wing size and symmetry directly influence the dispersion of flying individuals (De Block et al. 2008), here we hypothesized that orchid bee specimens from oil palm plantations would show both greater FA and wing sizes compared to individuals from LR areas, while bees from APP sites would show intermediate levels. This because larger wing sizes would permit great flight distances in the monocultured plantations.

## **Material and methods**

### **Study sites and sampling methods**

We broadly sampled the orchid bee communities in three oil palm plantations (PALM), three legal reserves (LR), and in three protected areas along river banks (APP), at the Agropalma Industrial Complex (approximately 02°20' and 02°40'S by 48°30' and 49°0'W), near Tailândia township, eastern Amazonian rainforest (Fig. 1). Sampling took place in the wet seasons of July 2015 and August 2016.

We collected male orchid bees with scent traps (2L PET plastic bottles with three openings for the entrance of bees; Fig. 1b) containing an internal swab cotton, on which we used one of the following scent attractants: vanillin, benzyl acetate, eucalyptol, eugenol, methyl cinnamate, and methyl salicylate. In each one of our nine sites, we set up six sampling stations with one set of six scent traps each, 500 m apart, and we sampled one site per day. The distance between different land-use types was 1–2 km, while the maximum distance was about 20 km. The LRs are natural unflooded forest fragments, ranging from 5,000 to 17,000 ha (Bolfe and Batistella 2011), while the APP sites are riparian corridors, mainly composed of secondary forests, at least in our study area (TB personal observation). The overall sampling methods applied are detailed in Brito et al. (2017).

From the total number of species collected, we selected two species that occurred in high numbers in all of our sampling sites (see Online Resource 1.). The choice of these species was also based on the large difference in body size between them, which we believed may be an important factor in the responses of the individuals to the different land-uses we evaluated. The first, *Euglossa ignita* (Fig. 2a), is a small-bodied orchid bee species, with total length of about 14.0 mm (Nemésio 2009). The second, *Eulaema meriana* (Fig. 2b), is much larger, with a body length of approximately 26.0 mm (Nemésio and Rasmussen 2011). Both species are widely distributed from Central América to southeastern Brazil (Nemésio and Rasmussen 2011; Oliveira 2007).

From the total number of specimens of *Eg. ignita* and *El. meriana* collected (106 and 270, respectively, from both years) in all land-use types, we selected 5 individuals from each species in each one of our nine sampled areas (excepting for PALM 3, in which we sampled two individuals; see Online Resource 1). In sites with more than five specimens sampled, we randomly choose only five representative bees. In total, 41 specimens of *Eg. ignita* and 45 of *El. meriana* were used in our analyses.

### **Orchid bees' wing traits**

We removed both fore and hind wings from specimens with tweezers and mounted the wings on microscope slides. The wings from both left and right slides were photographed with a digital camera with an achromatic objective 0.5X (diameter 58 mm) and a planapochromatic objective 1.0X (diameter 80 mm) coupled on a stereoscopic microscope (Leica DFC450). We measured eight wing venules in the fore wings and three in hind wings, following Pinto et al. (2015), with some adaptations (Fig. 2c). For each wing, we performed three different measurements, always done by the same researcher (author TB), but on different days, in order to account for measurement errors (Palmer and Strobeck 1986; Palmer 1994). The wing veins provide well-defined morphological markings and are commonly used in morphological analyses (Klingenberg and McIntyre 1998).

### **Statistical analysis**

We followed the same protocol used by Pinto et al. (2015) by calculating fluctuating asymmetry as the absolute difference between measurements made in the specimen's right (*R*) and left (*L*) wings (Palmer and Strobeck 1986). To assess the magnitude of the measurement error of each wing trait (ME) in the morphometric traits, we used a factorial mixed model ANOVA, with "individual" as a random explanatory factor and "side" as a fixed explanatory factor. The mean squares of the interaction between individual and side ( $MS_{\text{ind*side}}$ ) and the mean square of errors ( $MS_{\text{error}}$ ) were used to estimate FA, excluding ME (see Fig. 2 in Pinto et al. 2015). In this model, if the mean square of errors values are significantly higher than the mean squares of the interaction, then the variation of measurements between both *R* and *L* wings could not be attributed to the occurrence of FA (Palmer and Strobeck 1986). In this case, only wing traits with low ME were used in the subsequent analysis.



To exclude the possibility of the other types of asymmetry, we performed a *t* test of each measured feature against zero, and a Kolmogorov-Smirnov test to check for the bimodal distribution in our FA data (Palmer and Strobeck 1992). As demonstrated in other studies (e.g., Babbitt 2006), the distribution of FA is best described by a double Pareto-lognormal distribution, and not necessary it is adjust to a Gaussian distribution. We assumed that measurements with non-normal distributions were useful in the FA analysis, since we observed few categories of FA (leptokurtic distributions) in many traits, which may reflect false positives (Graham et al. 2003). Finally, we compared FA levels and the size of each trait of *Eg. ignita* and *El. meriana* individuals with a One-Way ANOVA, and evaluated whether these attributes of specimens sampled in PALM sites were bigger than those from LR sites. Finally, we performed *post hoc* Tukey test comparisons on the significant One-Way ANOVA results.

## Results

We found that the measurement error was smaller than FA in six traits of *Eg. ignita* (M1, M3, M4, M5, M9 and M10), and in nine traits of *El. meriana* (M1-M6, M9-M11), compared to the effects of both “individuals” and “side” (Table 1). According to our *t* tests of each measured trait against zero, some showed means different than zero on both orchid bee species (Table 2), indicating a level of antisymmetry. However, we discard antisymmetry as a possible cause of the observed variations in the morphological characters of the species analyzed because we found leptokurtic curves in the distributions of measurement data. Additionally, at least five traits of *Eg. ignita* (excepting M5) and two of *El. meriana* showed normal distributions (Table 2).

We found no effect of FA in relation to land-use types (LR, APP, and PALM areas) in any of the wing traits of either orchid bee species considered in the analysis (Table 3). Nevertheless, we observed that individuals of both *Eg. ignita* and *El. meriana* sampled in PALM plantations were bigger than those sampled from LR, in most of the wing traits (excepting for M10 of *Eg. ignita*, and M9 for *El. meriana*) (Fig. 3). Considering the mean values of all significant wing trait comparisons, *El. meriana* males collected in PALM were bigger than those from LR areas from between 1.59 to 5.78%, while in *Eg. ignita* the difference of M9 of males from PALM to LR was about 30.43% ( $F_{2,243} = 6.873$ ;  $P = 0.001$ ). Conversely, the wing trait M10 of *Eg. ignita* males was higher in LR and APP samples compared to PALM ( $F_{2,243} = 10.994$ ;  $P = 0.001$ ).

We also found that individuals from APP sites were similar to those sampled in both LR and PALM when we analyzed the traits M1 and M2 of *El. meriana* (Fig. 3). Additionally, on trait M5 of this same species, we found a gradual increase in wing measurements on the individuals from the LR to PALM, with specimens collected in APPs showing intermediate values ( $F_{2,267} = 15.003$ ;  $P < 0.001$ , Fig. 3).

## Discussion

In this study, we expected that *Eg. ignita* and *El. meriana* specimens sampled in PALM would show higher FA values in their wings traits compared to individuals sampled in LR, since we hypothesized that the human-modified habitat (and the consequent reduction in food sources) could act as stress factors to the bees. Contrary to our predictions, we did not find significant differences in the FA indexes of the individuals between the three land-use types we evaluated (LR, APP, and PALM). However, our findings indicate that orchid bee males sampled in PALM have larger wing measurements compared to LR areas, specifically two wing traits of *Eg. ignita* and six traits of *El. meriana*. Additionally, individuals of both species sampled in APP sites seem to be a mixture of what is found in LR and PALM sites.

Although anthropogenic stressors can show more severe effects on FA levels (Parsons 2005), in wild studies organisms are exposed to different environmental factors, and it is not always easy to detect which stressors different

measures of FA could be associated with, because of the presence of confounding effects that could potentially mask the response of FA to stressors (Beasley et al. 2013). Further, normally individual development is buffered against these "accidents" occurring by homeostatic mechanisms to produce symmetrical individuals (Palmer and Strobeck 1986). Also, morphological characteristics could react differently to stressing factors caused by land-use changes, by adjusting developmental instability and providing symmetrical individuals (Markow 1995).

Another factor that may have contributed to the absence of FA levels in our results relates to the flight distances of orchid bees naturally reaching in their environments. It has been reported that individual bees can fly as far as 2.5 km over open water (female bees; Janzen 1971), while others are able to travel more than 40 km across even terrain (Pokorny et al. 2015; Wikelski et al. 2010). In addition, they have specific foraging routes (known as "triplines"), which enable the bees to cross large areas composed of a mosaic of landscapes, especially when there are several small forest fragments severing as effective stepping-stones or corridors for their movement (Moura and Schlindwein 2009; Rosa et al. 2015). Therefore, the individuals we collected in the three land-use types may not have developed in their respective sampled areas, but rather in distant locations subjected to distinct environmental conditions during their development, as has been previously cited by Pinto et al. (2015). Consequently, the bees collected in our PALM sites, for example, may have been oviposited, may have hatched and developed in forests with adequate floral resources that were provisioned by their mothers and little environmental stressors that would cause malformed wings and increases in FA. We suspect that it is important to evaluate the effects of FA on bees from forest fragments adjacent to other land-use types than ours since our results showed that oil palm plantations may not enough to cause FA on the orchid bees.

Recent studies carried out on oil palm sites and preserved forest patches have shown that species richness and abundance of orchid bees declines with increasing distance to forests (Livingston et al. 2013), and that the species composition of these bees in the oil palm matrix is a smaller subset of that found in the forest, and in a lower abundance (Brito et al. 2017). Despite this, not all species are affected similarly. Some traits are correlated with vulnerability to multiple threats and stressors (Williams et al. 2010), and the use of morphological, behavioral and functional traits are useful attributes in ecological assessments to detect the susceptibility of species to differences in land-use (Rader et al. 2014; de Palma et al. 2015; Brito et al. 2018). These previous results reinforce the sensitivity these bees show to environmental changes, but also suggest that orchid bees are able to move between forest and oil palm plantations, and that some species are able to establish populations in landscapes having both kinds of habitats (Livingston et al. 2013).

Size variation in morphological traits of bees (e.g. body size) is usually associated with flight ability and the adaptive value of individuals (Cane 1987; Greenleaf et al. 2007). In our study, we found significant differences in two wing size traits of *Eg. ignita* and in six traits of *El. meriana*, comparing individuals sampled in three types of land-uses, with emphasis mainly on the differences between individuals collected in LR and those collected in PALM sites. Our results are consistent with a study carried in the Brazilian Cerrado, showing wing size differences between *Eulaema nigrata* Lepeletier, 1841 males sampled near intensely-used agricultural and natural areas (Pinto et al. 2015). These authors suggested that a possible mechanism driving wing size differences was the lack of food resources near agricultural areas as a consequence of human activities.

For some orchid bees, especially *Euglossa* species, changes in microhabitat characteristics such as forest canopy, understory vegetation and high temperatures caused by exposure in open areas appear to be negative predictors for some species occurrence (Viana et al. 2006). Our results show that, at least for *Eg. ignita* and *El. meriana*, there seems to be pressure exerted by the physical structure of the oil palm plantation favoring individuals with larger wings, while orchid bees with small wing size traits seems to be more restricted to forest patches. Although both species show substantial permeability of oil palm, we suspect that in addition to the physical structure, the low availability of food

resources for the bees in the oil palm plantations may be forcing the development of individuals with larger wings to allow them a greater flight capability.

Differences in wing traits were also recorded for *Euglossa pleosticta* Dressler, 1982 males sampled in Neotropical savannah (Brazilian cerrado), indicating that seasonal variation is an important predictor for the development of individuals of this species (Silva et al. 2009). These findings highlight the fact that the increase in food availability as a consequence of higher rainfall levels may have an important effect on the size of orchid bees (Crozier and Pamilo 1996; Peruquetti 2003).

Our results presented here indicate that land-use change associated with oil palm plantation have affected the structure of two orchid bee species' morphological traits, although the variation in wing size traits we observed occur during the developmental stages of the individuals, and are not the direct effect of the conditions of sites in which individuals were captured. The studies of FA on orchid bees in different land-uses or forest cover have not demonstrated significant effects of environmental stress on individuals' characteristics, and this could be the result of unmeasured factors, especially when the areas sampled are subject to uncontrolled conditions. Nevertheless, FA estimates can be a useful technique associated with analysis of multiple traits to identify which types of species are most vulnerable to land-use change and habitat conversion and loss.

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**Table 1** Factorial mixed model ANOVA (sides as a fixed factor and individuals as a random factor) results with mean squares of individuals ( $MS_{ind}$ ), side ( $MS_{side}$ ), interaction ( $MS_{ind*side}$ ), and error estimate ( $MS_{error}$ ) of the measurements in both left and right wings of two orchid bee species sampled in different land-use types at Agropalma Industrial Complex, state of Pará, Brazil (\*  $p < 0.05$ )

Specie	Wing trait	ANOVA			
		$MS_{ind}$	$MS_{side}$	$MS_{ind*side}$	$MS_{error}$
<i>Eg. ignita</i>	M1	0.0376	0.0177*	0.0032	0.0027
	M2	0.0446*	0.0269	<b>0.0093</b>	<b>0.0093</b>
	M3	0.0046*	0.0002	0.0014	0.0012
	M4	0.0184	0.0107*	0.0014*	0.0006
	M5	0.0117*	0.0278*	0.0053	0.0046
	M6	0.0866*	0.0254	<b>0.0145</b>	<b>0.0554</b>
	M7	0.0875*	0.0000	<b>0.0011</b>	<b>0.0420</b>
	M8	0.0679*	0.0415	<b>0.0079</b>	<b>0.0316</b>
	M9	0.0529	0.0876*	0.0180*	0.0020
	M10	0.0184	0.0001	0.0019*	0.0004
	M11	0.0562*	0.0025	<b>0.0117</b>	<b>0.0129</b>
<i>El. meriana</i>	M1	0.3091	0.0013	0.1716*	0.0357
	M2	0.2097	0.2655*	0.0893*	0.0070
	M3	0.0147	0.0052*	0.0070*	0.0003
	M4	0.2121	0.0044	0.0755*	0.0015
	M5	0.1326	0.1201*	0.0503*	0.0004
	M6	0.6561*	0.1992	0.1903	0.1705
	M7	1.0546*	0.0017	<b>0.1307</b>	<b>0.3316</b>
	M8	4.0855*	0.3554	<b>0.2951</b>	<b>1.1173</b>
	M9	0.1355	0.0023	0.0721*	0.0015
	M10	0.1413	0.0801*	0.0429*	0.0008
	M11	0.4511*	3.7296*	0.1929*	0.0839

Wing traits highlighted in bold were removed from the analyses because of the high measurement errors between the three different measures (see "Material and methods" for further explanation).



**Table 2** Normality distribution according to Kolmogorov-Smirnov test, and *t* tests of a sample against zero of the mean *R-L* (right minus left) wing traits of two orchid bee species sampled in different land-use types at Agropalma Industrial Complex, state of Pará, Brazil

Specie	Wing trait	One-sample t test		Normality test		
		T	<i>P</i>	K-S d	<i>P</i>	Mean FA
<i>Eg. ignita</i>	M1	2.350	<b>0.024</b>	0.083	> 0.05	0.0170
	M3	0.339	0.736	0.141	> 0.05	0.0016
	M4	2.805	<b>0.008</b>	0.086	> 0.05	0.0132
	M5	-2.288	<b>0.028</b>	0.213	< <b>0.05</b>	-0.0213
	M9	2.206	<b>0.033</b>	0.109	> 0.05	0.0377
	M10	-0.260	0.796	0.132	> 0.05	-0.0015
<i>El. meriana</i>	M1	0.088	0.930	0.326	< <b>0.01</b>	0.0045
	M2	-1.724	0.092	0.353	< <b>0.01</b>	-0.0627
	M3	-0.865	0.392	0.225	< <b>0.05</b>	-0.0088
	M4	-0.241	0.810	0.363	< <b>0.01</b>	-0.0081
	M5	-1.545	0.129	0.329	< <b>0.01</b>	-0.0422
	M6	-1.023	0.312	0.200	> 0.05	-0.0543
	M9	0.179	0.859	0.287	< <b>0.01</b>	0.0058
	M10	-1.366	0.179	0.294	< <b>0.01</b>	-0.0345
M11	4.398	< <b>0.001</b>	0.116	> 0.05	0.2351	

**Table 3** One-Way ANOVA results of the fluctuating asymmetry (FA) of wing traits for two orchid bee species sampled in different land-use types at Agropalma Industrial Complex, state of Pará, Brazil. Land-use codes: LR = legal reserves, APP = areas of permanent protection, PALM = oil palm plantations

Specie	Wing trait	Mean FA			One-Way ANOVA		
		LR	APP	PALM	d.f.	F	P
<i>Eg. ignita</i>	M1	0.026	0.016	0.007	38	0.5903	0.5592
	M3	0.004	0.004	-0.004	38	0.6582	0.5236
	M4	0.010	0.018	0.012	38	0.6656	0.5198
	M5	-0.023	-0.034	-0.005	38	1.2832	0.2889
	M9	0.027	0.061	0.023	38	2.0872	0.1380
	M10	-0.012	-0.014	0.027	38	0.4870	0.6182
<i>El. meriana</i>	M1	0.031	0.031	-0.049	42	1.9401	0.1564
	M2	-0.037	0.001	-0.153	42	1.8232	0.1741
	M3	0.003	0.001	-0.030	42	2.2222	0.1210
	M4	0.029	0.023	-0.077	42	0.9879	0.3808
	M5	-0.018	-0.011	-0.098	42	1.1558	0.3246
	M6	0.160	-0.098	-0.225	42	0.3963	0.6753
	M9	0.019	0.060	-0.062	42	0.6855	0.5094
	M10	-0.031	-0.018	-0.055	42	1.1533	0.3254
M11	0.332	0.384	-0.010	42	0.3109	0.7345	

## Figure Captions

**Fig. 1** Map of study region and sampling sites (a) at the Agropalma Industrial Complex, in state of Pará, Brazil. Image of a trail on a Legal Reserve with scent traps installed (b), a permanent protection area following a stream (c), and oil palm plantation (d) (Photos credit: T. Brito)

**Fig. 2** Image of individuals of *Euglossa ignita* (a) and *Eulaema meriana* (b), and representation of the measured venules (c) in both fore (M1–M8) and hind (M9–M11) wings of orchid bee males sampled in this study (Photo credits: Public domain images by Alejandro Santillana, available on [insectsunlocked.org](https://insectsunlocked.org)).

**Fig. 3** One-Way ANOVA results of the mean size of wing traits (in mm) of two orchid bee species sampled in forest reserves (LR), areas of permanent protection (APP) and oil palm plantations (PALM), in the municipality of Tailândia, state of Pará, Brazil. Significant One-Way ANOVAs are shown with  $p$ -values of Tukey test comparisons performed among land-use type

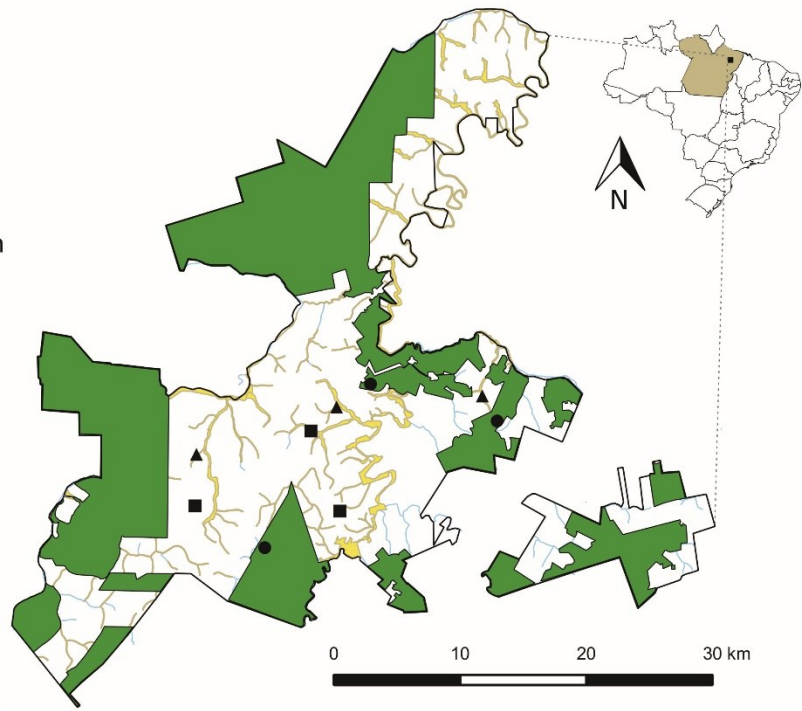
(a)

Legend

- Agropalma perimeter
- Streams
- Legal Reserves
- Areas of Permanent Protection
- Oil Palm Plantations

Sampling sites

- LR
- ▲ APP
- PALM



(b)

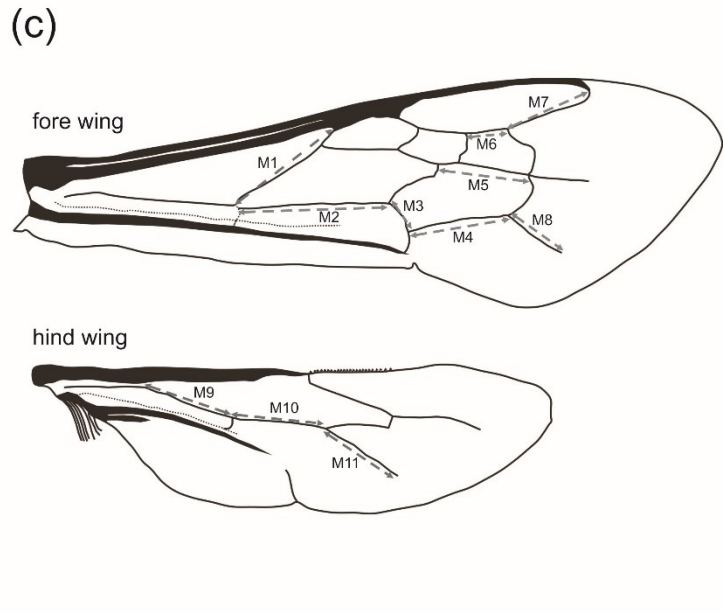


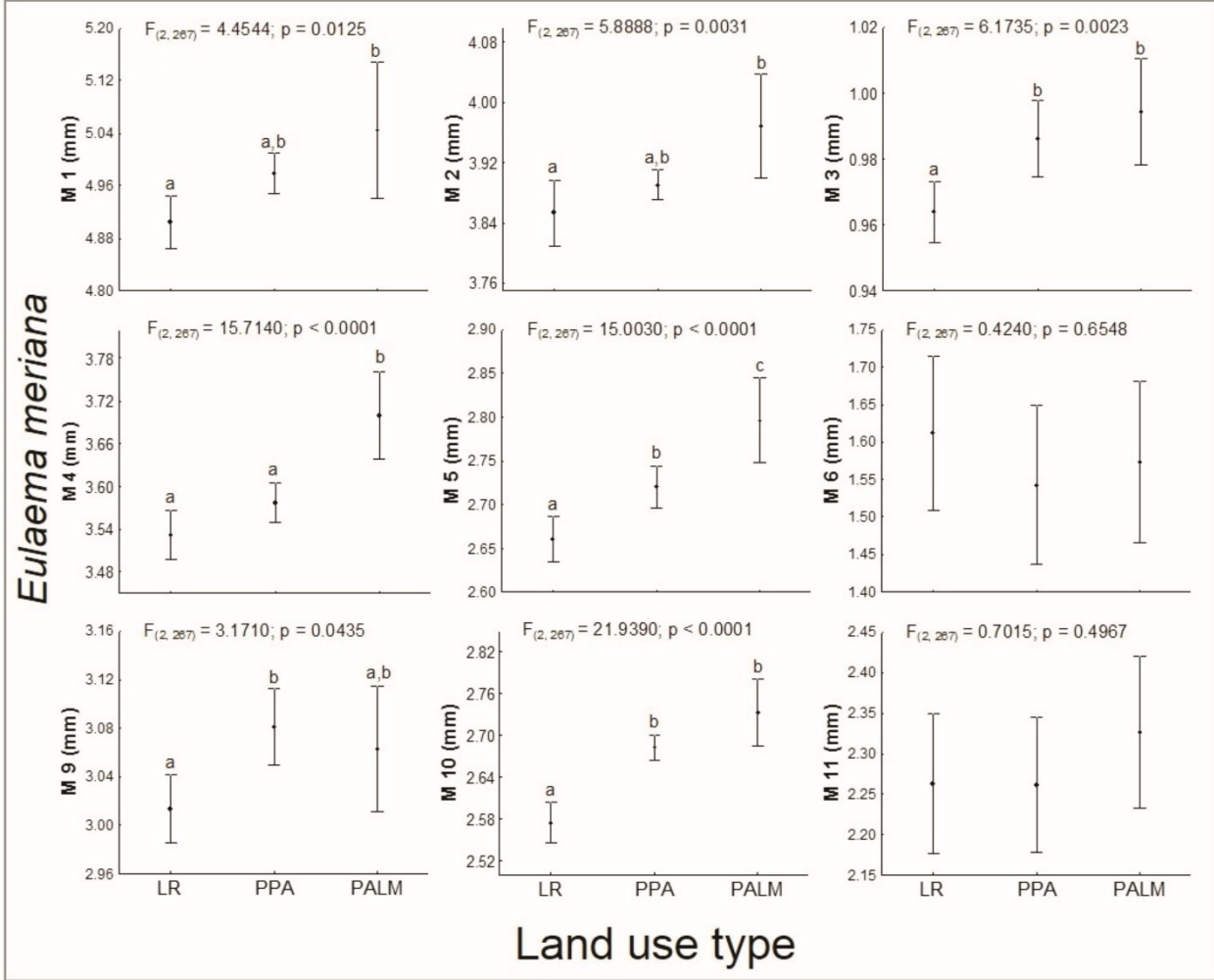
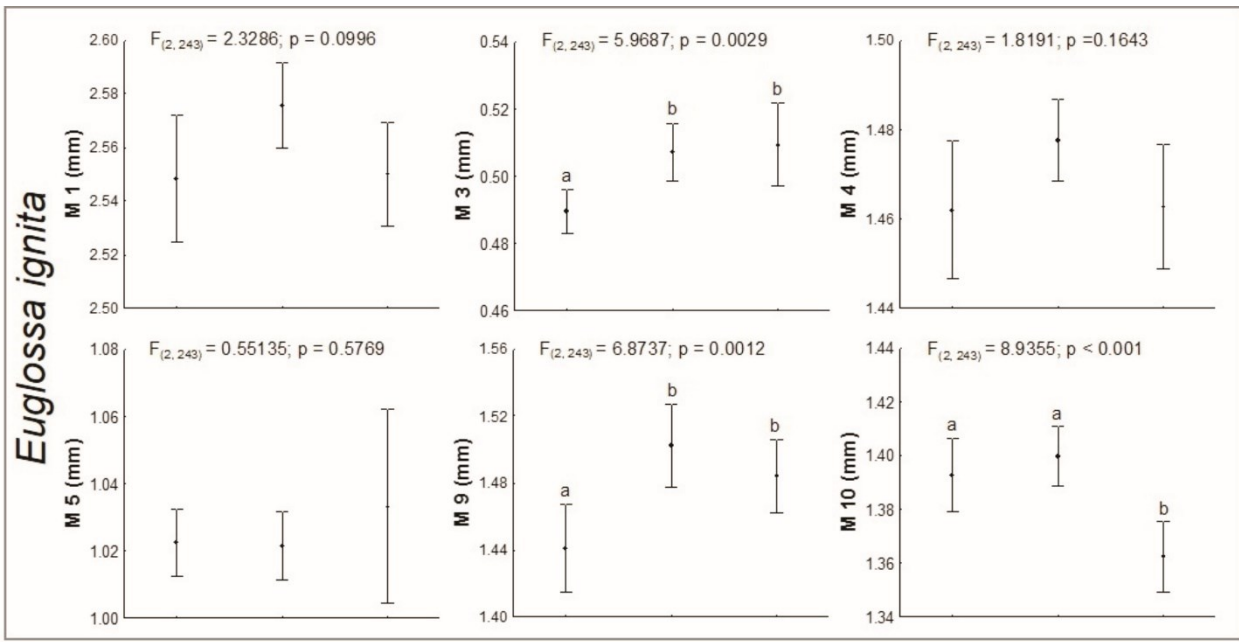
(c)



(c)







**Online Resource 1** Abundance of male orchid bee species collected with scent traps at the Agropalma Industrial Complex study areas in July 2015 and August 2016, municipality of Tailândia, Pará State, Brazil. Forest: Land-use codes: LR = legal reserves, APP = areas of permanent protection, PALM = oil palm plantations.

Species	LR			APP			PALM			Total
	LR 1	LR 2	LR 3	APP 1	APP 2	APP 3	PALM 1	PALM 2	PALM 3	
<i>Eufriesea auripes</i> (Gribodo, 1882)									3	3
<i>Eufriesea ornata</i> Mocsáry, 1896					1					1
<i>Euglossa (Euglossa) aff. mixta</i> Friese, 1899	1	1	4				1		1	8
<i>Euglossa (Euglossa) amazonica</i> Dressler, 1982	3	1	2			2				8
<i>Euglossa (Euglossa) bidentata</i> Dressler, 1982	5	4	6						1	16
<i>Euglossa (Euglossa) cognata</i> Moure, 1970			2							2
<i>Euglossa (Euglossa) gaianii</i> Dressler, 1982		1								1
<i>Euglossa (Euglossa) liopoda</i> Dressler, 1982			1		1	1			2	5
<i>Euglossa (Euglossa) magnipes</i> Dressler, 1982		1								1
<i>Euglossa (Euglossa) modestior</i> Dressler, 1982	3		7	6	3	2	4	2	4	31
<i>Euglossa (Euglossa) townsendi</i> Cockerell, 1904	1	1	2	2	3					9
<i>Euglossa (Glossura) chalybeata</i> Friese, 1925	7	8	44	3	8	6	3	3		82
<i>Euglossa (Glossura) ignita</i> Smith, 1874	13	5	7	9	46	4	8	12	2	106
<i>Euglossa (Glossura) imperialis</i> Cockerell, 1922	4	7	6						1	18
<i>Euglossa (Glossura) orellana</i> Roubik 2004	2		2		2					6
<i>Euglossa (Glossurella) augaspis</i> Dressler, 1982	16	4	9	4	1			1	3	38
<i>Euglossa (Glossurella) crassipunctata</i> Moure, 1968			2	1						3
<i>Euglossa (Glossurella) parvula</i> Dressler, 1982	1	2	3	1						7
<i>Euglossa (Glossuropoda) intersecta</i> Latreille, 1817	1	2		4	1	1				9
<i>Euglossa (Euglossa) sp.</i>		1							1	2
<i>Eulaema (Apeulaema) cingulata</i> Fabricius, 1804	16	7	10	20	110	28	39	73	29	332
<i>Eulaema (Apeulaema) mocsaryi</i> Friese, 1899	1	1		1		2			1	6
<i>Eulaema (Apeulaema) nigrita</i> Lepeletier, 1841			2	3	6	1	2	3	5	22
<i>Eulaema (Apeulaema) pseudocingulata</i> Oliveira, 2006	9	2	5	32	20	19	8	12	26	133
<i>Eulaema (Eulaema) bombiformis</i> Packard, 1869	7	4	4	2	2	5		3	1	28
<i>Eulaema (Eulaema) meriana</i> Olivier, 1789	31	8	7	34	67	29	14	28	52	270
<i>Eulaema (Eulaema) polyzona</i> Mocsáry, 1897	2				1					3
<i>Exaerete frontalis</i> Guérin, 1844	2	6	4	2	2	1				17
<i>Exaerete lepeletieri</i> Oliveira & Nemésio, 2003		1			1					2
<i>Exaerete smaragdina</i> Guérin, 1844	4		2	1						7



## CONCLUSÕES GERAIS

Mudanças no uso da terra, como a conversão de habitats naturais ou semi-naturais por atividades humanas, podem afetar significativamente as comunidades de abelhas. Os Euglossini, ou abelhas das orquídeas, são um grupo particularmente importante de abelhas neotropicais, devido sua contribuição como polinizadores de diversas espécies de orquídeas, bem como de muitas plantas nativas. As abelhas desse grupo possuem a capacidade de transpor longas distâncias em voo, o que os torna bons polinizadores especialmente nas florestas tropicais, onde a maioria das espécies vegetais apresenta distribuição espacial aleatória. Diversos estudos têm demonstrado que essas abelhas são suscetíveis às alterações ambientais, como a fragmentação, isolamento de habitats e mudanças climáticas, sugerindo que a manutenção da diversidade de abelhas das orquídeas requer a preservação de áreas florestais.

Os resultados do presente estudo demonstram que poucas espécies de Euglossini são capazes de suportar as condições ambientais presentes em áreas de plantio de palma de óleo, sendo encontradas com maior frequência nessas áreas espécies generalistas e de maior tamanho de corpo, como as espécies do gênero *Eulaema*. Analisando o padrão de tamanho de corpo de cada espécie nos três tipos habitat, era esperado que os indivíduos das espécies de maior tamanho corporal (e que conseqüentemente apresentam maior capacidade de voo), também fossem maiores nos plantios do que aqueles encontrados nas áreas de floresta. Contudo, pelo menos para quatro espécies (*Eulaema bombiformis*, *El. nigrita* e *El. pseudocingulata* e *Exaerete frontalis*) os maiores valores de tamanho corporal foram registrados para os indivíduos coletados no interior das florestas. Uma possível explicação para esse fato seria que as áreas de floresta são um habitat de alta qualidade, fornecendo recursos alimentares suficientes para os machos de Euglossini. Além disso, apesar de as espécies de *Eulaema* apresentarem uma alta capacidade de voo (cerca de 40 km, em Dressler 1982), é notável que algumas espécies deste gênero não são capazes de transpor fragmentos florestais para voar em áreas abertas, e que provavelmente o mesmo ocorra entre indivíduos da mesma espécie.

A avaliação dos caracteres morfológicos dos indivíduos pode fornecer informações valiosas sobre a intensidade da resposta das espécies frente às alterações ambientais. De maneira geral, embora não tenham sido evidenciadas variações na simetria dos indivíduos pertencentes às espécies *Eulaema meriana* e *Euglossa ignita*, as diferenças fenotípicas encontradas principalmente em termos de tamanho corporal (medida pela distância intertegular; Capítulo 2) e tamanho de asas (medida pelo comprimento das vênulas das asas anterior e posterior; Capítulo 3) sugerem uma seleção determinada pela estrutura física e pela baixa disponibilidade de recursos alimentares para as abelhas nas plantações de palma de óleo, o que pode estar forçando o desenvolvimento de

indivíduos com asas maiores para permitir voos mais distantes em áreas abertas. A diferença de tamanho encontrada entre os machos coletados no plantio comparada com aqueles das áreas florestadas (RLs e APPs) pode ainda, ser o reflexo da maior quantidade de espécies do gênero *Euglossa* nessas áreas preservadas, o que acaba diminuindo a média geral do tamanho das abelhas. Ainda assim, é importante ressaltar que os indivíduos coletados nos três diferentes tipos de hábitat podem não ter se desenvolvido nessas áreas, mas em locais distantes e submetidos a condições ambientais distintas durante o seu desenvolvimento.

Apesar da reputação negativa das plantações de palma de óleo para a biodiversidade, os resultados apresentados neste estudo destacam que os plantios em larga escala com a presença de áreas protegidas nas formas de reservas legais (RL) e áreas de preservação permanente (APP), servem ao propósito que preconiza o Código Florestal de proteger as comunidades, à exemplo dos Euglossini. As APPs se revelaram como eficientes corredores ecológicos, abrigando uma riqueza similar e uma abundância de abelhas das orquídeas superior à encontrada nas RLs, mesmo sendo formadas basicamente por vegetação secundária na região do estudo. Adicionalmente, foi possível indicar pelo menos cinco espécies com baixa tolerância aos plantios, das quais quatro (*Euglossa amazonica*, *Eg. augaspis*, *Eg. bidentata* e *Eg. imperialis*) estiveram intimamente relacionadas às RLs, demonstrando que essas espécies podem ser utilizadas como indicadores das florestas preservadas na Amazônia.

Considerando a capacidade de voo dos Euglossini, como mencionado acima, é importante destacar que o delineamento amostral utilizado neste estudo teve algumas limitações logísticas, não permitindo uma distribuição ideal dos locais de coleta, e esse fato pode ter contribuído para a presença de auto correlação espacial entre as unidades amostrais, embora relativamente baixa (< 15%). Efeito similar também foi verificado ao analisar a contribuição das distâncias entre as unidades amostrais sobre a composição taxonômica e funcional das abelhas das orquídeas, sugerindo que os reais efeitos das mudanças no uso da terra e de características do hábitat podem ter sido mascarados ou não detectados em função da proximidade entre os locais avaliados. Esses resultados reforçam a necessidade de abordagens em diferentes escalas, utilizando variáveis ou conjunto de variáveis que sejam capazes de captar a variação de cada ambiente, a fim de serem relacionadas com métricas morfológicas, funcionais e taxonômicas dos organismos, em especial, dos grupos de abelhas.

Nos estudos sobre a resiliência dos ecossistemas às mudanças ambientais e os serviços ecossistêmicos, tem sido cada vez mais apreciada a inclusão de análises funcionais dos grupos biológicos, e alguns índices de diversidade funcional são capazes de identificar com maior clareza essas funções ambientais. A dispersão funcional (FDis), por exemplo, apresenta, dentre outras características desejáveis, o fato de considerar a abundância relativa e de ser pouco influenciada

pelo número de espécies, ao contrário da riqueza funcional (FRic). Neste estudo, os índices de diversidade funcional utilizados foram capazes de detectar os efeitos dos diferentes tipos de hábitat sobre as assembleias de abelhas das orquídeas, sugerindo que, aliada à uma redução dos atributos populacionais, nos plantios de palma também são observadas perdas de funcionalidade das espécies desse grupo. Além disso, a similaridade funcional encontrada entre as RLs e APPs pode ser o reflexo de elementos estruturais comuns à essas áreas, embora não tenham sido constatadas relações entre a estrutura física do hábitat e as composições taxonômica e funcional dos Euglossini. Isso porque, em estudos realizados no campo, os organismos acabam sendo expostos à diferentes variáveis ambientais que muitas vezes não são mensuradas, ou tem seus efeitos confundidos.

Os resultados apresentados nos três capítulos dessa pesquisa, são consistentes e complementares em revelar as respostas das abelhas aos diferentes tipos de hábitat. Ao considerar áreas modificadas pela implementação de monocultura palma de óleo, é imperativa a manutenção de áreas florestais preservadas não somente na forma de grandes fragmentos florestais, sendo os corredores ripários (APPs) tão importantes quanto, por serem ambientes adequados para abelhas dependentes de florestas e intolerantes à locais expostos. Os padrões aqui encontrados são relevantes para as políticas de responsabilidade socioambiental e conservação da biodiversidade, considerados elementos chave para a produção sustentável de palma de óleo na Amazônia, e podem ser replicados em outros biomas a fim de verificar se os resultados obtidos são compatíveis ou ocorrem em diferentes níveis em outras localizações geográficas, e em outros tipos de cultivo.

## ANEXOS

**Anexo 1** - Normas da revista *Apidologie*, na qual foi publicado o Capítulo 1



### Instructions for Authors

#### SCOPE

*Apidologie* publishes original research articles, reviews and scientific notes on the biology of insects belonging to the superfamily Apoidea (Michener, 1944), the term “biology” being used in the broader sense. The main topics include: behavior, ecology, pollination, genetics, physiology, toxicology and pathology. Systematic research can also be submitted to the extent that it concerns the Apoidea. Also accepted are research papers, including economic studies, on the rearing, exploitation and practical use of Apoidea and their products, as far as they make a clear contribution to the understanding of bee biology. Preference will be given to studies that are hypothesis driven. Papers which are only of descriptive kind and of local interest are not accepted.

#### TYPES OF ARTICLES

The journal *Apidologie* publishes original articles, review articles, scientific notes, proceedings of scientific meetings and extensive bibliographies in English.

**It is the author's responsibility to ensure that the manuscript is written in appropriate English. Non English-speaking authors are strongly encouraged to consult a professional proof-reading service prior to submission.** The editorial board maintains the option of returning, before evaluation, manuscripts which do not meet the instructions and/or acceptable standards of English.

Original and review articles have an abstract in English.

A- *Original articles*: they should be no longer than ten pages as a rule, i.e. about 30,000 characters (spaces excluded), including tables and figures (see ‘Manuscript structure’ for more information).

B- *Review articles*: Their length is limited to about 60,000 characters, spaces excluded. The usual division into ‘materials and methods, results and discussion’ may be replaced by a more adapted structure.

C- *Proceedings of scientific meetings*: Summaries of communications are limited to 1700 characters, spaces excluded. They have no chapters, bibliographic references, tables or acknowledgements and are published by prior arrangement with the Editorial Board.

D- *Scientific notes*: *Apidologie* publishes brief notes to report information and observation **for which replication is not possible or additional data cannot be easily obtained and which have an exceptional scientific interest.** **The authors must justify in the cover letter the appropriateness of presenting their data as a Scientific Note.**

The length of such notes will be strictly restricted to 3 pages (i.e about 9,000 characters, spaces

excluded, if only text and references) and publication will depend on the availability of space in the journal and general interest to readers of *Apidologie*. This form is intended to augment scientific communication and is by no means for articles that are not of sufficient rigor to be published as full papers. All submissions must include ‘scientific note’ in the title. Only the title is translated in French and German; there is no summary.

E- *Extensive bibliographies*: A two-pages synopsis of introduction is published in the printed version, the bibliography itself being available online only. Before preparation and submission of such bibliographies, authors are advised to contact the Editorial office. References are published in HTML format in addition to PDF format.

## PEER REVIEW PROCESS

All manuscripts are examined initially by *Apidologie* scientific editors for their appropriateness to the journal. Those which do not match the scope of *Apidologie* or are of insufficient general interest are sent promptly to their authors. Other manuscripts are sent to a minimum of two experts chosen by the handling editor. Reviewers are invited to present their comments and/or suggestions within 4 weeks after getting access to the manuscript.

Reviewers’ comments are sent to the authors without their names to remain anonymous. Final acceptance is a decision of the handling editor and is based on the reviewers’ reports and the editorial board advice.

In case of revision, the authors must indicate in which ways the comments and suggestions were taken into account or why they were not. The corrected version should be returned to the handling editor within 2 months after the decision has been made. After this delay, it will be considered as a new manuscript. Depending on the handling editor’s decision, revised manuscripts may be sent out to reviewers a second time.

## SUBMISSION OF MANUSCRIPTS

**Please read these instructions carefully before submitting your manuscript: the Editorial Board maintains the option of returning to authors, before the reviewing process, any manuscript not in compliance with these recommendations.**

Submission of a paper implies that it reports original unpublished work, that it has not been accepted and is not under consideration for publication elsewhere. ***All authors must have read and approved the manuscript.***

The accepted language is English. The papers (original and review articles) are published with an abstract in English.

### How to submit

Authors have to submit their manuscripts online <https://www.editorialmanager.com/apid/> .

Electronic submission substantially reduces the editorial processing and reviewing times and shortens overall publication times. Please follow the hyperlink “Submit online” on the right and upload all of your manuscript files following the instructions given on the screen.

### Permissions

Authors wishing to include figures, tables, or text passages that have already been published elsewhere are required to obtain permission from the copyright owner(s) for both the print and online format and to include evidence that such permission has been granted when submitting their papers. Any material received without such evidence will be assumed to originate from the authors.

## Manuscript structure

The manuscript should be submitted in Word (please do not submit docx files) and typed in Times 12 double-spaced with margins of at least 3 cm at the top, bottom and sides for editor's marking. Lines and pages should be numbered.

The manuscripts (original articles) should be arranged as follows: title page, authors' names and addresses, short title, abstract and keywords, introduction, materials and methods, results, discussion/conclusion; acknowledgements, references, figures captions, tables, figures.

**Tables and figures, with their captions, should not appear in the text, but be placed together in the end of the text.**

### 1. Introduction

### 2. Material and Methods

### 3. Results

### 4. Discussion/ Conclusion

### Acknowledgements

The name of the funding organizations should be written in full.

Please do not use more than three levels of displayed headings.

### Title

With no more than 150 characters, spaces excluded (i.e. 3 lines max. on the printed page).

If there are Latin names of plants and animals, please do not mention the name of the author in the title. (This authority needs to appear only once in the article, with the first mention of the taxon in the text)

### Authors:

First names (in full) and last names of each author.

Address of all authors; detailed address of the corresponding author with his/her mail address.

### Short title:

No more than 45 characters, including spaces.

### Abstract

It should be no more than 850 characters and should contain no paragraphs, footnotes, references, cross-references to figures or tables and undefined abbreviations.

### Keywords

Up to five keywords should be supplied, separated by slashes, in bold lowercase letters.

### Acknowledgements

Acknowledgements of people, grants, funds, etc. should be placed in a separate section. The names of funding organizations should be written in full.

### References

The list of references should only include works that are cited in the text and that have been published or accepted for publication. An author citing a paper 'in press' should either provide a DOI or a proof of acceptance to the editors, otherwise it should be cited as 'unpubl. data'.

Unpublished data or personal communication should not appear in the list but should be cited in the text as 'unpubl. data'.

Reference list entries should be alphabetized by the last name of the first author of each work. In case of a reference with more than 10 authors, list only the first 5 authors and then 'et al.' If an author has several publications, the order is as follows: publications of the single author in chronological order, publications of this senior author with one co-author in chronological order, publications of this author with more than one co-author in chronological order.

The titles of the journals should be abbreviated, with punctuation marks, according to the ISSN List of Title Word Abbreviations (see: [www.issn.org/2-22661-LTWA-online.php](http://www.issn.org/2-22661-LTWA-online.php)) The authors' initials should be punctuated as well.

Examples of the layout and punctuation to be used are given below:

*Article of a journal:*

Burgett, M., Burikam, I. (1985) Number of adult honey bees (Hymenoptera: Apidae) occupying a comb: a standard for estimating colony populations. *J. Econ. Entomol.* **78** (6), 1154-1156

*Article by DOI:*

Bevk, D., Kralj J., Cokl, A. (2011) Coumaphos affects food transfer between workers of honeybee *Apis mellifera*. *Apidologie*, DOI:10.1007/s13592-011-0113-x

*Book:*

Bailey, L., Ball, B. V. (1991) *Honey Bee Pathology*. Academic Press Ltd., London.

*Book Chapter:*

Henderson, P. J. F. (1992) Statistical analysis of enzyme kinetic data, in: Eienthal, R. and Danson, M. J. (Eds.), *Enzyme assays: a practical approach*. Oxford University Press, Oxford, pp. 277-316

*Electronic material:*

Agreste, MAAPRAT (2011) Répartition du Territoire. 2009-2010 semi-définitive [online] <http://www.agreste.agriculture.gouv.fr/thematiques/territoire-environnement> (accessed on 05 July 11)

Citation in the text: refer to author(s) and year of publication (Dupont 1956). When there are more than two authors, give the first author's name followed by 'et al.'.

## Miscellaneous points

### Abbreviations:

The acronyms and scientific abbreviations should be defined at first mention in the text, except for the common ones (DNA, RFLP, PCR, ANOVA, etc.).

The authors' initials and the abbreviated titles of the journals should be presented with punctuation marks in the list of references.

### Units

Units should be from the International System of Units (SI) (English version available at: <http://www.bipm.org/en/si/>).

For example, hectares and ppm do not belong to the SI and should be changed into m<sup>2</sup> and mg/kg or µL/L, respectively.

On the SI website you also find the official abbreviation of each unit. For example: 1 h = 60 min = 3600 s and 1 d = 24 h

The official abbreviation of liter is L. We use L to discriminate from 1 (one).



Time is expressed as follows: 1150 h for 11h50 a.m. and 1715 h for 5h15 p.m.

### **Latin names**

The Latin names as well as the authority must be cited in full at the first mention in the text and then the genus abbreviated in the following citations. The authority should not appear in the title or the abstract. Latin genus and species must be italicized.

### **Varroa**

The word should not be used like a common noun (*varroa*) but be replaced either by the Latin binomial (*V. destructor* or *V. jacobsoni*) or by « mites » when the meaning is unequivocal.

### **Races of honeybees**

The honeybee subspecies should be mentioned in Latin *only* if morphometric or genetic proof of the race can be produced. If not, use a circumlocution such as « derived from Carnolian honeybees ». For the sake of accuracy, the terms European-derived and African-derived should be used for studies involving honey bees in the New World in which the origins or racial makeup of the study population needs to be stated.

### **Geographical coordinates**

When the location of the experiment is meaningful, geographic coordinates of the place should be added.

### **DNA Sequences**

Apidologie requires that sequence data generated and used in studies published in the journal be submitted to Genbank prior to publication and the Accession numbers then placed in the manuscript text (or in figures and tables). [<http://www.ncbi.nlm.nih.gov/genbank/submit.html>]

## **TABLES AND ARTWORKS**

### **Tables**

- All tables are to be numbered using Latin numerals.
- Tables should always be cited in text in consecutive numerical order.
- For each table, please supply a table caption (title) explaining the components of the table.
- Identify any previously published material by giving the original source in the form of a reference at the end of the table caption.
- Footnotes to tables should be indicated by superscript lower-case letters (or asterisks for significance values and other statistical data) and included beneath the table body.

### **Artwork**

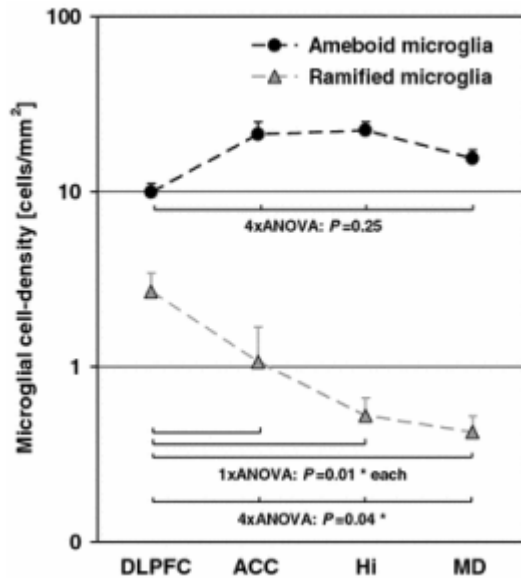
For the best quality final product, it is highly recommended that you submit all of your artwork – photographs, line drawings, etc. – in an electronic format. Your art will then be produced to the highest standards with the greatest accuracy to detail. The published work will directly reflect the quality of the artwork provided.

### **Electronic Figure Submission**

- Supply all figures electronically.
- Indicate what graphics program was used to create the artwork.
- For vector graphics, the preferred format is EPS; for halftones, please use TIFF format. MS Office files are also acceptable.

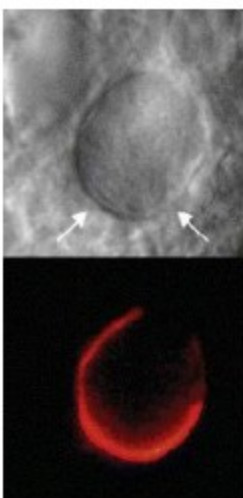
- Vector graphics containing fonts must have the fonts embedded in the files.
- Name your figure files with "Fig" and the figure number, e.g., Fig1.eps.

### Line Art



- Definition: Black and white graphic with no shading.
- Do not use faint lines and/or lettering and check that all lines and lettering within the figures are legible at final size.
- All lines should be at least 0.1 mm (0.3 pt) wide.
- Scanned line drawings and line drawings in bitmap format should have a minimum resolution of 1200 dpi.
- Vector graphics containing fonts must have the fonts embedded in the files.

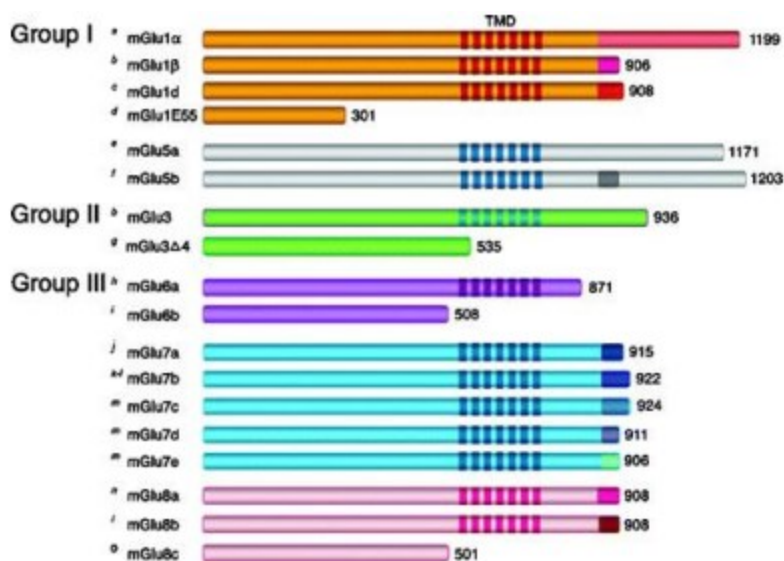
### Halftone Art



- Definition: Photographs, drawings, or paintings with fine shading, etc.
- If any magnification is used in the photographs, indicate this by using scale bars within the figures themselves.

- Halftones should have a minimum resolution of 300 dpi.

## Combination Art



- Definition: a combination of halftone and line art, e.g., halftones containing line drawing, extensive lettering, color diagrams, etc.
- Combination artwork should have a minimum resolution of 600 dpi.

## Color Art

- Color art is free of charge for online publication.
- **If black and white will be shown in the print version, make sure that the main information will still be visible.** Many colors are not distinguishable from one another when converted to black and white. A simple way to check this is to make a xerographic copy to see if the necessary distinctions between the different colors are still apparent.
- If the figures will be printed in black and white, do not refer to color in the captions.
- Color illustrations should be submitted as RGB (8 bits per channel).

## Figure Lettering

- To add lettering, it is best to use Helvetica or Arial (sans serif fonts).
- Keep lettering consistently sized throughout your final-sized artwork, usually about 2–3 mm (8–12 pt).
- Variance of type size within an illustration should be minimal, e.g., do not use 8-pt type on an axis and 20-pt type for the axis label.
- Avoid effects such as shading, outline letters, etc.
- Do not include titles or captions within your illustrations.

## Figure Numbering

- All figures are to be numbered using Arabic numerals.
- Figures should always be cited in text in consecutive numerical order.
- Figure parts should be denoted by lowercase letters (a, b, c, etc.).
- If an appendix appears in your article and it contains one or more figures, continue the consecutive numbering of the main text. Do not number the appendix figures, "A1, A2, A3, etc." Figures in online appendices (Electronic Supplementary Material) should, however, be numbered separately.

### Figure Captions

- Each figure should have a concise caption describing accurately what the figure depicts. Include the captions in the text file of the manuscript, not in the figure file.
- Figure captions begin with the term Fig. in bold type, followed by the figure number, also in bold type.
- No punctuation is to be included after the number, nor is any punctuation to be placed at the end of the caption.
- Identify all elements found in the figure in the figure caption; and use boxes, circles, etc., as coordinate points in graphs.
- Identify previously published material by giving the original source in the form of a reference citation at the end of the figure caption.

### Figure Placement and Size

- When preparing your figures, size figures to fit in the column width.
- For most journals the figures should be 39 mm, 84 mm, 129 mm, or 174 mm wide and not higher than 234 mm.
- For books and book-sized journals, the figures should be 80 mm or 122 mm wide and not higher than 198 mm.

### Permissions

If you include figures that have already been published elsewhere, you must obtain permission from the copyright owner(s) for both the print and online format. Please be aware that some publishers do not grant electronic rights for free and that Springer will not be able to refund any costs that may have occurred to receive these permissions. In such cases, material from other sources should be used.

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Springer accepts electronic multimedia files (animations, movies, audio, etc.) and other supplementary files to be published online along with an article. This feature can add dimension to the author's article, as certain information cannot be printed or is more convenient in electronic form.

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- Supply all supplementary material in standard file formats.
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- To accommodate user downloads, please keep in mind that larger-sized files may require very long download times and that some users may experience other problems during downloading.

### Audio, Video, and Animations

- Always use MPEG-1 (.mpg) format.

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- Submit your material in PDF format; .doc or .ppt files are not suitable for long-term viability.
- A collection of figures may also be combined in a PDF file.

### Spreadsheets

- Spreadsheets should be converted to PDF if no interaction with the data is intended.
- If the readers should be encouraged to make their own calculations, spreadsheets should be submitted as .xls files (MS Excel).

### Specialized Formats

- Specialized format such as .pdb (chemical), .wrl (VRML), .nb (Mathematica notebook), and .tex can also be supplied.

### Collecting Multiple Files

- It is possible to collect multiple files in a .zip or .gz file.

### Numbering

- If supplying any supplementary material, the text must make specific mention of the material as a citation, similar to that of figures and tables.
- Refer to the supplementary files as “Online Resource”, e.g., “... as shown in the animation (Online Resource 3)”, “... additional data are given in Online Resource 4”.
- Name the files consecutively, e.g. “ESM\_3.mpg”, “ESM\_4.pdf”.

### Captions

- For each supplementary material, please supply a concise caption describing the content of the file.

### Processing of supplementary files

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The article will be published online after receipt of the corrected proofs. This is the official first publication citable with the DOI. After release of the printed version, the paper can also be cited by issue and page numbers.

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At acceptance, you can provide a list of max. 10 email addresses of colleagues: the journal will send them a complimentary copy of the PDF of your paper. This may definitely help disseminating your study and increasing its potential impact, as well as the impact of the journal.



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Apidologie

Official journal of the Institut National de la Recherche  
Agronomique (INRA) and Deutschen Imkerbundes e.V.  
(D.I.B.)

Managing editor: Dufay, A.

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Journal no. 13592

## Anexo 2 - Normas da revista Journal of Insect Conservation, na qual foi publicado o Capítulo 2.



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### Journal of Insect Conservation

An international journal devoted to the conservation of insects and related invertebrates

Editor-in-Chief: D. Maes; J.S. Pryke; J.L. León-Cortés

ISSN: 1366-638X (print version)

ISSN: 1572-4753 (electronic version)

Journal no. 10841



## Instructions for Authors

### MANUSCRIPT SUBMISSION

#### Manuscript Submission

Submission of a manuscript implies: that the work described has not been published before; that it is not under consideration for publication anywhere else; that its publication has been approved by all co-authors, if any, as well as by the responsible authorities – tacitly or explicitly – at the institute where the work has been carried out. The publisher will not be held legally responsible should there be any claims for compensation.

#### Permissions

Authors wishing to include figures, tables, or text passages that have already been published elsewhere are required to obtain permission from the copyright owner(s) for both the print and online format and to include evidence that such permission has been granted when submitting their papers. Any material received without such evidence will be assumed to originate from the authors.

#### Online Submission

Please follow the hyperlink “Submit online” on the right and upload all of your manuscript files following the instructions given on the screen.

#### Additional request

Upon submission, the e-mail addresses of all authors will be requested. At the end of the submission process, the corresponding author will receive an acknowledgement e-mail and all co-authors will be contacted automatically to confirm their affiliation to the submitted work.

### TITLE PAGE

#### Title Page

The title page should include:

- The name(s) of the author(s)
- A concise and informative title



- The affiliation(s) and address(es) of the author(s)
- The e-mail address, and telephone number(s) of the corresponding author
- If available, the 16-digit ORCID of the author(s)

## Abstract

Please provide an abstract of 150 to 250 words. The abstract should not contain any undefined abbreviations or unspecified references.

## Keywords

Please provide 4 to 6 keywords which can be used for indexing purposes.

TEXT

## Text Formatting

Manuscripts should be submitted in Word.

- Use a normal, plain font (e.g., 10-point Times Roman) for text.
- Use italics for emphasis.
- Use the automatic page numbering function to number the pages.
- Do not use field functions.
- Use tab stops or other commands for indents, not the space bar.
- Use the table function, not spreadsheets, to make tables.
- Use the equation editor or MathType for equations.
- Save your file in docx format (Word 2007 or higher) or doc format (older Word versions).

Manuscripts with mathematical content can also be submitted in LaTeX.

[LaTeX macro package \(zip, 182 kB\)](#)

## Headings

Please use no more than three levels of displayed headings.

## Abbreviations

Abbreviations should be defined at first mention and used consistently thereafter.

## Footnotes

Footnotes can be used to give additional information, which may include the citation of a reference included in the reference list. They should not consist solely of a reference citation, and they should never include the bibliographic details of a reference. They should also not contain any figures or tables.

Footnotes to the text are numbered consecutively; those to tables should be indicated by superscript lower-case letters (or asterisks for significance values and other statistical data). Footnotes to the title or the authors of the article are not given reference symbols. Always use footnotes instead of endnotes.

## Acknowledgments

Acknowledgments of people, grants, funds, etc. should be placed in a separate section on the title page. The names of funding organizations should be written in full.

## Important note:

**All authors are requested to use the continuous line numbering function for their manuscripts.**

## SCIENTIFIC STYLE

Please always use internationally accepted signs and symbols for units (SI units).

## SCIENTIFIC STYLE

Nomenclature: Insofar as possible, authors should use systematic names similar to those used by Chemical Abstract Service or IUPAC.

## REFERENCES

### Citation

Cite references in the text by name and year in parentheses. Some examples:

Negotiation research spans many disciplines (Thompson 1990).

This result was later contradicted by Becker and Seligman (1996).

This effect has been widely studied (Abbott 1991; Barakat et al. 1995a, b; Kelso and Smith 1998; Medvec et al. 1999, 2000).

### Reference list

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Gamelin FX, Baquet G, Berthoin S, Thevenet D, Nourry C, Nottin S, Bosquet L (2009) Effect of high intensity intermittent training on heart rate variability in prepubescent children. *Eur J Appl Physiol* 105:731-738.

<https://doi.org/10.1007/s00421-008-0955-8>

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Smith J, Jones M Jr, Houghton L et al (1999) Future of health insurance. *N Engl J Med* 341:325–329

- Article by DOI

Slifka MK, Whitton JL (2000) Clinical implications of dysregulated cytokine production. *J Mol Med*.

<https://doi.org/10.1007/s001090000086>

- Book

South J, Blass B (2001) *The future of modern genomics*. Blackwell, London

- Book chapter

Brown B, Aaron M (2001) The politics of nature. In: Smith J (ed) *The rise of modern genomics*, 3rd edn. Wiley, New York, pp 230-257

- Online document

Cartwright J (2007) Big stars have weather too. IOP Publishing PhysicsWeb.

<http://physicsweb.org/articles/news/11/6/16/1>. Accessed 26 June 2007

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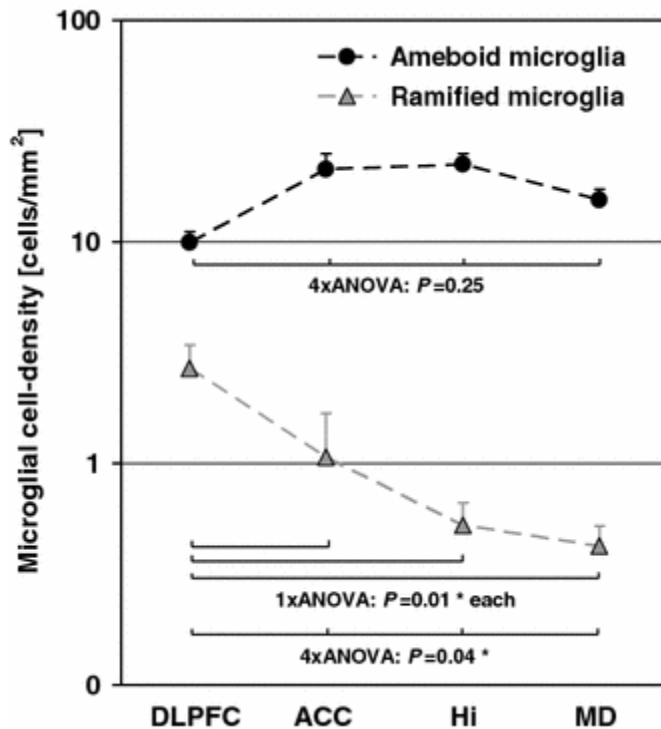
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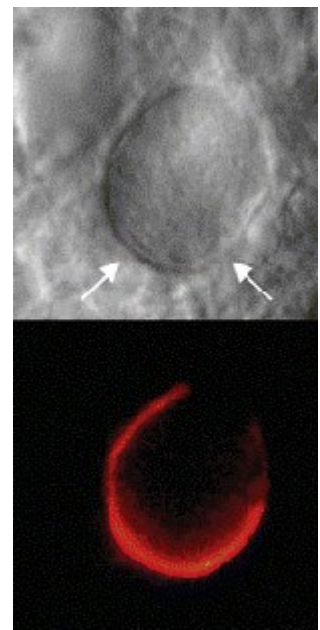
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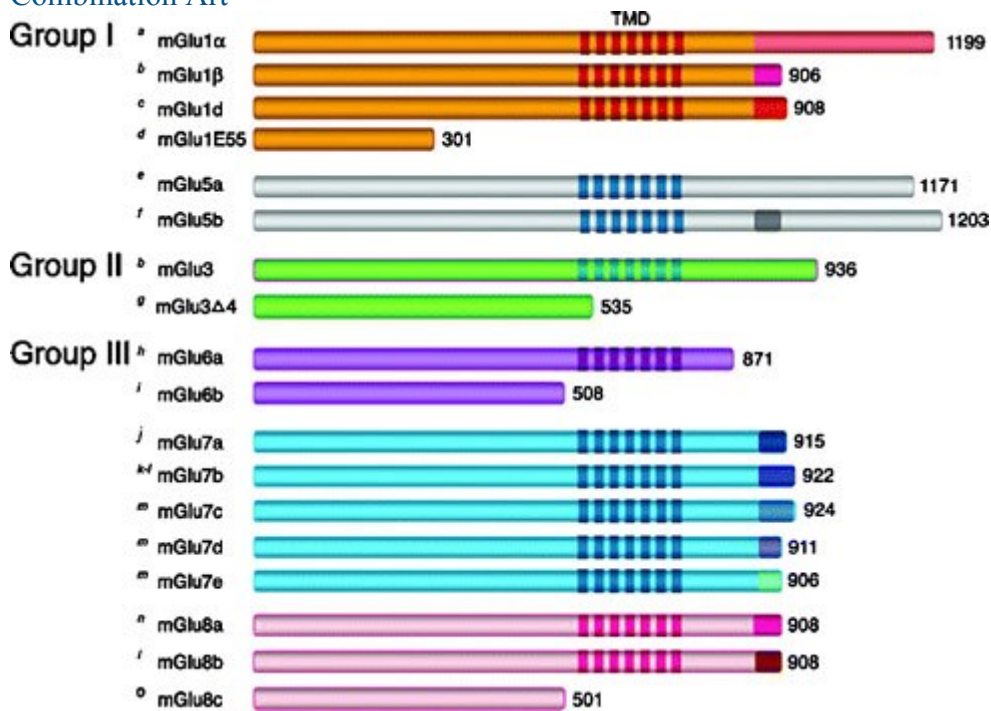
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## Anexo 3 - Normas da revista *Insectes Sociaux*, para a qual foi submetido o Capítulo 3 dessa Tese.



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International Journal for the Study of Social Arthropods

Editor-in-Chief: Michael **Breed**

ISSN: 0020-1812 (print version)

ISSN: 1420-9098 (electronic version)

Journal no. 40

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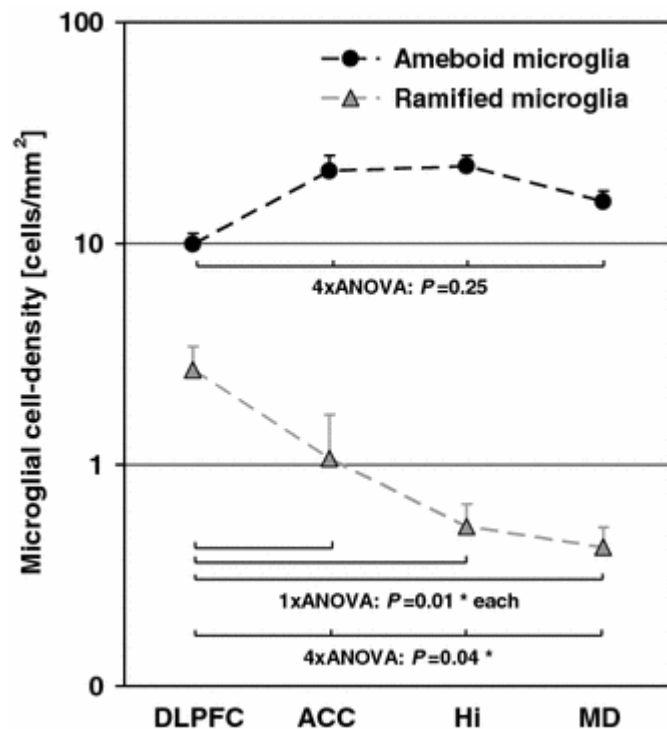
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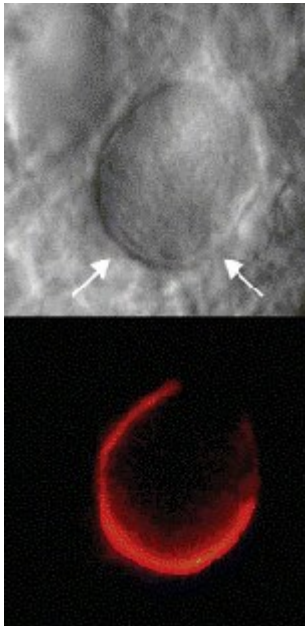
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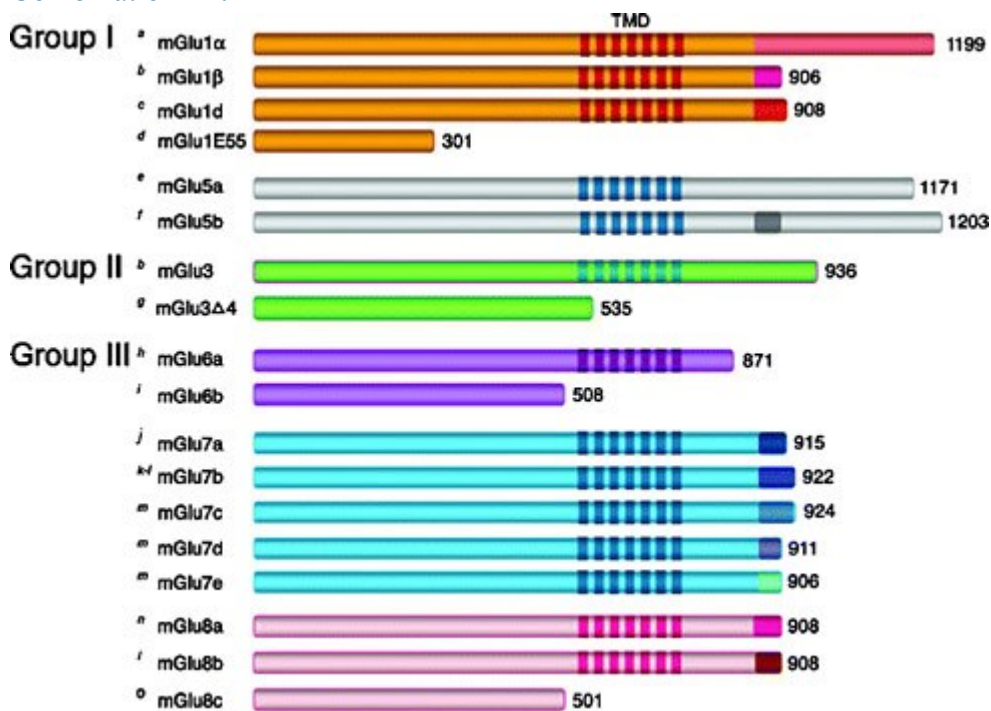
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