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ORIGINAL ARTICLE

Orchid bees in riparian and terra-firme forest fragments in an urban matrix in southwestern Brazilian Amazonia

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ABSTRACT

Riparian forests are important ecosystems that support an enormous biodiversity in Brazil. Despite being protected under Brazilian legislation, these forests suffer great impact from the fragmentation of habitats. Orchid bees are a key group of pollinators in the Neotropical region, yet few data are available on the assamblage structure of these bees in riparian forests. We evaluated the role of fragments of riparian and terra-firme forest on the conservation and maintenance of orchid bees in an urban landscape in the southwestern Amazon basin. Specifically, we evaluated whether bee assemblages in riparian and terra-firme forests differed significantly in abundance, species richness and composition. We also evaluated whether species richness and abundance of bees vary with the size of the forest fragment. Male bees were attracted using odoriferous baits and collected with entomological nets in 10 forest fragments. There was no significant difference between riparian and terra-firme fragments in species abundance, richness and composition, but there was a positive correlation between fragment size and species richness and abundance. Our results suggest that, in an urban landscape, the remaining riparian and terra-firme forest fragments still could maintain 62.7% of the orchid bee species known to occur in the region, reinforcing the conservation value of these forest remnants. Our findings indicate that these fragments provide a potentially important habitat for the maintenance of local bee populations in the landscape.

KEYWORDS: Euglossini, forest fragmentation, pollination, urban landscape

Abelhas das orquídeas em fragmentos de floresta ripária e de terra-firme em uma matriz urbana no sudoeste da Amazônia brasileira

RESUMO

As florestas ripárias no Brasil são importantes ecossistemas que sustentam uma enorme biodiversidade. Apesar de protegidas pela legislação brasileira, elas têm sofrido grandes impactos decorrentes da fragmentação florestal. As abelhas das orquídeas constituem um grupo chave de polinizadores na região Neotropical, porém, pouco se sabe sobre suas assembleias em florestas ripárias. Nós avaliamos o papel de fragmentos de floresta ripária e de terra-firme na conservação e manutenção da fauna de abelhas das orquídeas em uma paisagem urbana no sudoeste da Amazônia. Especificamente, avaliamos se assembleias de abelhas de fragmentos ripários e de terra-firme diferem significativamente em abundância, riqueza e composição de espécies. Também avaliamos se a abundância e a riqueza de espécies variam em função do tamanho do fragmento. Machos de abelhas foram atraídos por iscas odoríferas e coletados com redes entomológicas em 10 fragmentos florestais. Não houve diferença significativa entre fragmentos ripários e de terra-firme quanto à abundância, riqueza e composição de espécies, mas houve uma correlação positiva entre o tamanho do fragmento e a riqueza e abundância de espécies. Nossos resultados sugerem que, em uma paisagem urbana, os fragmentos de floresta ripária e de terra firme ainda podem manter 62,7% do número de espécies de abelhas das orquídeas conhecido para a região, reforçando o valor da conservação desses remanescentes florestais. Nossos dados indicam que esses fragmentos fornecem um habitat potencialmente importante para a manutenção das populações locais de abelhas na paisagem.

PALAVRAS-CHAVE: Euglossini, fragmentação florestal, polinização, paisagem urbana

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INTRODUCTION

Riparian forests provide important ecosystem services, such as the maintenance and protection of water resources, geological stability and biodiversity, the facilitation of gene flow of both fauna and flora, and the protection of soils, while also supporting the wellbeing of human populations (Borges *et al.* 2011; Monteiro *et al.* 2013; Martins 2014). In Brazil, despite being protected under forestry legislation, which requires the maintenance of riparian zones on private properties as permanent reserves (BRASIL 2012), riparian forests have been widely impacted by deforestation, habitat fragmentation, and urbanization (Martins 2014; Ferreira *et al.* 2015).

Concomitantly, the recent worldwide decline of pollinators has reinforced fears of a potential global crisis (Novais *et al.* 2016). Anthropogenic factors, such as habitat loss, changes in land use, the application of pesticides, and the intensification of farming activities, may all have a major impact on many groups of insect pollinators, including bees (Ferreira *et al.* 2015; Araújo *et al.* 2018; Almeida *et al.* 2020).

In the Neotropical region, the orchid bees (Apidae: Euglossini) are a key group of insect pollinators (Roubik and Hanson 2004), more abundant and diverse in well-preserved environments (Antonini *et al.* 2016; Allen *et al.* 2019), although some, more generalist species are found in degraded areas (Silva and De Marco-Júnior 2014; Aguiar *et al.* 2015). They are pollinators of native and cultivated plants and the conservation of this group of bees is a fundamental prerequisite for the conservation of many orchids and a wide variety of other plants found in tropical forests (Cavalcante *et al.* 2012). The fragmentation and loss of forest habitat impact orchid bee communities through the interruption of ecological processes, such as pollination, and a reduction in the availability of flowers that produce pollen, nectar, and aromatic substances (Armbruster 1993; Tonhasca *et al.* 2002, Livingston *et al.* 2013, Brito *et al.* 2018). Larger fragments are expected to contain a higher number of species (MacArthur and Wilson 1967), as they tend to have greater environmental heterogeneity, diversity of food sources and floral fragrances, and nesting sites, which favor greater richness and abundance of bees (Morato and Campos 2000; Tonhasca *et al.* 2002). Higher visitation rates to odoriferous baits and greater species richness of orchid bees have been reported in larger forest fragments (Powell and Powell 1987), but data on this subject are generally scarce for orchid bees (Powell and Powell 1987; Ramalho *et al.* 2009; Brosi 2009).

Most studies of orchid bees have focused on fragments of terra-firme forest (Storti *et al.* 2013; Storck-Tonon *et al.* 2013; Brito *et al.* 2018, but see Storck-Tonon and Peres 2017). However, some bees are known to prefer riparian habitats (Moura and Schlindwein 2009; Brito *et al.* 2017), which could be related to favorable conditions of temperature and humidity, necessary for the development of the brood. Futhermore, the plants found in tropical riparian forests offer floral resources all year round for a wide range of pollinators, including many species of solitary and social bees that nest in riparian forests and their marginal habitats (Moura and Schlindwein 2009; Pires *et al.* 2012; Montoya-Pfeiffer *et al.* 2020).

Relatively few data are available on the diversity and ecology of euglossine in riparian forests (Carvalho *et al.* 2006; Moura and Schlindwein 2009; Faria and Silveira 2011), in particular in the Amazon biome (Brito *et al.* 2017). Another little known aspect in the Amazon is the adaptability of euglossines to urban environments. Many species of orchid bees occur and nest in urban landscapes (Storti *et al.* 2013). Relatively small forest fragments, such as public parks, in urban areas can act as dispersion corridors and increase habitat connectivity for bee assemblages (Nemésio and Silveira 2007; Storck-Tonon *et al.* 2013; Storti *et al.* 2013; Nemésio 2014).

No previous study in the Amazon biome has compared the orchid-bee fauna in remnants of riparian and terra-firme forest in an urban matrix. In this context, we evaluated the diversity and abundance of orchid bees in urban fragments of riparian and terra-firme forest in the southwestern Brazilian Amazon, to assess their role in the maintenance of the orchid bee fauna of an urban landscape in the region. Our predictions were: (i) riparian and terra-firme forest fragments differ in abundance, species richness and species composition of orchid bees; and (ii) larger fragments, independently of forest type, have greater abundance and richness of bees.

MATERIAL AND METHODS

Study area

We sampled male orchid bees from September 2015 to February 2016 in 10 forest fragments in the urban landscape of the city of Rio Branco, Acre state, in northern Brazil (Table 1; Figure 1). We selected forest fragments with an area between 1.6 and 162.2 ha, which were assigned to one of two forest categories, either riparian or terra-firme (forest that is never flooded), based on their proximity to the nearest water course (Table 1). In general, the terra-firme fragments were larger (average size = 55.5 ha) than the riparian ones (average size = 45.4 ha), with the exception of the Via Parque private area, which was the smallest sampled fragment (Table 1). All the selected fragments were located within a predominantly urban matrix, including some open habitat (built areas, streets, roads, vacant lots and small pastures) in the areas surrounding the fragments. The distance between fragments varied from 2.1 to 13.9 km (average = 7.7 km). Only three fragments were at an average distance above 7.7 km from other fragments. The predominant vegetation of the study region is open tropical terra-firme forest with bamboo and palm trees, and dense forest (Silveira 2005). The local climate is tropical

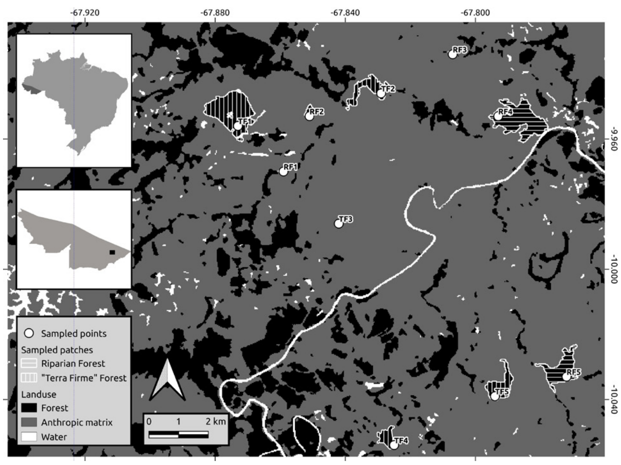

Figure 1. Location of the study area in the state of Acre in Brazil, and of the sampling sites in the urban matrix of the municipality of Rio Branco, Acre, Brazil (RF = riparian forest, TF= terra-firme forest).

Table 1. Location, size and classification of the forest fragments sampled for orchid bees in the urban landscape of Rio Branco, Acre, Brazil.

Forest fragment	Forest type	Coordinates	Area (ha)
Batista Stream	Riparian	09°58'11"S, 67°51'31"W	5.2
Tucumã Stream	Riparian	09°57'11"S, 67°51'02"W	12.7
Ouricuri Stream	Riparian	09°56'02"S, 67°48'24"W	5.3
São Francisco Stream	Riparian	09°57'11"S, 67°47'33"W	121.4
Judia Stream	Riparian	10°02'00"S, 67°46'20"W	82.5
Zoobotanical Park	Terra-firme	09°57'23"S, 67°52'21"W	162.3
Municipal Forest Nursery	Terra-firme	09°56'47"S, 67°49'44"W	22.1
Via Parque Private Property	Terra-firme	09°59'11"S, 67°50'31"W	1.6
Amapá Environmental Protection Area	Terra-firme	10°03'15"S, 67°49'30"W	35.5
Chico Mendes Environmental Park	Terra-firme	10°02'20" S, 67°47'38"W	56.1

hot and humid, with a mean annual temperature of 32°C (ACRE 2010). During the study period, the mean monthly precipitation was 171 mm, with November being the rainiest month (327.1 mm) and January the driest month (96.3 mm). The mean relative humidity was 83.8 ± 7.7%, with mean daily temperatures of 23.5 ± 1.2 °C (INMET 2016).

Bee sampling

In each fragment, we collected bees at three sampling points that were at least 50 m from the edge of the fragment, and 100 m from each of the other two points. Each point was sampled twice, on different days within the study period, totalling six samples and approximately 48 hours of sampling time in each fragment. This sampling effort has been successfully used to sample bees from orchids in the region (Storck-Tonon *et al* 2009; Storck-Tonon *et al*. 2013; Cândido *et al*. 2018). The average sampling interval in almost all fragments varied around 30 days, although the interval between sampling occasions withn fragments was quite variable, from three to 86 days (Supplementary Material, Appendix S1). At the end of six months, all fragments were sampled six times.

On each sampling day and at each sampling point, we soaked two cotton swabs in each of the odoriferous substances benzyl acetate, cineol, skatole, eugenol, methyl salicylate, and vanillin, and hung them from a horizontal nylon line at a height of 1.5 m above the ground, with an interval of 2 m between each pair of swabs, following the protocol of Storck-Tonon *et al*. (2009). We captured bees from 7:00 to 15:00 using an entomological net, as this method is more efficient in the region than trapping with plastic bottles (Nemésio and Morato 2006).

We collected data on the ambient and soil temperatures, luminosity, and relative humidity on an hourly basis during each sampling period using a portable digital thermo-hygro-anemometer-luximeter (THAL-300, Instrutherm, São Paulo, Brasil) and an infrared soil thermometer (± 2°C, MT-350, Minipa, São Paulo, Brasil). We estimated the area (in hectares) of each fragment in ArcGis 10.1, analyzing the polygon of each area derived from LANDSAT8 OLI sensor (Orbit/point: 002/067) satellite images, which have a 30 m spatial resolution in the multispectral band and a 15 m resolution in the panchromatic band.

We identified most of the collected bees to species level by comparing the specimens with the vouchers deposited in the reference collection of Universidade Federal do Acre (UFAC), in Rio Branco, Acre, Brazil. The specimens of the genus *Eufriesea* were identified by Dr. José Eustáquio dos Santos (Universidade Federal de Minas Gerais, UFMG), and some of the specimens of the genera *Euglossa*, *Eulaema* and *Exaerete* were identified by Dr. Danielle Storck-Tonon (Universidade do Estado de Mato Grosso, UNEMAT) and Dr. Marcio Luiz de Oliveira (Instituto Nacional de Pesquisas da Amazônia, INPA). The specimens were deposited in the Entomological Collection at the Center for Biological and Nature Sciences of UFAC.

Statistical analyses

To assess the sampling efficiency, we constructed species accumulation curves for the riparian and terra-firme fragments separately, using the *specaccum* function in the 'vegan' package (Oksanen *et al*. 2020) in R 3.2.3 (R Development Core Team 2016). This function sequentially samples random individuals from a data set and measures the number of novel species encountered as additional individuals are sampled. We use the 'random' method, which finds sites in random order and samples individuals without replacement. Each curve was plotted as the average of 1000 permutations.

We used generalized linear mixed models (GLMMs) (Bolker *et al*. 2009) and linear mixed-effects models (LMMs) (Crawley 2012) to test whether the abundance and richness of bees and the microclimatic variables (luminosity, relative humidity, and air and soil temperatures) differed between riparian and terra-firme fragments. We considered the abundance and species richness of bees and each of the microclimatic variables as a response variable and habitat (riparian or terra-firme fragment) as explanatory variable. We also included the identity of each area as random effect in the models to account for variance associated with random site effects, using the two samplings in each of the three sampling points as sampling repetitions. We tested model significance by comparing the evaluated model and the null model (intercept and random effect only) by analysis of variance. The adequacy of model prediction was assessed through residual analysis and tests for overdispersion (Crawley 2012). Due to the overdispersion of residues, which occurs when the deviance of the response is greater than that expected by the chosen distribution (Hinde and Demétrio 1998), we analyzed the abundance of bees through a GLMM with negative binomial error distribution. No data overdispersion was detected for species richness of bees, which was thus analyzed with a GLMM using Poisson error distribution. Finally, each of the microclimatic variables was analyzed with a LMM using Gaussian error distribution. GLMM and LMM were created with the 'lme4' package (Bates *et al.* 2020), the analysis of variance between each model and the null model with the 'vegan' package (Oksanen *et al*. 2020), and the residual analysis of GLMM and LMM with the 'DHARMa' package (Florian 2020) in R 3.2.3 (R Development Core Team 2016).

To compare the species composition between riparian and terra-firme fragments, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001) based on Jaccard distance. The method computes a pseudo F-ratio, which is the ratio of the composition dissimilarity within a treatment to the ratio between treatments, and the significance is tested by permutation. Subsequently, we carried out a permutational analysis of multivariate dispersions (PERMDISP) (Anderson 2006). PERMDISP is a multivariate analyses analogue to Levene's test for homogeneity of variances, and the statistic (average distance of group members to the PCoA group centroid) is tested by permutation (Anderson 2006). PERMANOVA and PERMIDISP were performed with the 'vegan' package (Oksanen *et al.* 2020) in R 3.2.3 (R Development Core Team 2016).

Finally, we adjusted models of simple linear regression to predict the abundance and species richness of bees in the riparian and terra-firme fragments as a function of fragment area. For this analysis, we used the log values of the area of each fragment (Sokal and Rohlf 2011).

RESULTS

Overall, we collected 3,166 bees, representing four genera and 38 species (Table 2). We collected 1,805 (57%) bees belonging to 35 species in the terra-firme fragments, and 1,361 (43%) belonging to 32 species in the riparian fragments. *Euglossa ignita* was the most common species overall, in both riparian and terra-firme fragments, with 703 individuals (22.2%) overall, followed by *Eulaema nigrita*, with 371 individuals (11.7%) and *Eulaema cingulata*, with 321 (10.1%). Six species were recorded only in the terra-firme fragments, and three only in the riparian fragments (Table 2). For both riparian and terra-firme fragments, the cumulative number of species collected approached the asymptote by the 25th sample (Figure 2).

The abundance of bees (mean ± standard deviation) did not differ between riparian and terra-firme fragments (riparian, 48.3 ± 24.3 individuals; terra-firme, 57.2 ± 31.5 individuals; ANOVA: χ^2 = 1.49, *df* = 1, *p* = 0.2220). The species richness of bees also did not differ between riparian and terra-firme fragments (riparian, 12.2 ± 5.7 species; terra-firme, 13.3 ± 3.6 species; ANOVA: χ^2 = 0.61, *df* = 1, *p* = 0.4340).

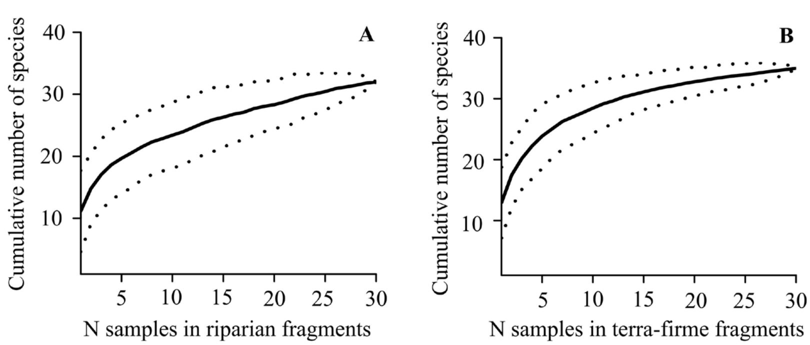

Figure 2. Accumulation curve of orchid-bee species (continuous line) and 95% confidence intervals (dashed lines) for riparian-forest fragments (A) and terra-firme forest fragments (B) located within the urban matrix of Rio Branco, Acre, Brazil. N samples = number of samples.

Table 2. Number of bees collected per species in five fragments of riparian forest and five fragments of terra-firme forest in the urban landscape of Rio Branco, Acre, Brazil.

Species	Riparian	Terra-firme	Total
Eufriesea convexa (Friese, 1899)	–	1	1
Eufriesea flaviventris (Friese, 1899)	2	2	4
Eufriesea ornata (Mocsáry, 1896)	–	1	1
Eufriesea pulchra (Smith, 1854)	3	1	4
Eufriesea superba (Hoffmannsegg, 1817)	1	8	9
Euglossa allosticta Moure, 1969	41	39	80
Euglossa amazonica Dressler, 1982	104	100	204
Euglossa augaspis Dressler, 1982	33	35	68
Euglossa avicula Dressler, 1982	1	7	8
Euglossa bidentata Dressler, 1982	3	7	10
Euglossa chalybeata Friese, 1925	–	2	2
Euglossa chlorina Dressler, 1982	1	1	2
Euglossa cognata Moure, 1970	15	15	30
Euglossa despecta Moure, 1968	–	4	4
Euglossa ignita Smith, 1874	221	482	703
Euglossa imperialis Cockerell, 1922	11	37	48
Euglossa intersecta Latreille, 1817	3	6	9
Euglossa gaianii Dressler, 1982	1	–	1
Euglossa laevicincta Dressler, 1982	–	1	1
Euglossa aff. *mixta* Friese, 1899	13	26	39
Euglossa modestior Dressler, 1982	143	175	318
Euglossa mourei Dressler, 1982	80	67	147
Euglossa orellana Roubik, 2004	1	54	55
Euglossa prasina Dressler, 1982	11	5	16
Euglossa pleosticta Dressler, 1982	–	1	1
Euglossa rugilabris Moure, 1967	1	–	1
Euglossa securigera Dressler, 1982	1	2	3
Euglossa townsendi Cockerell, 1904	1	10	11
Eulaema bombiformis (Packard, 1869)	7	13	20
Eulaema cingulata (Fabricius, 1804)	156	165	321
Eulaema meriana (Olivier, 1789)	125	154	279
Eulaema mocsaryi (Friese, 1899)	26	26	52
Eulaema nigrita Lepeletier, 1841	182	189	371
Eulaema pseudocingulata Oliveira, 2006	92	98	190
Exaerete frontalis (Guérin, 1844)	3	5	8
Exaerete aff. *frontalis*	1	–	1
Exaerete lepeletieri Oliveira & Nemésio, 2003	24	18	42
Exaerete smaragdina (Guérin, 1844)	54	48	102
Total abundance	1,361	1,805	3,166
Total species richness	32	35	38

Regarding climatic variables, the riparian fragments differed from the terra-firme fragments by registering significantly higher values of air temperature (mean ± standard deviation) (riparian, 30.3 ± 1.8 °C; terra-firme, 28.6 ± 1.2 °C; ANOVA: $\chi^2 = 10.05$, $df = 1$, $p = 0.0015$) and luminosity (riparian, 785.3 ± 285.9 Lux; terra-firme, 529.3 ± 216.0 Lux; ANOVA: $c^2 = 13.05$, $df = 1$, $p < 0.0003$), and significantly lower values of relative humidity (riparian, 66.7 ± 6.1%; terra-firme, 76.4 ± 3.5%; ANOVA: $c^2 = 14.47$, $df = 1$, $p < 0.0001$) (Figure 3). Soil temperature did not differ significantly between fragment type (riparian, 23.8 ± 5.2 °C; terra-firme, 26.0 ± 5.0 °C; ANOVA: $\chi^2 = 0.94$, $df = 1$, $p = 0.3329$) (Figure 3).

There was no significant difference in species composition (PERMANOVA: F = 1.110, $r^2 = 0.121$, $p = 0.3826$), and species composition heterogeneity (PERMDISP: F = 0.001, $p = 0.9676$) between riparian and terra-firme fragments.

No significant correlation was found between fragment area and species richness in riparian ($r = 0.74$, $p = 0.1513$, $df = 3$) and terra-firme fragments ($r = 0.48$, $p = 0.4151$, $df = 3$). However, when the joint dataset for all fragments was considered, a significant and positive regression was observed for species richness ($y = 4.7\log(x) + 14.4$, $r^2 = 0.47$, $p = 0.0283$, $df = 8$) and abundance ($y = 141.2\log(x) + 124.3$, $r^2 = 0.44$, $p = 0.0346$, $df = 8$) on fragment size (Figure 4a,b). Overall, larger fragments tended to have a larger number of both bee species and individuals than smaller fragments.

DISCUSSION

The fact that the cumulative number of species approached the asymptote for both categories of fragments, indicates that the sampling effort was adequate for a reliable estimate of the species richness of orchid bees in the study area, including more exclusive and less abundant species.

Our results point to that there is no significant difference between riparian and terra-firme fragments in the abundance and species richness of orchid bees, independently of forest type. While riparian forests are considered to be relatively humid environments (Silva *et al*. 2015), the temperature and luminosity were higher and relative humidity significantly lower in riparian fragments, contrary to our expectations. This indicates that, despite the proximity of the sampling points to streams, the riparian fragments were more open than the primary terra-firme forests. These variables influence the activity of insects in general (Marques 2012), and of orchid bees in particular (Nemésio and Vasconcelos 2013; Vilhena *et al*. 2017). However, the environmental differences between the forest types were not enough to significantly influence the structure of the respective bee assemblages.

We found no significant difference in species composition between riparian and terra-firme forest fragments, in contrast with other studies that found low similarity in species composition between riparian forests and other types of habitat in the surrounding matrix for neotropical savanna (Faria and Silveira 2011) and environments in the northern hemisphere (Williams 2011). One factor contributing to the overall similarity among the bee faunas in our study may be the proximity among the fragments (2.1 to 13.9 km), as euglossine bees can fly and forage over a number of kilometers each day in search of widely-dispersed food sources and aromatic substances (Pokorny *et al*. 2015). Many

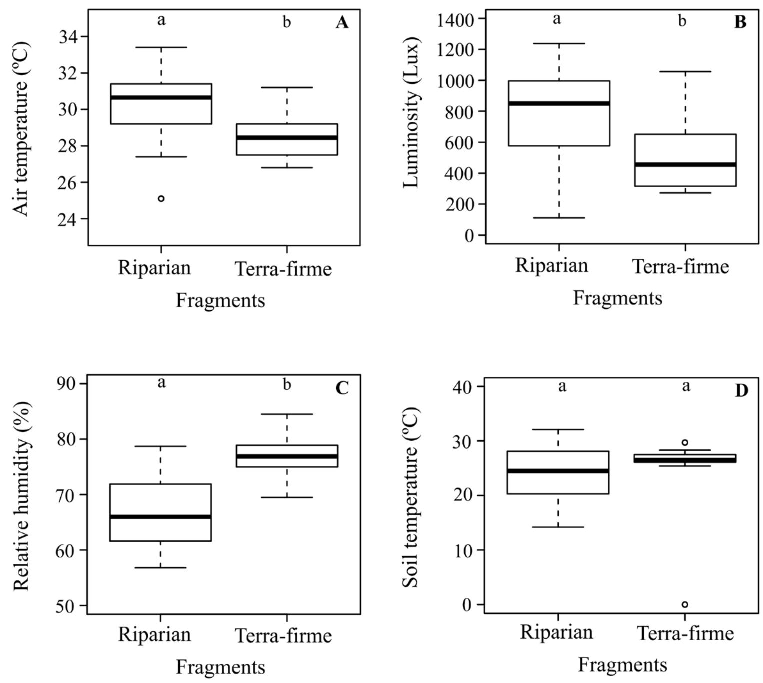

Figure 3. Values of the climatic variables air temperature (A), luminosity (B), relative humidity (C) and soil temperature (D) in riparian and terra-firme forest fragments sampled for orchid bees in the urban matrix of Rio Branco, Acre, Brazil. The box represents the 25-75% quartiles, the line the median and the bars the standard error. Circles represent outlier values. Different letters above the boxes represent statistically significant differences between the categories.

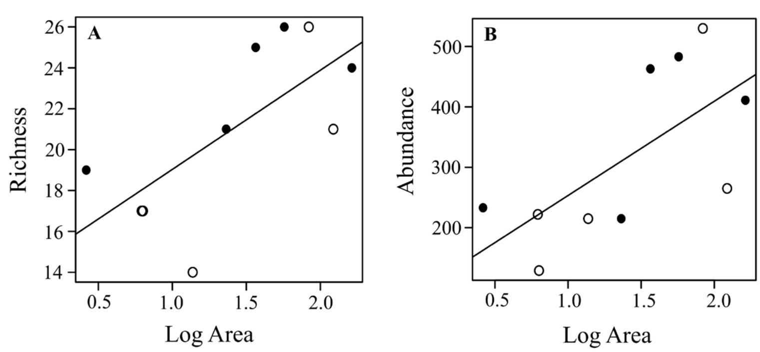

Figure 4. Relationship between the log area of riparian and terra-firme forest fragments with species richness (A) and abundance (B) of orchid bees in the urban matrix of Rio Branco, Acre, Brazil. In both plots, the white circles represent the riparian fragments and the black circles, the terra-firme fragments.

generalist species are also able to forage over long distances, far from their nests, and in anthropogenic environments in the urban matrix (Raw 1989; Nemésio and Silveira 2007). In the Atlantic Forest, males of these bees were observed to disperse recurrently both within and among forest fragments in search of resources (Tonhasca *et al*. 2003). Another factor that may have contributed to this result is that the fragments are inserted in an urban matrix and their vegetation structure is more uniform and dominated by open ombrophilous forest (Daly and Silveira 2009; ACRE 2010).

Although no significant difference in species composition was found, some species (*Euglossa gaianii*, *Eg. rugilabris*, and *Exaerete* aff. *frontalis*) occurred only in riparian fragments, and others (*Eufriesea convexa*, *Ef. ornata*, *Eg. chalybeata*, *Eg. despecta*, *Eg. laevicincta* and *Eg. pleosticta*) only in terra-firme fragments, although in low abundance (1-4 individuals). Some of these species had already been collected in the region (Nemésio and Morato 2006; Storck-Tonon *et al*. 2011; Storck-Tonon *et al*. 2013). Of the three species collected in the riparian fragments, only *Eg. gaianii* had been recorded in an urban fragment in Rio Branco. Regarding the species collected in the terra-firme fragments, *Ef. convexa* and *Eg. laevicincta* had not yet been recorded in the region. *Eufriesea ornata* was previously recorded in two fragments in a rural area in the vicinity of Rio Branco. *Euglossa despecta* was recorded in eight rural and urban fragments. *Euglossa pleosticta* was recorded in a rural fragment and in a forest relatively distant from the urban matrix of Rio Branco. *Euglossa chalybeata* was recorded in the region of Rio Branco in high abundance but only in two fragments in rural areas. Thefore, except for *Eg. chalybeata*, all other exclusive species recorded in this study were collected previously in low abundance in the region and could be considered of low density. *Euglossa chalybeata, Eg. pleosticta* and *Ef. ornata* were also recorded in forests of the Juruá River basin, Acre (Nemésio and Morato 2005), which suggests that they are widely distributed in the southwestern Amazon.

The number of species recorded in our study represents 62.7% of the orchid-bee species known to occur in the southwestern Brazilian Amazon (Nemésio and Morato 2006, Storck-Tonon *et al.* 2009; Cândido *et al.* 2018), indicating that the sampled fragments are occupied by a considerable proportion of the known total regional diversity of orchid bees. Considering that the abundance and diversity of arthropods is declining in tropical forests due to climate change (Novais *et al.* 2016), and the important role of orchid bees in trophic webs (Lister and Garcia 2018), urban forest fragments may play a fundamental role in the conservation of ecosystems in the landscape as a whole. Riparian and terra-firme fragments may provide orchid bees with nesting sites, refuge from solar radiation (Moura and Schlindwein 2009; Faria and Silveira 2011), and feeding resources (Neves and Viana 1999). Additionally, riparian forests are considered to be areas of permanent preservation under Brazilian legislation (BRASIL 2012). Both riparian and terra-firme habitats are important in the provision of ecosystem services, such as pollination, production of fruit and seeds, carbone storage, regulation of the hydrological cycle and prevention of erosion and silting (Martins 2014; Mello *et al.* 2016; Lense *et al.* 2020). Both types of forest fragments may also provide important ecological corridors for the dispersal of bee populations, contributing to the maintenance of gene flow and the structure of assemblages, and reducing the potential for local extinction (Souza *et al.* 2010; Storti *et al.* 2013; Gray *et al.* 2016; Lense *et al.* 2020).

The species richness and abundance of orchid bees may also be affected by the quality and heterogeneity of the matrix surrounding forest fragments (Livingston *et al.* 2013; Aguiar *et al.* 2015; Brito *et al.* 2017). Given the ongoing urbanization of the study area in the municipality of Rio Branco, the size of local forest fragments (both riparian and terra-firme) is decreasing progressively. The modification of the urban landscape, with the reduction in forest cover and the ongoing expansion of the urban matrix, may result in a reduction in the availability of natural resources (Santos *et al.* 2019), such as nesting sites and materials, and sources of pollen and nectar, which combine to limit the species richness and abundance of bees (Zanette *et al.* 2005; Storck-Tonon *et al.* 2013). This process affects solitary bees in particular, such as the majority of the Euglossine bees, including the forms that nest on the ground and in tree holes (Zanette *et al.* 2005; Cardoso and Gonçalves 2018). In this context, areas of natural vegetation located within the urban matrix, no matter how small or disturbed, can be important refuges for bees and other organisms associated with the urban landscape (Aronson *et al.* 2017).

As in our study, larger fragments generally tend to harbor higher species richness (Santos *et al.* 2013). In the case of bees, larger areas imply a greater availability of sources of odoriferous substances, feeding resources, resin, and potential nesting sites. While some studies have found evidence that the size of the fragment influences the structure of orchid-bee assemblages (Powell and Powell 1987; Aguiar *et al.* 2015; Botsch *et al.* 2017), the empirical data are inconclusive (Nemésio and Silveira 2007). Powell and Powell (1987) recorded a decrease in the visitation rates of bees at odoriferous baits with decreasing fragment size in central Amazonia. In a previous study in the southwestern Amazon, which focused on fragments located within both the urban matrix and the rural zone, Storck-Tonon *et al.* (2013) found no significant relationship between the area of the fragment and the abundance and species richness of bees. The divergence between these findings and the results of the present study may be related primarily to the configuration of the respective study areas and the sampling procedures adopted in each study. The habitat complexity, in terms of vegetation structure, also may be an important determinant of the distribution of orchid bees (Aguiar *et al.* 2014). In the Brazilian Atlantic Forest, Antonini *et al.* (2016) showed that relatively complex habitats tend to have a greater species richness and abundance of bees than less complex environments, even though the species composition was not affected systematically. Further research is needed to evaluate the long-term impacts of the urbanization process on these environments and the biodiversity they support in a more conclusive way.

CONCLUSIONS

Our prediction that species abundance, richness and composition of orchid bees differs between riparian and terra-firme forest fragments in an urban landscape in the southwestern Amazon has not been corroborated. However, the size of the fragment was a predictor of richness and abundance. Therefore, our findings highlight the importance of maintaining large areas of forest within the urban matrix for the conservation of orchid-bee species. Furthermore, riparian and terra-firme forest fragments widely dispersed in the urbanized landscape may provide important habitat for the maintenance of bee populations and their foraging patterns. The fact that a major proportion of the regional species complement of orchid-bees was found in these fragments emphasizes the functional importance of this type of habitat in the urban matrix.

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SUPPLEMENTARY MATERIAL (only available in the electronic version)

Cândido *et al*. Orchid bees in riparian and terra-firme forest fragments in an urban matrix in southwestern Brazilian Amazonia

Appendix S1. Sampling dates of orchid bees in five riparian (RF1-RF5) and five terra-firme (TF1-TF5) forest fragments (FRAG) from September 2015 to February 2016 in Rio Branco, Acre state, Brazil. Tabulated values are the numbers of orchid-bee individuals captured on each day. The black bars mark periods over 10 days in which there was no field work.

FRAG	September																				October																		
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
RF1				20																	47																		
RF2																		18				39																	
RF3	6																																				17		
RF4										27																						37							
RF5					55																												86						
TF1		40																	68																				
TF2									27																					31									
TF3			35																	28														39					
TF4																	23																			77			
TF5								40																					70										

FRAG					November													December					January													
	20	21	22	23	16	17	18	19	20	21	22	23	24	25	26	27	28	10	11	12	13	14	7	8	9	10	11	12	13	14	15	17	18	19	20	21
RF1																							21													
RF2	31													14			59		54																	
RF3													32																							
RF4									65																											
RF5				71																												86				
TF1		105																								50										
TF2																																				
TF3																		37																		
TF4						58						83										59														
TF5					67																															

FRAG											February																										
	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
RF1																31							32														
RF2																																					
RF3			16															25												33							
RF4					20							44					72																				
RF5																					136																96
TF1													80													68											
TF2									45											34								38									
TF3														45																			49				
TF4							103																														
TF5				120																					106						80						