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Community Ecology

Forest Matrix Fosters High Similarity in Bee Composition Occurring on Isolated Outcrops Within Amazon Biome

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Abstract

Most studies analyze fragmentation due to habitat loss caused by anthropogenic activities and few of them analyzed fragmentation on naturally fragmented areas. In the Eastern Amazon, it is possible to find areas naturally open and surrounded by pristine forest. Understanding how species respond to isolation in these areas is an important challenge for decision-making processes aiming conservation and restoration. Using standardized methods of bee collection (entomological nets, bait trap, pan trap, and nest trap), the objective of this study was to analyze the composition and diversity of bees occurring on six isolated outcrops located in two protected areas within Amazon biome. More specifically, we tested 1) if the dissimilarity in bee species composition is explained by the isolation of outcrops and 2) if bee richness, abundance, and Shannon diversity can be explained by the outcrop size. We found 118 species, with the Meliponini and Euglossini (Hymenoptera: Apidae) tribes representing the highest number of species. The similarity in species composition across all outcrops is high and is not explained by the isolation. In addition, the richness, abundance, and Shannon diversity are not explained by outcrop size. Forest does not seem to be a barrier to bee movement, and although most species probably nest in the forests, they use the highly diverse plants of the outcrops as a complementary food source.

Key words: diversity, pollinator, tropical forest, Carajás

Land use change has negatively affected biodiversity (Allan et al. 2015), with habitat fragmentation being one of the most common consequence (Krauss et al. 2010). Studies have shown a loss of diversity in fragmented areas (Wilson et al. 2016), including functional (Hatfield et al. 2018) and genetic (Frankham et al. 2017) diversity, and changes in species composition (Hill and Curran 2001) due to fragmentation. However, most studies analyzed fragmentation due to habitat loss caused by anthropogenic causes (Tilman et al. 2001), and few analyzed naturally fragmented areas (Boff et al. 2014, Soro et al. 2017). However, understanding how species respond to isolation in areas of different sizes surrounded by pristine forest matrix is an important challenge for decision-making processes aiming conservation and restoration.

More than 90% of tropical flowering plant species depend on animal pollination for reproduction (Klein et al. 2007, Ollerton et al. 2011), and among all pollinators, bees are the most important ones for plant species in native forests (Michener 2007). However, little is

known about diversity of Amazon native bees and their relationship with local flora and, one possible explanations for this is the general knowledge gap about insects (Eisenhauer et al. 2019, Montgomery et al. 2020), especially in tropical regions. Fieldwork involving standardized sampling methods is urgent in areas with scarce data, as an initial step towards species conservation plans. Standardized sampling methods can provide not just a list of species but a comprehensive and comparable approach to understanding species composition in an area.

Two important protected areas in the eastern Amazon are the Carajás National Forest and the Campos Ferruginosos National Park located in the southeast Pará (northern Brazil, eastern Amazon). They are located within a set of protected areas that is a fragment of pristine forest within an area highly degraded by anthropogenic impacts (Souza-Filho et al. 2016), known as the Amazon Arc of Deforestation. Carajás is a rich mineral province, and iron ores can be found on ferruginous outcrops. These

outcrops are called 'cangas' and present a distinguished flora characterized by herbs and shrubs adapted to a high solar incidence and shallow soil with high concentration of iron (Mota et al. 2018). The cangas of Carajás are located in the ridges of mountain ranges known as Serra Norte and Serra Sul (referring to its location inside the Carajás National Forest), and Serra do Tarzan and Serra da Bocaina (which currently belongs to the Campos Ferruginosos National Park) (Souza-Filho et al. 2019). Such characteristics of soil and vegetation can be found in the ferruginous 'campos rupestres' located in the Quadrilátero Ferrífero in the state of Minas Gerais (southeastern Brazil), where bee surveys have already been conducted in some localities (Araújo et al. 2006, Azevedo et al. 2008).

The cangas in the two abovementioned protected areas are naturally isolated and surrounded by tropical Amazon forest and have areas of different sizes. The bee species list found on Carajás was recently published (Borges et al. 2020), based mostly on specimens deposited in entomological collections. However, no standardized sampling of bee species was conducted until now, which hinders ecological analysis. In addition, the configuration of these natural open areas as isolated islands of differing size and surrounded by pristine tropical Amazon forest presents an important opportunity for research.

Following the theory of island biogeography (MacArthur and Wilson 1967), it may be reasonable to consider the combined effects of area and isolation on bee diversity. According to this theory, one could expect that isolated and distant areas would be more prone to present a lower number of species. However, the presence of forest among isolated and distant areas probably could not prevent the movement of bees, since it is reasonable to suppose that bee species are able to move freely between canga areas and forests. Additionally, most bee species reported for Carajás are widespread (Borges et al. 2020).

Using four standardized bee collection methods, our aim was to analyze the composition and diversity of bees occurring in six isolated canga outcrops within two protected areas in the eastern Amazon, Carajás National Forest and the Campos Ferruginosos National Park (hereafter Carajás). More specifically, we built the first list of bee species occurring on the cangas of Carajás, and tested if (i) bee species composition dissimilarity in all studied cangas is explained by the isolation of cangas and (ii) richness, abundance, and Shannon diversity can be explained by the canga size. Considering that previous studies showed that the reported bee species are mainly widely distributed, we hypothesized that there is no difference on bee composition, since the forest probably represents no barrier to bee movement.

## Materials and Methods

Study Site

Our study was conducted during 2017 in cangas located in Carajás (−50.7409 W, −5.8699 N, −49.7989 W, −6.5357 S) (Fig. 1). The climate in the region is classified as the Aw type according to Köppen (tropical wet), and the average altitude is 670 m (maximum 904 m) (Souza-Filho et al. 2019). The region experiences high annual rainfall (~2000 mm), with maximum precipitation occurring between January and March and minimum precipitation occurring between June and August. Monthly average temperatures vary between 25 and 26°C (Sahoo et al. 2016). Cangas are natural open areas surrounded by forest with intense solar incidence (Fig. 1). The rocky vegetation (herbaceous-shrub) grows directly on the mineral iron

deposits (Silva et al. 1996, Mota et al. 2018), and the soil is an outcrop of ores.

Two areas are located in the Serra Norte (known as N2 and N8), three areas are located in the Serra Sul (known as S11A, S11B, and S11C), and one area is located in the Serra da Bocaina. We used the QGIS software (Open Source Geospatial Foundation Project) to calculate the size of each canga (Table 1). To determine the isolation of the cangas (i.e., the minimum distance between two canga areas), we used the nearest-neighbor distance function in the postGIS software (Spatial and Geographic Objects for PostgreSQL). We considered Serra Sul as a unit for the analysis of isolation and we consider this area in three parts for the analysis of size (S11A, S11B, and S11C). We did this because the isolation between the parts of Serra Sul is not as evident as in Serra Norte.

Bee Survey

Our initial planning was to visit the six cangas once a month throughout the year to capture annual variations in temperature and precipitation in the region. However, some logistical problems (high precipitation, mist, and damaged roads) prevented us for doing that, and each area was visited in the months of January, March, April, May, July, August, and November. Each area was visited once a month. Initially, we marked four points 300 m apart (point 0, 300, 600, and 900 m; see below) with a GPS in each of the six cangas, and visited one canga per day on each of the 7 months. We used four methods of bee sampling to estimate the richness and abundance of bee species (Fig. 2): 1) Entomological nets: we conducted a census based on the observation and capture of bees on flowers with the aid of entomological nets (Sakagami et al. 1967) (Fig. 2A). Bee sampling with entomological nets was performed along a pre-established transect of 900 m in length and 2 m wide in each canga, which was inspected once during each survey. A single collector (U.M.M.) collected from 9:00 a.m. in the morning until 12:00 a.m., traversing the 900 × 2 m pre-established transect of each canga. On average, there were 18 h of collection per month (3 h × 6 areas), totaling 126 h of collection (18 h × 7 mo). Each flowering plant in the transect was observed for 5 min and all the bees that visited the flowers were collected. 2) Trap nests: trap nests were constructed to supply artificial cavities for the nesting of solitary bees (Fig. 2B) (Krug and Alves-Dos-Santos 2008). They were formed by two pieces of wood measuring 28 × 28 × 95 mm that were perforated longitudinally with holes of different diameters (6, 8, 10, 13 mm) and a length of 140 mm (based on Marinho et al. 2018). The nests were organized into one set consisting of two blocks containing eight trap nests each (totaling four trap nests of each diameter). Thus, each set contained 16 blocks. The sets were fixed in small shrubs available and, due to the great exposure to solar incidence, they were protected using thermal material (styrofoam). Four sets separated by 300 m were installed in each canga (point 0, 300, 600, and 900 m), totaling 64 blocks per canga that remained in the area for the entire collection period (January–November). They remained in the cangas until some of the blocks in the set were occupied by one bee species. When a block was removed, we placed a new block with the same diameter. 3) Pan traps: plastic cups were painted with three different colors (yellow, white, and blue) to visually attract bees and filled with a solution of water and detergent (Fig. 2C). The pan traps were placed in the same transect used for the samples with entomological net. They were separated by an approximate distance of 3m from each other. At each point (0, 300, 600 and 900 m), four sets were placed separated by a distance of approximately 15 m (totaling 48 units). On average, there were 48 h of collection per month (8h ×
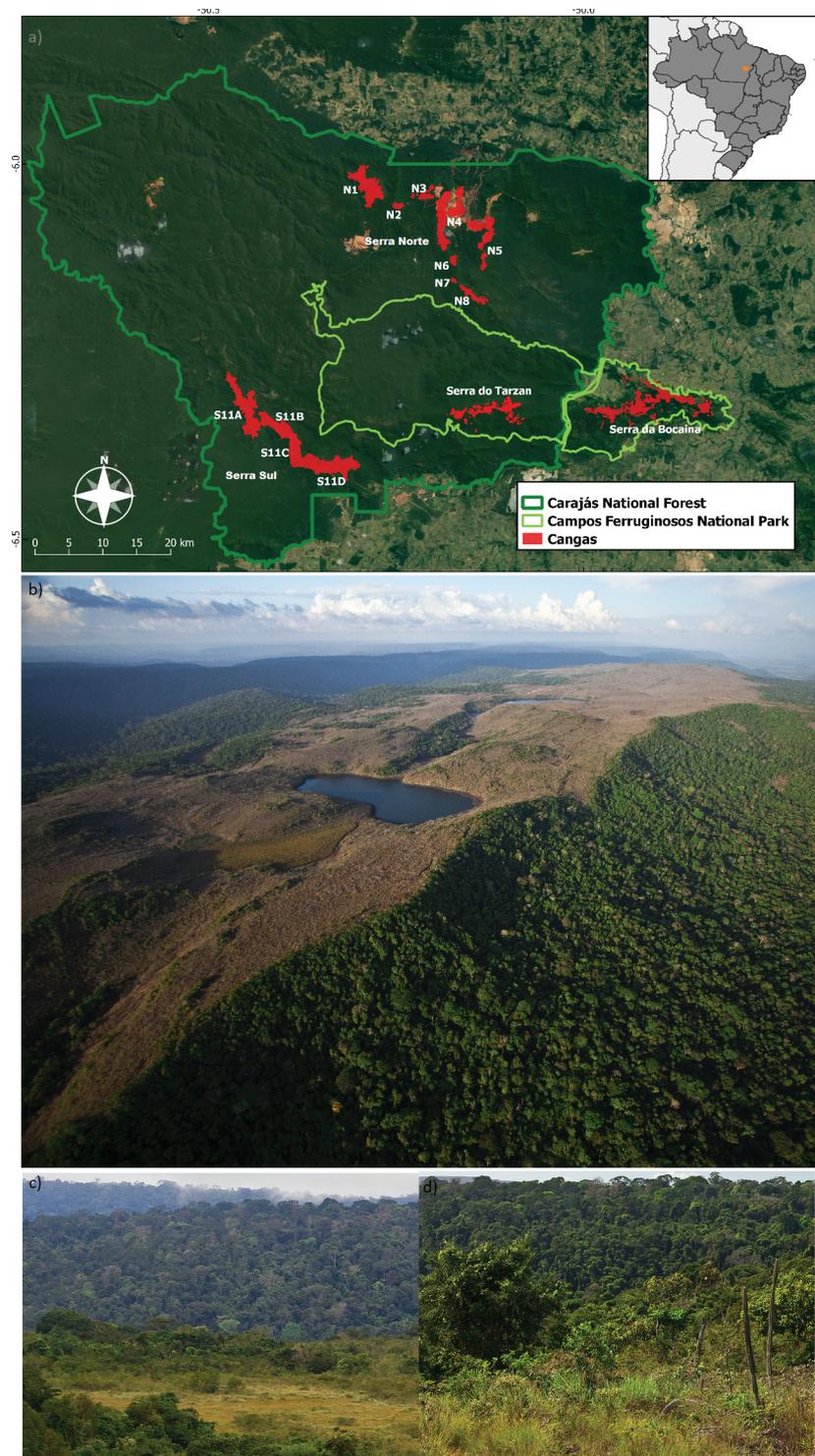
Fig. 1. (A) Canga outcrops in the Carajás National Forest and the Campos Ferruginosos National Park (Pará, Brazil). The six cangas where bees were collected are N2, N8, S11A, B, C, and Bocaina. The acronyms N and S refer to Serra Norte and Serra Sul, respectively. (B) Aerial photo showing the striking view of a canga outcrop surrounded by pristine Amazon forest. (C and D) Views of canga vegetation (Photos: João Rosa).

6 areas), totaling 336 h of collection (48 h × 7 mo). 4) Bait traps (Fig. 2D): these traps are widely used and specifically designed for sampling males of the Euglossini tribe (Hymenoptera: Apidae) tribe (Krug and Alves-dos-Santos 2008). They are made of plastic bottles (bottles made of polyethylene terephthalate or PET bottles) with four openings and remained in the cangas for 8 h (6 a.m. to 2 p.m.). To attract the Euglossini bees, we used four different artificial essences: eucalyptol, vanillin, eugenol, and methyl salicylate. Sets of four traps were used in each point (point 0, 300, 600, and 900 m) totaling 16 units in each canga (Storck-Tonon et al. 2009). The bottles contained different essences and were placed 5 m apart. They were tied in the bushes at a height of approximately 1.5 m above the ground. On average, there were 48 h of collection per month (8h × 6 areas), totaling 336 h of collection (48 h × 7 mo).

Table 1. Abundance, richness, and Shannon diversity of bee species collected in six cangas in the eastern Amazon

	Carajás National Forest					Campos Ferruginosos National Park
	Serra Sul			Serra Norte		Serra da Bocaina
	S11A	S11B	S11C	N2	N8	
Size (ha)	1,527	844	626	86	34	2,145
Isolation (m)	32,192			14,212	14,212	25,570
Abundance	214	339	297	415	217	309
Richness	47	47	49	67	44	48
Diversity	3.0	2.5	2.9	3.2	3.0	2.3

The area of each canga is shown in hectares. Isolation (in meters) was measured considering the minimum distance between the studied cangas. The measurements for the cangas in Serra Sul are equal because the three cangas are contiguous; the isolation values for the cangas in Serra Norte are also equal because N2 and N8 are the closest each other.

Fig. 2. Methods for sampling bees: (A) Entomological net; (B) Trap nest; (C) Pan trap; and (D) Bait trap.

All collected bees were identified by specialists (B.W.T.C., J.E.S.J., and R.L.R.) with the support of a stereo microscope and taxonomic keys (e.g., Silveira et al. 2002, Nemésio and Ferrari 2011, Santos Júnior et al. 2015) and deposited in the Museu Paraense Emílio Goeldi (MPEG, Pará, Brazil).

Statistical Analyses

To evaluate the representativeness of the sampling methods, species rarefaction/extrapolation curves were computed for each method and for all methods pooled based on Hill numbers (iNEXT R package; Chao et al. 2014, Hsieh et al. 2016), which also calculate the diversity of bees at the study sites using the Shannon index.

We compared the bee species composition among sites using the unweighted pair group method with arithmetic mean (UPGMA) as the aggregation algorithm for the Bray–Curtis dissimilarity index (Legendre and Legendre 2012). The Bray–Curtis index compares two species in terms of minimum abundance between sites and the value ranges from zero to one, which facilitates comparison. The UPGMA takes into account differences in measures of dissimilarity, regardless of how the original data was. Therefore, we used the cophenetic correlation coefficient to evaluate the difference between the estimated cluster and original dissimilarities as a measure of efficiency of the clustering method. This approach is often used to better understand the structure and relationships in the data, and a common way to suggest a specific number of clusters is to visually inspect the produced dendrogram (e.g., Borges et al. 2017, Devecchi et al. 2020, see also Legendre and Legendre 2012). However, here we used three methods to infer the optimal number of clusters to minimize that subjectivity: the elbow, silhouette, and gap statistic methods. The statistical analyses were conducted in R (R Core Team 2018) using the vegan (Oksanen et al. 2018) and factoextra (Kassambara and Mundt 2018) packages.

We also verified if bee dissimilarity was explained by the isolation of canga patches using the Mantel test, also implemented in the vegan package. To assess the relationship between area and bee richness, bee abundance, and bee diversity (Shannon index), we performed linear regression.

Results

Canga Bee Diversity

A total of 1,705 specimens belonging to 118 species and 37 genera were captured in all surveyed areas (Supp Table S1 [online only]). The Apidae family presented the highest number of species (95), followed by Halictidae (21), and Megachilidae (2) (Supp Table S1 [online only]). The highest values of abundance, richness, and Shannon diversity were recorded in N2 (Table 1).

A total of 37 species (31.1%) of orchid bees (Euglossini) was collected; this group was the most abundant, with 1,203 individuals collected (70.6%) (Supp Table S1 [online only]). Species from four genera were collected: 26 species of *Euglossa* Letreille, 1802 (Hymenoptera: Apidae), 1802, five of *Eulaema* Lepeletier, 1841 (Hymenoptera: Apidae), four of *Eufriesea* Cockerell, 1908 (Hymenoptera: Apidae), and two of *Exaerete* Hoffmannsegg, 1817 (Hymenoptera: Apidae). Considering all surveyed areas, *Eulaema nigrita* Lepeletier, 1841 (Hymenoptera: Apidae) was the most abundant species (478 individuals; 28% of total collection), followed by *El. cingulata* (Fabricius, 1804) (Hymenoptera: Apidae) (250; 14.7%) and *El. meriana* (Olivier, 1789) (Hymenoptera: Apidae) (125; 7.3%).

Stingless bees (Hymenoptera: Apidae: Meliponini) represented the highest number of species (38 species; 32.7%) and were the second most abundant group (332 specimens; 19.5%) (Supp Table S1 [online only]). Seventeen genera were collected; *Trigona* Jurine, 1807 (Hymenoptera: Apidae) presented the highest number of species (11 species), followed by *Melipona* Illiger, 1806 (Hymenoptera: Apidae) (five species). *Trigona recursa* Smith, 1863 (Hymenoptera: Apidae), *T. pallens* (Fabricius, 1798) (Hymenoptera: Apidae), and *Scaptotrigona xanthotricha* (Hymenoptera: Apidae) were the most abundant species, with 72, 30, and 25 specimens collected, respectively.

With the use of bait traps, 1,269 specimens corresponding to 60 different species were collected. As expected, most of the species collected with bait traps were from Euglossini (1,196 specimens). *Eulaema* was the genus most abundantly collected (867 specimens) with this methodology. However, 17 species of Meliponini bees and five species of Augochlorini were also collected. Of the four essences used, eucalyptol was the most attractive (582 specimens; 33 species). Vanillin facilitated the capture of 320 specimens and 25 species; methyl salicylate, 188 specimens and 29 species; and eugenol, 179 specimens and 22 species.

The use of entomological nets resulted in the capture of 364 specimens corresponding to 56 different species. Most of the species collected with this method belong to the Meliponini tribe (32 species).

The use of pan traps allowed the capture of bees that are difficult to collect (43 specimens; 25 species). Most of the species collected by the pan traps were from the Augochlorini, Emphorini, Halictini, Megachilini, Meliponini, and Xylocopini tribes.

Nest traps captured only 27 specimens of two species (*Centris analis* (Fabricius, 1804) (Hymenoptera: Apidae) and *Euglossa townsendii* Cockerell, 1904 (Hymenoptera: Apidae). *Centris analis* was exclusively collected by the nest traps.

The species accumulation curves for the bait traps and for the total survey effort were the closest ones to reach stabilization, but it would still be necessary to conduct a supplementary effort to record all bee species occurring in the cangas of Carajás (Fig. 3). The data from the entomological net methodology produced the curve that was closest to that of the total bee sample, showing that it is a particularly efficient methodology at capturing a diverse representation of species, even if the specimen count was low.

Bee Species Community Composition

The optimal number of clusters indicated by the methods mentioned earlier (the elbow, silhouette, and gap statistic methods) was three (Fig. 4): one cluster contained the S11A, S11C, and N8 cangas, another contained S11B and Bocaina, and one contained N2 only. According to the cophenetic correlation coefficient, the dissimilarity indicated in the dendrogram represents 70% of the actual dissimilarity in the Bray–Curtis index values.

Data regarding the isolation of each canga can be found in Table 1. Similarity in the bee communities was not explained by the distance between cangas ($P = 0.19$, $R = 0.22$). Of the total number of species collected, eight were common in the six areas, seven were collected exclusively in S11A, 10 were collected exclusively in S11B, four were collected exclusively in S11C, 11 were collected exclusively in Bocaina, 15 were collected exclusively in N2, and three were collected exclusively in N8 (Supp Table S1 [online only]). The results obtained corroborated our hypothesis that forest probably is not a barrier to bee movement.

Relationships Between Bee Richness, Abundance, and Diversity and Canga Size

We found no significant relationships between canga size and richness ($R^2 = 0.07$, $P = 0.3$), abundance ($R^2 = -0.23$, $P = 0.8$), or Shannon diversity ($R^2 = 0.41$, $P = 0.1$) (Fig. 5). Interestingly, our results also showed that small areas of canga harbor similar values of bee diversity when compared with the largest areas sampled (Fig. 5). Overall, these results also corroborate our main hypothesis that forest probably represents no barrier to bee movement.

Discussion

Our study is the first one describing and evaluating the bee diversity of open and isolated areas in the cangas within Amazon forest. We found no effect of area and distance on the diversity and abundance of bees considering the six cangas analyzed using standardized sampling methods. Our species accumulation curve suggested that additional sampling effort are still a necessary further step.

We surveyed a total of 118 bee species, which is a similar figure found in a previous study that analyzed the bees in four 'campos rupestres' in the state of Minas Gerais (south-eastern Brazil) at a higher altitude (>800 m); authors have found between 115 and 141 species in each studied area (Azevedo et al. 2008). Another study analyzed the bee species occurring in the same type of open areas ('campos rupestres') in Ouro Preto (Minas Gerais; 1,230 m altitude) using only entomological nets to collect the bees on flowers and found 46 species (Araújo et al. 2006). However, in addition to the fact that the biomes are different and contain different species of bees, the different methodological procedures (transect size, types of traps, sampling effort) of those studies preclude
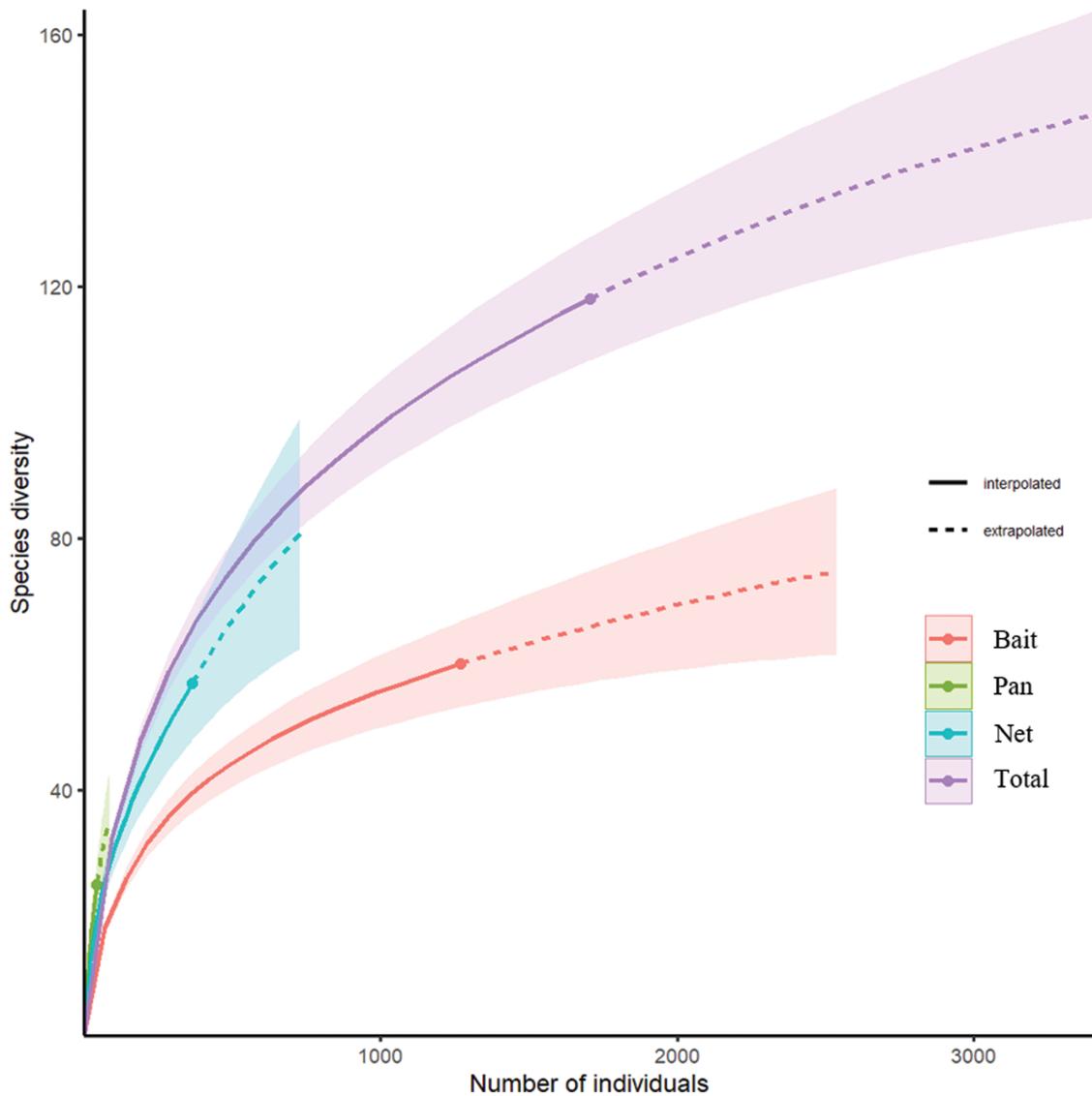
Fig. 3. Species accumulation curve for the bait trap, pan trap, entomology net, and the all methods together, except nest trap.
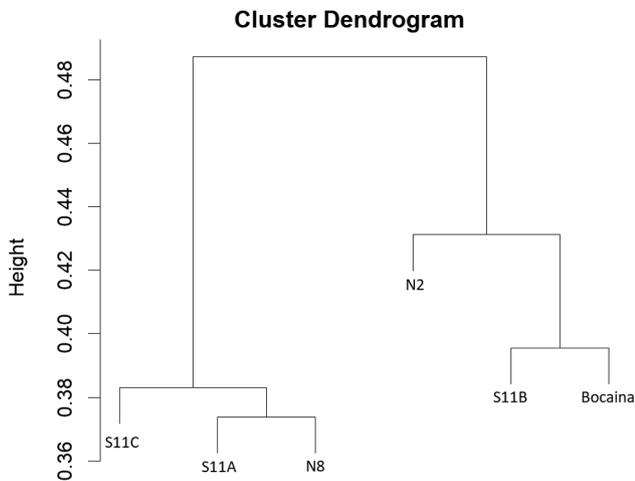

Fig. 4. Bray-Curtis clustering of bee species composition in cangas.

comparisons and reinforce the importance of using standardized survey methods.

As expected, our results showed that most Euglossini bees were attracted by bait traps. Previous studies have showed that orchid bees, the most abundant group of bees, inhabit densely forested environments (Ducke 1902, Braga 1976, Roubik and Ackerman 1987, Oliveira and Campos 1995, Nemésio and Silveira 2007) and are able to fly long distances (Pokorny et al. 2015). Therefore, this great diversity of species associated with great flight capacity, allowed that bees of this tribe to be abundantly collected in areas of canga. Stingless bees were the second most diverse group and were mainly collected by entomological nets, followed by bait traps. Stingless bees constitute a diverse group of highly eusocial bees that occur throughout tropical regions (Michener 2007). Entomological nets are useful for capturing species of this group since stingless bees are the main visitors of numerous flowering plants in the tropics and likely the principal pollinators of many of them (Heard 1999). Among the four methodologies applied to collect bees, the efficiency
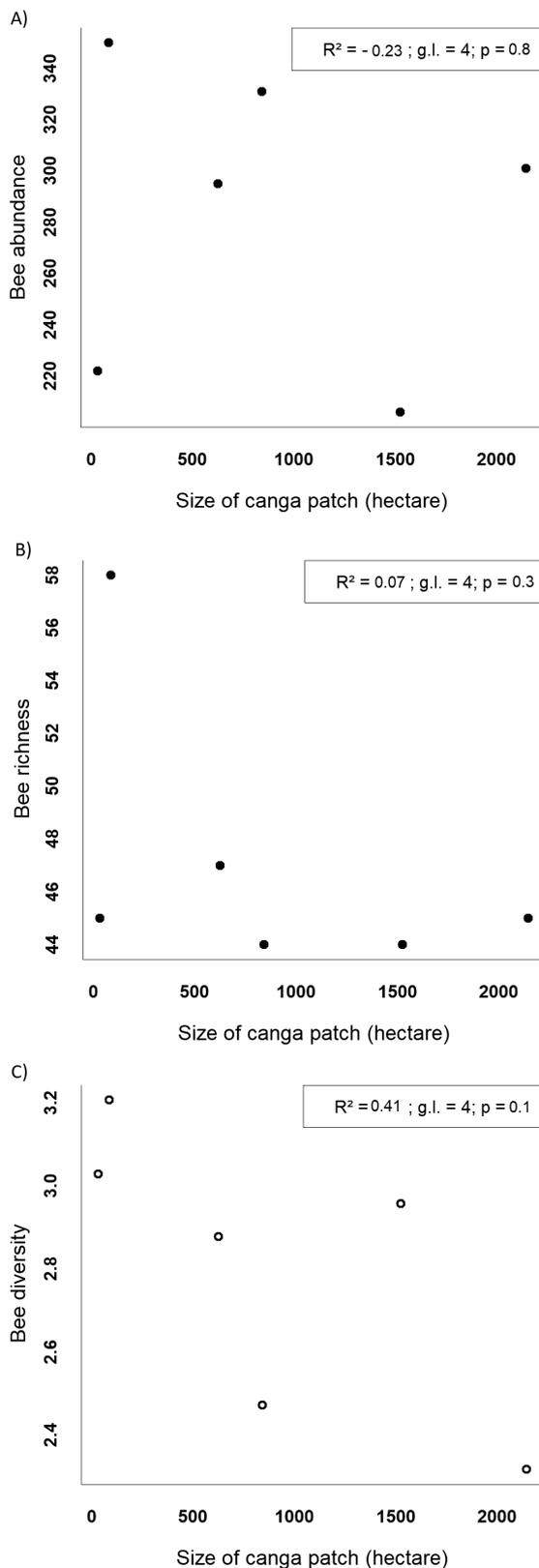
Fig. 5. Linear regressions of (A) richness, (B) abundance, and (C) Shannon diversity of bees and canga area (hectares).

of pan traps is the only one not well studied in tropical forests, but may be dependent on the local vegetation type, water availability, and both type and placement of the traps (Gonçalves et al. 2012).

In addition, the exposure time of pan trap can be a factor in low bees' capture, especially on tropical forests with high rates of daily precipitation. Previous studies have reached different conclusions about the performance of this last sampling method, and some of them showed its success (Krug and Alves-Dos-Santos 2008, Lebuhn et al. 2013, Ramírez-Freire et al. 2014) or its poor performance (Gonçalves et al. 2012). The efficiency of nest traps in capturing bees was low probably due to the high abundance of nesting sites found in the well-preserved forests located around cangas. There are no large trees in the canga areas, which is mostly occupied by herbs and shrubs. Moreover, it seems unlikely that bee species that build their nest in the soil can find suitable soil conditions in the cangas. The shallow soil rich in iron ore is difficult to excavate and can reach high temperatures under high solar incidence. Therefore, it is likely that bees use cangas mainly for exploring food resource and not for nesting.

The species of bees in Carajás formed three groups with little difference between them and without geographic agreement. This finding contradicts island biogeography theory predicting that the largest and nearest areas would present more similar communities compared to smaller areas (MacArthur and Wilson 1967). Additionally, the canga patches size did not explain the bee richness and abundance. These results suggest that the Amazon forest is not a barrier to the bees found in the study area. Forested areas, for example, did not impede the gene flow of a Morning Glory plant species from cangas and genetic diversity was not affected by the size of the areas (Lanes et al. 2018). One possible explanation for this finding is that the homogeneity of the forest areas that surround the cangas represents a suitable habitat for most Amazon bee species. They can live in the forest, finding floral and nest resources in the dense vegetation, also using the areas of cangas to collect nectar and pollen. One could expect that the largest and nearest cangas of Serra Sul and Bocaina would present more similar communities when compared with smaller cangas of Serra Norte, according to the main predictions of island biogeography theory (MacArthur and Wilson 1967), but this was not supported by our data. Most bee species collected in this study does not seem to be specialist in the canga habitat; in fact, most of the bees collected presents broad geographical distribution, and provably none is restricted to the study area. Moreover, forest habitats present lower solar radiation exposure and lower precipitation impact than open areas of cangas, which could offer milder conditions to bees, and wide opportunities to find nesting sites. Probably, the vast majority of bees make their nests in the forest areas that surround the canga areas, especially those species that nest on ground (such as *Geotrigona* Moure, 1943 (Hymenoptera: Apidae); Camargo and Pedro 2013) and on large tree trunks (such as *Melipona* species; Camargo and Pedro 2013). The Euglossini tribe is also well known as forest bees (Dressler 1982, Roubik and Hanson 2004). This probably also explain why small cangas close to pristine forest presented high bee diversity, as specially observed in the canga N2. This area showed a particularly high diversity of bees, exhibiting the highest number of exclusive species, despite being the second smallest canga and completely surrounded by forest. Other recent work conducted on the same cangas of Carajás showed that size and isolation do not explain the structure of bee-plant interaction networks (Pinto et al. in press), reinforcing the idea that forest does not seem to be a barrier to the movement of bees.

Open areas can offer an important complementary site for bee foraging, as previously noted (Azevedo et al. 2008). A preliminary study analyzing 118 plant species in the cangas of Carajás showed that 80% are pollinated by animals (Giannini et al. 2017). More

recently, a total of 856 species of seed plants were recorded in the cangas of Carajás (Mota et al. 2018), and a new study based on pollination syndromes that analyzed 771 of those cangas' plant species showed that 50% rely mostly on bees as their main pollinators (Pinto et al. in press). Thus, the cangas of Carajás likely provide complementary food resources.

However, we show that the data produced here need to be complemented, and future work should be conducted in order to increase the sampling effort and reinforce the results obtained. New areas inside cangas could be sampled, which would increase the knowledge about bee community. Moreover, the forest around cangas could also be surveyed, in order to compare both bee communities occurring on forest and cangas.

Our study is the first one to address bee community in the open areas within Amazon forest, and that the forest probably does not act as a barrier to bee movement. However, new bee surveys are necessary to complement the sampling effort. The cangas offer a complementary habitat with a rich flora for the bees to find their food resources, although most likely they depend primarily on the forests for their nesting. The effort to address the current gap in knowledge about bees occurring on Amazon is an important step to achieve robust data for helping biodiversity conservation (Green et al. 2005, Loh et al. 2005) and restoration (Montoya et al. 2012).

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Table S1. Bee species collected on cangas located on two protected areas in the Eastern Amazon.

Acknowledgments

Data Accessibility Statement

All relevant data are within the manuscript and its Supporting Information files.

References Cited

Allan, E., P. Manning, F. Alt, J. Binkenstein, S. Blaser, N. Blüthgen, S. Böhm, F. Grassein, N. Hölzel, V. H. Klaus, *et al.* 2015. Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. Ecol. Lett. 18: 834–843.

Araújo, V. A., Y. Antonini, and A. P. Araújo. 2006. Diversity of bees and their floral resources at altitudinal areas in the Southern Espinhaço Range, Minas Gerais, Brazil. Neotrop. Entomol. 35: 30–40.

Azevedo, A. A., F. A. Silveira, C. M. L. Aguiar, and V. S. Pereira. 2008. Fauna de abelhas (Hymenoptera, Apoidea) nos campos rupestres da Cadeia do Espinhaço (Minas Gerais e Bahia, Brasil): riqueza de espécies, padrões de distribuição e ameaças para conservação. Megadiversidade. 4: 127–157.

Boff, S., A. Soro, R. J. Paxton, and I. Alves-dos-Santos. 2014. Island isolation reduces genetic diversity and connectivity but does not significantly elevate diploid male production in a neotropical orchid bee. Conserv. Genet. 15: 1123–1135.

Borges, S. H., M. P. Santos, L. Soares, and A. S. Silva. 2017. Avian communities in the Amazon cangas vegetation: biogeographic affinities, components of beta-diversity and conservation. Anais da Academia Brasileira de Ciências 89: 2167–2180.

Borges, R. C., K. Padovani, V. L. Imperatriz-Fonseca, and T. C. Giannini. 2020. A dataset of multi-functional ecological traits of Brazilian bees. Sci. Data 7: 120.

Braga, P. I. S. 1976. Atração de abelhas polinizadoras de Orchidaceae com auxílio de iscas-odores na campina, campinarana e floresta tropical úmida da região de Manaus. Ciência e Cultura. 28: 767–773.

Camargo, J. M. F., and S. E. M. Pedro. 2013. Meliponini Lepeletier, 1836. *In* J. S. Moure, D. Urban, and G. A. R. Melo (eds.), Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region—online version. http://www.moure.cria.org.br/catalogue. Accessed 27 April 2019.

Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84: 45–67.

Devecchi, M. F., J. Lovo, M. F. Moro, C. O. Andrino, R. G. Barbosa-Silva, P. L. Viana, A. G. Giulietti, G. Antar, M. T. C. Watanabe, and D. C. Zappi. 2020. Beyond forests in the Amazon: biogeography and floristic relationships of the Amazonian savannas. Bot. J. Linn. Soc. 193(4): 478–503.

Dressler, R. L. 1982. Biology of the orchid bees (Euglossini). Annu. Rev. Ecol. Syst. 13: 373–394.

Ducke, A. 1902. As espécies Paraenses do gênero Euglossa. Boletim do Museu Paraense 3: 561–577.

Eisenhauer, N., A. Bonn, and C. A Guerra. 2019. Recognizing the quiet extinction of invertebrates. Nat. Commun. 10: 50.

Frankham, R., J. D. Ballou, K. Ralls, M. Eldridge, M. R. Dudash, C. B. Fenster, R. C. Lacy, and P. Sunnucks. 2017. Genetic management of fragmented animal and plant populations. Oxford University Press. Oxford Scholarship Online. doi: 10.1093/oso/9780198783398.001.0001.

Giannini, T. C., A. M. Giulietti, R. M. Harley, P. L. Viana, R. Jaffe, R. Alves, C. E. Pinto, N. F. O. Mota, C. F. Caldeira Jr., V. L. Imperatriz-Fonseca, *et al.* 2017. Selecting plant species for practical restoration of degraded lands using a multiple-trait approach. Austral. Ecol. 42: 510–521.

Gonçalves, R. B., E. F. Santos, and C. F. Scott-Santos. 2012. Bees (Hymenoptera: Apoidea: Apidae) captured with Malaise and pan traps along an altitudinal gradient in the Parque Estadual da Serra do Mar, Ubatuba, São Paulo, Brazil. Chek List. 8: 53–56.

Green, R. E., A. Balmford, P. R. Crane, G. M. Mace, J. D. Reynolds, and R. K. Turner. 2005. A framework for improved monitoring of biodiversity: responses to the World Summit on Sustainable Development. Conserv. Biol. 19: 56–65.

Hatfield, J. H., M. L. Harrison, and C. Banks-Leite. 2018. Functional diversity metrics: how they are affected by landscape change and how they represent ecosystem functioning in the tropics. Curr. Landscape Ecol. Rep. 3: 35–42.

Heard, T. A. 1999. The role of stingless bees in crop pollination. Annu. Rev. Entomol. 44: 183–206.

Hill, J. L., and P. J. Curran. 2001. Species composition in fragmented forests: conservation implications of changing forest area. Appl. Geogr. 21: 157–174.

Hsieh, T. C., K. H. Ma, and A. Chao. 2016. iNEXT: An R package for interpolation and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7: 1451–1456.

Júnior, J. E. S., F. R. Santos, and F. A. Silveira. 2015. Hitting an unintended target: phylogeography of *Bombus brasiliensis* Lepeletier, 1836 and the first new Brazilian bumblebee species in a century (Hymenoptera: Apidae). PLoS One 10: e0125847.

Kassambara, A., and F. Mundt. 2018. factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.7. https://CRAN.R-project.org/package=factoextra

Klein, A. M., B. E. Vaissière, J. H. Cane, I. Steffen-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proc. Biol. Sci. 274: 303–313.

Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, E. Ockinger, M. Pärtel, J. Pino, *et al.* 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol. Lett. 13: 597–605.

Krug, C., and I. Alves-dos-Santos. 2008. O uso de diferentes métodos para amostragem da fauna de abelhas (Hymenoptera: Apoidea), um estudo em floresta ombrófila mista em Santa Catarina. Neotrop. Entomol. 37: 265–278.

Lanes, É. C., N. S. Pope, R. Alves, N. M. Carvalho Filho, T. C. Giannini, A. M. Giulietti, V. L. Imperatriz-Fonseca, W. Monteiro, G. Oliveira, A. R. Silva, *et al.* 2018. Landscape genomic conservation assessment of a narrow-endemic and a widespread morning glory from Amazonian savannas. Front. Plant Sci. 9: 532.

Lebuhn, G., S. Droege, E. F. Connor, B. Gemmill-Herren, S. G. Potts, R. L. Minckley, T. Griswold, R. Jean, E. Kula, D. W. Roubik, *et al.* 2013. Detecting insect pollinator declines on regional and global scales. Conserv. Biol. 27: 113–120.

Legendre, P., and L. F. Legendre. 2012. Numerical ecology. Elsevier, Amsterdam.

Loh, J., R. E. Green, T. Ricketts, J. Lamoreux, M. Jenkins, V. Kapos, and J. Randers. 2005. The Living Planet Index: using species population time series to track trends in biodiversity. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 360: 289–295.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Marinho, D., D. B. Muniz, and G. G. Azevedo. 2018. Nesting biology of three Megachile (Hymenoptera: Megachilidae) species from Eastern Amazonia, Brazil. Rev. Bras. Entomol. 62: 97–106.

Michener, C. D. 2007. The bees of the World, 2nd ed. Johns Hopkins University Press, Baltimore, MD.

Montgomery, A., R. R. Dunn, R. Fox, E. Jongejans, S. R. Leather, M. E. Saunders, C. R. Shortall, M. W. Tingley, and D. L. Wagner. 2020. Is the insect apocalypse upon us? How to find out. Biol. Conserv. 241: 108327.

Montoya, D., L. Rogers, and J. Memmott. 2012. Emerging perspectives in the restoration of biodiversity-based ecosystem services. Trends Ecol. Evol. 27: 666–672.

Mota, N. F. O., M. T. C. Watanabe, D. C. Zappi, A. L. Hiura, J. Pallos, R. S. Viveros, A. M. Giulietti, and P. L. Viana. 2018. Amazon canga: the unique vegetation of Carajás revealed by the list of seed plants. Rodriguesia 69: 1435–1488.

Nemésio, A., and R. R. Ferrari. 2011. Species of Euglossa (Glossura) and E.(Glossuropoda)(Hymenoptera: Apidae: Euglossina) occurring in the Amazon, including new records for Brazil. Zootaxa 2885: 1–13.

Nemésio, A., and F. A. Silveira. 2007. Orchid bee fauna (Hymenoptera: Apidae: Euglossinae) of Atlantic forest fragments inside an urban area in southeastern Brazil. Neotropical Entomol. 36: 186–191.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, *et al.* 2018. Vegan: community ecology package. R package version 2.5–6. https://CRAN.R-project.org/package=vegan.

Oliveira, M. L., and L. A. O. Campos. 1995. Abundância, riqueza e diversidade de abelhas Euglossinae (Hymenoptera: Apidae) em florestas contínuas de terra firme na Amazônia central, Brasil. Rev. Brasil Zool. 12: 547–556.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos. 120: 321–326.

Pinto, C. E., M. Awade, M. T. C. Watanabe, R. M. Brito, W. F. Costa, U. M. Maia, V. L. Imperatriz-Fonseca, and T. C. Giannini. 2020. Size

and isolation of naturally isolated habitats do not affect plant-bee interactions: A case study of ferruginous outcrops within the eastern Amazon forest. PLoS ONE 15(9): e0238685. doi:10.1371/journal.pone.0238685.

Pokorny, T., D. Loose, G. Dyker, J. J. G. Quezada-Euán, and T. Eltz. 2015. Dispersal ability of male orchid bees and direct evidence for long-range flights. Apidologie. 46: 224–237.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 27 April 2018.

Ramírez-Freire, L., G. Alanís-Flores, R. Ayala-Barajas, C. Velazco-Macías, and S. Favela-Lara. 2014. El uso de platos trampa y red entomológica en la captura de abejas nativas en el estado de Nuevo León, México. Acta Zoológica Mexicana. 30: 508–538.

Roubik, D. W., and J. D. Ackerman. 1987. Long-term ecology of euglossine orchid-bees (Apidae: Euglossini) in Panama. Oecologia. 73: 321–333.

Roubik, D. W. and P. E. Hanson. 2004. Abejas de orquídeas de la América tropical: biología y guía de campo. Editorial INBio. Santo Domingo de Heredia, San José, 370 pp.

Sahoo, P. K., J. T. Guimarães, P. W. Souza-Filho, M. S. Silva, R. O. Silva, Júnior, G. Pessim, B. C. Moraes, P. F. Pessoa, T. M. Rodrigues, M. F. Costa, *et al.* 2016. Influence of seasonal variation on the hydro-biogeochemical characteristics of two upland lakes in the Southeastern Amazon, Brazil. An. Acad. Bras. Cienc. 88: 2211–2227.

Sakagami, S., S. Laroca, and J. Moure. 1967. Wild bee biocenotics in São José dos Pinhais (PR), South Brazil, preliminary report. J. Fac. Sci. Hokkaido Univ. 16: 253–291.

Silva, M. F. F., R. S. Secco, and M. G. Lobo. 1996. Aspectos ecológicos da vegetação rupestre da Serra dos Carajás, Estado do Pará, Brasil. Acta Amaz 26: 17–44.

Silveira, F. A., G. A. Melo, and E. A. Almeida. 2002. Abelhas brasileiras. Sistemática e Identificação, p. 253. Fundação Araucária, Belo Horizonte.

Soro, A., J. J. G. Quezada-Euan, P. Theodorou, R. F. Moritz, and R. J. Paxton. 2017. The population genetics of two orchid bees suggests high dispersal, low diploid male production and only an effect of island isolation in lowering genetic diversity. Conserv. Genet. 18: 607–619.

Souza-Filho, P. W., E. B. de Souza, R. O. Silva Júnior, W. R. Nascimento, Jr, B. R. Versiani de Mendonça, J. T. Guimarães, R. Dall'Agnol, and J. O. Siqueira. 2016. Four decades of land-cover, land-use and hydroclimatology changes in the Itacaiúnas River watershed, southeastern Amazon. J. Environ. Manage. 167: 175–184.

Souza-Filho, P. W. M., T. C. Giannini, R. Jaffé, A. M. Giulietti, D. C. Santos, W. R. Nascimento, Jr, J. T. F. Guimarães, M. F. Costa, V. L. Imperatriz-Fonseca, and J. O. Siqueira. 2019. Mapping and quantification of ferruginous outcrop savannas in the Brazilian Amazon: a challenge for biodiversity conservation. PLoS One 14: e0211095.

Storck-Tonon, D., E. F. Morato, and M. L. Oliveira. 2009. Fauna de Euglossina (Hymenoptera: Apidae) da Amazônia Sul-Ocidental, Acre, Brasil. Acta Amazonica 39: 693–706.

Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. Science. 292: 281–284.

Wilson, M. C., X. Y. Chen, R. T. Corlett, R. K. Didham, P. Ding, R. D. Holt, M. Holyoak, G. Hu, A. C. Hughes, L. Jiang, *et al.* 2016. Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landscape Ecology. 31: 219–227.