The impact of agricultural colonization and deforestation on stingless bee (Apidae: Meliponini) composition and richness in Rondônia, Brazil

J. Christopher BROWN[1], Marcio Luiz de OLIVEIRA[2]

[1] Department of Geography, University of Kansas, 1475 Jayhawk Blvd., 223, Lawrence, KS 66045, USA. jcbrown2@ku.edu

[2] Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, Caixa postal 2223, Manaus, AM 69060-971, Brazil. mlolivei@inpa.gov.br

Short title: Deforestation and stingless bees

Abstract

Stingless bees were collected throughout the state of Rondônia in the southwestern Brazilian Amazon for one year. The impact of agricultural colonization and subsequent deforestation on species composition and richness is explored. Deforestation, around each of 187 sample sites, was characterized at meso, micro, and local spatial scales. At the micro-scale, deforestation was measured using a data layer generated by satellite remote sensing and analyzed with the assistance of a geographic information system. We report perhaps the greatest richness of stingless bees ever recorded in the tropics, collecting 9,555 individuals from 98 species of stingless bees. Ten of these are new species and 16 were first-ever records for Rondônia. Five new species were scientifically described from the study. We report statistical relationships between deforestation and species richness at all spatial scales of analysis, and we tentatively identify species that appear to be especially sensitive to deforestation.

Key-words: social bees; redundancy analysis; forest fragmentation; land use; Amazon

1. INTRODUCTION

Bees are considered to be some of the most important pollinators of both wild and cultivated plants (Michener 2000), responsible for pollinating at least 60% of the nearly 1500 species cultivated by humans (Garófalo 2009). Stingless bees have attracted the attention of researchers interested in the effects of deforestation and forest fragmentation on pollinators (Liow et al. 2001, Cairns et al. 2005, Villanueva-Gutiérrez et al. 2005, Ricketts et al. 2008, Brosi 2009, Brosi et al. 2007, 2008, Freitas et al. 2009, Fierro et al. 2012). The main conclusion from this work is that tropical deforestation affects greatly the abundance, diversity and composition of stingless bees, and that deforestation could have serious consequences for the pollination and reproduction of both native and cultivated plants. Few studies exist, however, from the Brazilian Amazon, in spite of its putative high diversity of bees (Oliveira et al. 1995, Oliveira 2001, Dick 2001, Brown and Albrecht 2001).

In Brazil, stingless bees comprise one of the country's most species-rich groups, with 192 recorded species (Silveira et al. 2002); the actual number of species is likely much higher, considering how poorly sampled bees are in the Brazilian Amazon (Overal 2001, Baccaro et al. 2008). There is a nearly forty-year gap in the generation of knowledge of these bees in the region. That gap runs from the last study of Adolpho Ducke (Ducke 1925), who pioneered the study of these bees in the region, to expeditions that began in the region in 1963 (Camargo 1994). There are also major spatial gaps in our knowledge. Most of the work cited above was carried out along the margins of major rivers (Camargo 1994) and near major urban areas (Oliveira et al. 1995, Oliveira 2001), with almost no work in the immense areas between rivers, near headwaters or in mountainous areas (Oliveira et al. 2010). While our knowledge of these bees is relatively sparse in the region, deforestation due to development of infrastructure, mining, and agricultural colonization continues throughout the Amazon, in spite of notable decreases in Brazil and several other Amazonian countries from 2005-2010 (Colombia, French Guiana, and Peru actually saw increases in deforestation rates) (PRODES 2011, RAISG Amazonian Network of Georeferenced Socio-Environmental Information 2013).

The landscape of the state of Rondônia, Brazil, the focus of the present study, is emblematic of the effects of development in the Brazilian Amazon on forest cover and biodiversity. Up until the 1960s, the forests of Rondônia were relatively intact, the main forest type being "tropical moist forest" in the northern half of the state and "subtropical moist forest" according the Holdridge Life-Zones map (International Institute for Applied Systems Analyses (IIASA 1989). Agricultural colonization projects were established there beginning in the 1960s. Ouro Preto do Oeste (hereafter "Ouro Preto") was the first colonization project established in Rondônia, it is one of thirteen meso-regions of the state surveyed for the present study, and unlike the other regions, it was chosen for intensive monthly sampling during the study period for the following reasons. Ouro Preto's landscape is a microcosm of the range of deforestation landscapes found across the state, with environments representing some of the longest settlement history in the state and some much more recent, leading to areas ranging from very high to very low levels of deforestation, respectively (Figure 1). In general, then, farm lots within 16 km of the main BR-364 highway bisecting the state from southeast to northwest had very little forest remaining by 1996, when the present study was conducted, in contrast, there is much more forest remaining on farm lots in Mirante da Serra near the indigenous reserve and the national park. Other reasons for choosing Ouro Preto for year-round surveys include its convenient central location in the state, and availability of laboratory space. Regular sampling in Ouro Preto during the entire study allowed us to test whether seasonality needs to be taken into account when conducting more rapid, one-time surveys of stingless bees in the state.

The present study examines the relationship between deforestation, caused by modern settlement in the Amazon, and the composition and richness of stingless bees.

2. MATERIALS AND METHODS

2.1. Dependent and independent variables

Species composition and richness data (dependent variables) for each collection location were grouped in three main ways for analysis, each way representing the impact of colonization and subsequent deforestation at meso, micro, and local-scales. Deforestation levels at the meso and micro-scale (independent variables) were determined by overlaying points recording the latitude and longitude of the sample locations over a data layer depicting forest and non-forest cover available from PRODES (Amazon Deforestation Calculation Program) from INPE (National Institute of Space Research) (Câmara et al. 2006). Circles with radii of numerous distances (.5, 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10 km) were drawn around each collection point, and the percent area deforested within each circle was calculated using ArcGIS (ESRI). (As shown below, the .5 km deforestation parameter was determined to be the most significantly related to the species variables, so it was used as the main deforestation variable at the meso-region level.)

Every meso-region of the state surveyed that has undergone modern agricultural settlement was characterized in terms of the year it received its first major influx of agricultural colonists, allowing two main types to be recognized: those settled 1980 and before are considered “older,” and those 1981 and after are considered “newer”. These designations were made based on the history of each colonization area provided by Fearnside (1989). Meso-regions are labeled “areas of preservation” when they are under some form of permanent state or federal protection and have not undergone any modern agricultural settlement (indigenous reserves, extractive reserves, state and national parks).

1. Meso-regional scale: This scale of analysis allows comparisons of species composition and richness among colonization areas of different ages and to compare these with meso-regions that have experienced little or no impact of modern settlement, because older areas have been disturbed for longer periods of time and have higher levels of deforestation and higher forest fragmentation.
2. Micro-regional scale: This scale allows for analysis of impacts in the more immediate area of collection locations. Deforestation variables were generated for each sample location as described above using the latitude and longitude of sample locations and a data layer from INPE depicting forest and non-forest cover in 1997.
3. Local scale: This scale of analysis accounts for the immediate landcover of the collection location at the sub-location level. Each sub-location was characterized as closed canopy forest or open vegetation formations, which included savanna, secondary vegetation, cropland, and pasture.

Statistical analyses involved a number of different techniques to explore the relationships among deforestation, species richness and composition at the above spatial scales. These included scatterplots, ordination (conducted using Canoco 5), Ordinary Least Squares regression, and by comparing the summary statistics of all locations within particular ranges of deforestation level using boxplots. Regarding ordination, detrended correspondence analysis of species composition across sample locations indicated the use of linear methods, so redundancy analysis was used for all ordination. Before conducting the ordination, rare species were removed from the dataset by excluding species that appeared in less than 5% of sample sites. For analyses involving just the Ouro Preto meso-region, this left 62 species, and for the state-wide dataset, this left 63 species.

2.2. Choice of collection locations

Fieldwork was sponsored by the Second Approximation Project of the Socio-Economic-Ecological Zoning of Rondônia, funded by the World Bank and executed by Tecnosolo/DHV Consultants. Selection of locations for sampling species composition and richness had to take into account the main access ways to the priority areas of the research for the zoning exercise: the federal highways BR-364, and 429, secondary roads, and the Ouro Preto and Cautário Rivers (Figure 1). Collections were most often done where access was easiest. Factors such as heavy rains, poor road conditions, and the need to obtain permission from landowners to enter properties often limited access. Examination of the number and spatial distribution of sample locations throughout the state, however, suggests that the data are unprecedented in spatial coverage in comparison to other stingless bee surveys, and they are representative of the state and its varied forest cover conditions. It bears repeating that the meso-region of Ouro Preto was surveyed every month of the study to allow for testing the hypothesis that seasonality must be taken into account when conducting stingless bee surveys. Other meso-regions of the state were surveyed only once.

<Figure 1 about here>

2.3. Collection methods

From September 1996 to September 1997, six locations were sampled each month in the Ouro Preto meso-region. Each month, a separate meso-region of the state was selected for a survey expedition that lasted from 5-10 days. Independent of the location, collections were always made beginning after 7 h and ending before 18 h. Bees were sampled in a total of 187 locations during the study. In each meso-region sampled, care was taken to ensure that collections were done at least 1.5 km apart in an effort to decrease the chances of capturing bees from the same colony. The latitude and longitude of every location was recorded with the aid of a Garmin 45 GPS.

Collections were standardized in order to allow for comparisons across locations. Each location was divided into three sub-locations:

1. Open area sub-location 1 (open canopy): landcover in these areas was characterized by crops, savanna, pasture, or fallow, secondary vegetation. The nearest forest was approximately 250-500 m away, forming in most cases the very back of a farm lot. Each of three collectors then located a bush, with each bush separated by 50 m along a straight line parallel to the forest edge. Each collector took a plastic spray bottle filled with a 1:1 mixture of honey and water and

sprayed an approximately 0.25 m^2 surface area on each bush with 15 pumps of the spray bottle. Then, collectors waited at each bush for 60 minutes and captured bees as they arrived. This is a variation on a common technique first published by Wille (1962).

2. Forest area sub-location (closed canopy): collectors penetrated the nearest forest area by approximately 250 m, repeating the same honey and water spray procedure described above. With an hour spent collecting in both sub-location 1 and 2, two hours were spent at spray locations as a whole in each sample location.

3. Open area sub-location 2 (open canopy): collectors returned to the initial open area sub-location and collected bees randomly found on flowers in the open.

The order of these collections was altered each time in order to generate heterogeneity in the relationship between landcover and the timing of the collections. At all times and in all landcovers, bees were opportunistically collected when found on the following substrates: mud, human skin (collecting sweat), water, feces, and carcasses. When discovered, bees were collected at their nest entrances.

2.4. Mounting and identification of specimens

After capture, bees were killed with ethyl acetate and placed in labeled plastic film canisters lined with tissue paper. Samples were transported to Drs. João M. F. Camargo and Sílvia R. M. Pedro for species identification.

3. RESULTS

3.1. Overall species composition in Rondônia

The study resulted in collection of 9,555 individuals from 98 species of stingless bees, with 10 new species and 16 recorded for the first time ever in the state of Rondônia (supplementary material, Table A) (see Camargo and Pedro 2007). This diversity is very high in comparison to other surveys in the tropics (Table I). Five new species were scientifically described from the study: *Dolichotrigona mendersoni*, *D. browni*, *D. rondoni*, *Celetrigona hirsuticornis* and *Leurotrigona gracilis*. All indications are that *D. rondoni* is endemic to Rondônia (see Camargo and Pedro 2005). The other five new species are still waiting for description (supplementary material, Table A).

<Table I about here>

3.2. State-wide species composition by capture/substrate type

Most of the species in the current study were found on many different substrates (Table A, supplementary materials). The exceptions are *Duckeola ghilianii*, *Frieseomelitta flavicornis*, *F. portoi*, *Lestrimelitta limao*, *Melipona illustris*, *Schwarzula coccidophila*, and some species of *Paratrigona*. Moreover, many *Trigonisca*, all relatively rare in the collection, were found on no more than two substrates.

3.3. Ouro Preto meso-region analysis

In 73 locations sampled during the year in the Ouro Preto meso-region, there were 82 species of stingless bees (Figure 2), which equals almost 74% of the total species (98) that were found in the entire state of Rondônia. In an analysis of sampling effort and species accumulation, it was determined that sampling in five locations led to collection of 70% of the species that would be found in the Ouro Preto meso-region.

<Figure 2 about here>

In figure 3a the number of species found at each location is plotted with the distance in kilometers the location lies along the road that runs perpendicular to the BR-364, from Ouro Preto (km 0) southwest through the urban centers of Nova União and Mirante da Serra all the way to the border with the area of Uru-Eu-Wau-Wau Indigenous Reserve and the Pacaás Novos National Park (km 84). There is great variation in the number of species per location, independent of the distance from the BR-364. A Lowess smoother drawn through the scatter plot (Velleman 1980), however, shows a very slight trend toward more species with greater distance from the BR-364. An ordinary least squares regression line fit to the data shows a statistically significant slope of positive correlation, but the slope is very slight. The effect of deforestation on species richness is most visible when plotting richness and the percent of area deforested within 0.5 km of the sample location (Figure 3b), independent of distance from the BR-364. Redundancy analysis (RDA) of the deforestation variables from all the distances indicated that deforested area within .5 km of the sample location had the greatest fit of all the deforestation variables in characterizing species composition (Figure 3c), though the results are marginally significant. The first axis eigenvalue in the RDA was .0435 (Monte Carlo permutation test (499 permutations), F-ratio=2.8, p=.066). In forward selection using just the .5, 1, and 2 km deforestation variables, the .5 km variable explained 3.3% of species composition, and out of the three variables it contributed 56% to species variation (pseudo-F=2.4, p=.004)(Figure 3d).

<Figure 3 about here>

Data were grouped into collections made during the dry season (May-September) and those made during the wet season (October-April), and the null hypothesis that there is no difference in species richness between them was tested. A visual examination of box plots showing the distribution of data in both the wet and dry season shows there is no statistically significant difference between the groups, because the shaded areas of the box plots (marking 95% confidence intervals around the median) overlap one another (Figure 4).

<Figure 4 about here>

3.4. Meso-regional analysis

Because of logistical reasons, the number of locations sampled in each meso-region was variable. The most extreme cases are Ouro Preto with 73 locations and some samples taken near the BR-364 near Porto Velho with only 3 (Table II).

<Table II about here>

3.4.1. Species composition

The species found in each meso-region are listed in supplementary materials (Table B). 38 species appeared in 10 (2/3) of the 15 meso-regions sampled in the state, independent of the history of colonization or level of deforestation. 40 species were found in 5 (1/3) or less regions. Six of the least common species were found exclusively in areas of preservation and four exclusively in areas of newer colonization, and hence less deforested (supplementary materials, Table B).

3.4.2. Species richness

The highest mean bee species richness was found in Extrema, Machadinho-Cujubim, São Miguel do Guaporé, Campo Novo and Costa Marques, meso-regions of the state where we would expect to find a greater richness of species, given that they were colonized most recently and where deforestation levels are lower. In comparison, Linha D, Ouro Preto, Rolim de Moura, Chupinguaia and Pimenteiras all with a low mean number of species, were colonized much longer and thus have experienced much more deforestation. The difference between species richness found in older vs. newer settlements is statistically significant, as evidenced by the box plots in figure 5.

<Figure 5 about here>

There was an unexpected low of mean species richness in official environmental preservation areas (AP in figure 5): the Reserva Extrativista do Rio Cautário, the

Reserva Extrativista do Rio Ouro Preto, the Estação Ecológica Cuniã, and the Parque Estadual Guajará-Mirim.

3.5. Micro-regional analysis

3.5.1. Species composition

Sixty-one species (62%) were found at least once, no matter the level of deforestation, suggesting these bees may have some level of tolerance to deforestation and fragmentation of the landscape (supplementary materials, Table C). In contrast, twenty-seven species (27%) were the only species absent from highly deforested areas (80-100% deforestation) suggesting a susceptibility to deforestation. Redundancy analysis showed statistically significant explanation of the variation in species composition using dummy variables for the meso-region of each sample site and the .5 km deforestation variable as environmental variables (adjusted explained variation 3.5%; Monte Carlo permutation test results (499 permutations): first axis (pseudo F-ratio=4.4, p=.004) all axes (pseudo F-ratio=1.5, p=.002)(Figure 6). The .5 km deforestation variable by itself was insignificant (results not shown).

<Fig 6 about here>

3.5.2. Species richness

A scatterplot of the percent of area deforested within 0.5 km of the location of each sample site and species richness for all locations across Rondônia (Figure 7a) shows a similar situation to that found for the Ouro Preto meso-region (Figure 3). Results for the analyses performed using other radii (1, 2 km) were insignificant, suggesting that the bees respond to more local, less regional deforestation patterns (results not shown). This test matched the results for species composition found using redundancy analysis (Figure 3). There is a wide diversity of bees that can be found at each level of deforestation. There is, however, a slight trend toward decreasing diversity when deforestation percentage rises. The scatterplot shows a line fit to the data using Ordinary Least Squares regression, which is statistically significant ($p \leq .0001$). The data were then grouped into sample sites of four different deforestation levels (0 to <10%, 10 to <45%, 45 to <80%, 80 to 100%), with no significant differences among the groups (results not shown). A significant difference did appear, however, when a medium deforestation category was created from 10 to <80%, compared to the 0 to <10% and 80 to 100% categories (figure 7b).

<Figure 7 about here>

3.6. Local-scale analysis

3.6.1. Species composition

A total of 79 (80%) species were found in both open vegetation and closed canopy landcovers, seven only in closed canopy forest and eight only in open vegetation (Table D, supplementary material). Redundancy analysis of a dataset that considered each open and closed canopy collection as a separate sample (n=401) showed a significant difference in species composition between open and closed canopy sites (3% adjusted explained variation, all axis permutation test (Monte Carlo, 499 permutations, pseudo-F-ratio=13.5, p=0.004)(Figure 8).

<Figure 8 about here>

3.6.2. Species richness

Species mean richness was slightly higher in open canopy vs. closed canopy environments (8.6 vs. 7.5 species), but as shown in the accompanying box plots, there is no significant difference between the two distributions (Figure 9).

<Figure 9 about here>

We also analyzed a subset of our samples for only those bees found in nests at each location (Table E, supplementary materials). Seven species were found only under open canopy, 15 only in closed canopy environments, and nine in both closed and open canopy formations.

4. DISCUSSION

There are at least 12 bees that have been recorded in the state, but they were not found in the present study, in spite of the immense spatial coverage and number of locations sampled: *Lestrimelitta rufa, L. rufipes, L. maracaia, Melipona dubia, M. amazonica, Oxytrigona mulfordi, Plebeia alvarengai, Trigona lacteipennis, T. guianae, Trigonisca nataliae, T. pediculana* and *Scaptotrigona* sp. n. (Camargo and Pedro 2007).

Rondônia can be said now to have 110 species, known as one of the most species-rich and sampled in the tropics with respect to stingless bees. A discussion of potential taxonomic issues with our list of species can be found in supplementary materials. The large number of substrates examined for collecting in this study likely helped maximize the number of species found in each location, with nearly 80% of all species captured from flowers, honey baits, and on skin (collecting sweat) (Table A, supplementary materials).

The evidence for the impact of colonization and subsequent deforestation on stingless bees was most visible from the more intensive yearlong collection in the Ouro Preto meso-region. More species were found there than in any other meso-region, likely due to the large number of samples taken throughout the year. On the left side of figure 3a are data from collection sites that are closest to the BR-364 and the urban center of Ouro Preto. Thus, they are within the oldest areas of colonization, ones that consequently are the most deforested as well. From km 4 to km 32, the number of species tends to rise, indicating that with distance from the BR-364, the species richness rises. From km 32 to 60, however, richness decreases somewhat, which could be attributed to deforestation and urban impact, because km 40 is the center of the urban area of Nova União, and km 60 is Mirante da Serra. Past km 60 to km 84, the end of colonization and the border of the indigenous reserve and national park, richness tends to rise again, with three sites of very high richness at km 84. There was, however, a statistically significant relationship between species richness and deforestation within .5 km of the sample locations (Figure 3 a and b). The redundancy analysis bi-plot in figure 3d shows the 15 best-fitting species, with all but *Melipona fuliginosa* strongly negatively correlated with the deforestation variable, indicating sensitivity to higher levels of deforestation. The .5 km deforestation variable appears the most significantly related to species composition and richness (over other radii). We would expect a short-range variable like this to be significant given our understanding from the literature that stingless bee activity cannot be expected to extend greater than 2-3 km (Kerr et al. 1962, Roubik and Aluja 1983, Souza et al. 1996, Nogueira-Neto 1997: 89, Carvalho-Zilse and Kerr 2004, Kuhn-Neto et al. 2009). Our results from Ouro Preto also indicate species richness is not affected by seasonality, as evidenced by Figure 4. This matches our understanding that stingless bee nests are permanent and individuals are actively foraging throughout the year.

The meso-regional analysis showed that stingless bee richness is affected by deforestation in a statistically significant way, but not very substantively, with perhaps a few species less found on average between the most and least deforested sites across the state. Aggregating the numerical values to categorical levels of deforestation (high, medium and low) did show significantly higher richness at medium levels when compared with high and low levels (Figure 7). High and low levels of deforestation with similar richness are difficult to explain. The low level areas involve a significant number of samples from areas of preservation, where deforestation levels were near zero. Collections there did result in some sites with high richness, but many sites were very low, bringing down the mean. The low mean in the Estação Ecológica Cuniã, an official environmental preservation area, could be because of a strong cold front from Antarctica that penetrated the southern Amazon in June during the fieldwork. The temperature could have been outside the range of tolerance for the bees those days, explaining the low numbers found. The low mean species richness found in the other areas of preservation, however, was not related to any abnormal weather. One possible explanation for low richness is that in very large preserved areas, the sampling methods used simply were inadequate to detect the existing diversity. In smaller forested patches, the chances may be higher to find greater diversity. M.L. Oliveira (personal observation) found a similar situation when sampling orchid bees (Euglossini) in the region of Manaus, and J. M. F. Camargo (Unpubl. data) remarked that stingless bees in the Amazon express very patchy distribution, with many species concentrated in few places, leaving some larger areas with low diversity within forested areas.

The redundancy analysis at the meso-region level revealed some important results. The .5 km deforestation variable alone was insignificant in explaining species composition, unlike the case when only the Ouro Preto meso-region alone was analyzed. An ordination that included dummy variables for the meso-region of each sample site, however, was statistically significant (Figure 6), and showing the 20 best-fitting species in the species-environmental variables bi-plot showed a group of species highly negatively corrected to deforestation, indicating possible susceptibility to deforestation. Finally, the local-scale analysis showed no statistically significant difference in species richness, but redundancy analysis of species composition showed a statistically significant difference between closed and open canopy environments. An examination of the 20 best-fitting species along the horizontal axis allowed for identification of potentially susceptible species (Figure 8).

To sum up the effects of agricultural colonization and subsequent deforestation, we look to the redundancy analyses to identify particular species and groups that appear most strongly affected (Figures 3, 6, and 8). We start by selecting the best-fit species in each of the three ordinations, and from those selecting the most negatively correlated with the deforestation variable. We then list those species as a first cut of the most affected by deforestation. Relative susceptibility within this list can be further determined by seeing which species appear most frequently in the list across the ordinations.

Table III marks with an "x" the species that appear in the corresponding ordinations according to the above rules. It bears repeating that these ordinations are based on datasets that exclude rare species, so they are all species that are widespread in Rondônia and independent of the region in which they were found showed negative correlation with the .5 km deforestation variable and were mainly found in closed canopy environments.

Clearly, not all species known to prefer cavities in live trees are in our list of species most likely affected by deforestation. This may be because they were too rare in our survey to be included in the redundancy analyses or their presence has yet to be affected by deforestation. For any species to persist in an area undergoing deforestation, stingless bees must survive the physical destruction that occurs during tree felling, the initial burning of the trees, and subsequent burns, sometimes annual, especially in areas of cattle pasture. Bees that persist must have the ability immediately to rectify and rebuild nest architecture and then survive repeated burning and predation. As an example *M. seminigra abunensis* and *M. grandis* appears able to do this better than other *Melipona* species in the Ouro Preto meso-region, or perhaps these larger *Melipona* species respond to disturbance over a longer period of time (Brown and Albrecht 2001). We do not know whether the species and colonies found in open areas moved into those areas after disturbance, or whether they survived the disturbance. In the long term, species must survive potential isolation and inbreeding.

There appears to be a consensus that stingless bees are essentially a forest group, but as generalists, they are able to forage away from their nests into disturbed environments in many cases, as supported by our analysis of species composition in open and closed canopy environment. There are likely to be several species that can survive quite well in disturbed environments, the classic species in this case being *Tetragonisca angustula*; it is very common in disturbed areas in the Americas (Oliveira 2001, Fierro et al. 2012), and is even well adapted to urban environments where it is commonly found in buildings, wooden posts, walls, and it is widely managed for honey production. On the whole, it seems prudent to follow Brosi et al. (2008) and Brosi (2009) who recommend preservation of forest fragments wherever possible to maximize the possibility of colony survival.

Numerous questions remain for future research. It seems clear that stingless bee sampling is currently ineffective in very large, forested areas (Oliveira 2001). The bees may simply be easier to find and capture in deforested areas, so it would be helpful to understand better the spatial pattern of foraging by bees, perhaps by experimentation with managed colonies in forested areas and accompanying studies of pollen types found in honey throughout the year to determine the relative contributions of environments of various disturbance levels to colony survival. We also have little idea of how colonies survive the process of deforestation and subsequent burning of agricultural plots by settlers. It would seem plausible that maintenance of forest fragments is essential for stingless bee conservation, but future studies should attempt to determine what the minimum size and ideal spatial configurations are for species conservation.

It is our hope that this work brings greater attention to this group of bees as a resource that provides pollination services for both native and non-native plants and crops (Santos and Absy 2010, Rech and Absy 2011a and 2011b). These bees are affected by agricultural settlement and deforestation and we have an opportunity to plan for their conservation as areas undergo development in years to come.

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FIGURE CAPTIONS

Figure 1. Map of study locations and the meso-regions studied in the state of Rondônia, Brazil.

Figure 2. Stingless bee species accumulation curve, across 73 collection locations, during one year of sampling in Ouro Preto do Oeste meso-region, Rondônia, Brazil.

Figure 3. (a) Scatterplot of stingless bee species richness in each sample location vs. the distance of the location from the BR-364 highway, Ouro Preto meso-region, Rondônia, Brazil. (b) Number of species found in each location vs. the percent area deforested within 0.5 km of sample locations. Both linear regression lines are significant ($p \leq 0.0001$). (c) Bi-plot of species and .5 km deforestation variable, all species. (d) Bi-plot showing only the 15 best-fitting species (DolcLong-*Dolochotrigona longitarsis*, FrieSilv-*Frieseomelitta silvestrii*, MelBr-*Melipona brachychaeta*, MelpFulg – *Melipona fuliginosa*, MelpSchw-*Melipona schwarzi*, PartVici-*Partamona vicina*, PlbAffMn-*Plebeia* aff. *minima*, PlebKerr-*Plebeia kerri*, PlebMarg-*Plebeia margaritae*, PlebeSp1-*Plebeia* sp. 1, PlebeSp2-*Plebeia* sp. 2, SchwTimd-*Schwarzula timida*, TetrgSpN-*Tetragona* sp.n., TrigGrae-*Trigonisca graeffei*, TrigHirt-*Trigonisca hirticornis*,

Figure 4. Comparison of stingless bee richness during wet (w; n=38) and dry (d; n=35) seasons in Ouro Preto do Oeste meso-region in Rondônia state, Brazil. Shaded areas of box plots are 95% confidence intervals around the median.

Figure 5. Comparison of stingless bee species richness per sample location across type of meso-region in Rondônia state, Brazil. Shaded areas are 95% confidence intervals around the median. (AP n=54; newer n=31; older n=102). AP=Area of preservation; newer=meso-regions receiving greatest influx of migrants 1981 and later; older=meso-regions receiving greatest influx of migrants 1980 and earlier.

Figure 6. (a) Redundancy analysis species-environmental variables bi-plot of samples from all meso-regions (63 most common species, .5 km deforestation variable, and dummy variables for all meso-regions). (b) Plot from same analysis as a, but showing only the 20 species with the best fit; species arrows with dotted lines are the most negatively correlated to the .5 km deforestation variable. DolcLong-*Dolichotrigona longitarsis*, LeurMuel-*Leurotrigona muelleri*, MelBr-*Melipona brachychaeta*, MelpSchw-*Melipona schwarzi*, NannMeln-*Nannotrigona melanocera*, PartTest-*Partamona testacea*, PlbAffMn-*Plebeia* aff. *minima*, PlebeSp1-*Plebeia* sp. 1, PlebeSp2-*Plebeia* sp. 2, PtlLr-*Ptilotrigona lurida,* ScaptSp2-*Scaptotrigona* sp. 2, TetrAngs-*Tetragonisca angustula*, TetrDors-*Tetragona dorsalis*, TrigAmaz-*Trigona amazonensis*, TrgCilCl-*Trigona cilipes*, TrigChan-*Trigona chanchamayonensis*, TrigCras-*Trigona crassipes*, TrignSp2-*Trigona* sp. 2, TrignSp3-*Trigona* sp. 3, TrigTruc-*Trigona truculenta*,

Figure 7. Relationship of stingless bee species richness and deforestation across the state of Rondônia, Brazil. (a) Scatterplot of percent of area deforested within 0.5 km of sample points and species richness. Slope of ordinary least squares regression line is significant at $p \leq 0.0001$. (b) Summary statistics and box plots of distribution of data for

groups of deforestation level (low – 0<10%; medium – 10<80%; high – 80-100%). Shaded areas of box plots are 95% confidence intervals around the median.

Figure 8. Redundancy analysis species-environmental variable bi-plot of 401 sample sites of open vs. closed canopy collections. (a) all species, (b) 20 best-fitting species on horizontal axis. DolcLong-*Dolichotrigona longitarsis*, FrieTric-*Frieseomelitta trichocerata*, MelpGran-*Melipona grandis*, ParatSpN-*Paratrigona* sp. n. aff. *lineata*, PartNham-*Partamona nhambiquara*, PartVici-*Partamona vicina*, PlbAffMn-*Plebeia* aff. *minima*, PlebeSp1-*Plebeia* sp. 1, PlebeSp2-*Plebeia* sp. 2, PlebVari-*Plebeia variicolor*, ScauLati-*Scaura latitarsis*, ScauLong-*Scaura longula*, TetrClav-*Tetragona clavipes*, TetrGoet-*Tetragona goettei*, TetrAngs-*Tetragonisca angustula*, TetrWeyr-*Tetragonisca weyrauchi*, TrigAmaz-*Trigona amazonensis*, TrigCras- *Trigona crassipes*, TrigChan-*Trigona chanchamayoensis*, TrignSpN-*Trigona* sp. n.

Figure 9. Box plot and summary statistics of stingless bee species richness with sub-locations grouped by landcover type in Rondônia state, Brazil. Shaded areas of box plots are 95% confidence intervals around the median.

Table I. Comparison between the richness of stingless bees recorded in Rondônia state (Brazil) and other places in the Tropics.

Place	Number of species	area (km^2)	reference
Madagascar	4	587,041	Camargo and Pedro (1992)
New Guinea	5	462,840	Camargo and Pedro (1992)
Australia	8-10	7,692,024	Camargo and Pedro (1992)
Central Sumatra	24	473,000	Salmah et al. (1990)
Africa	50	30,221,532	Camargo and Pedro (1992)
Brazil: Manaus	54	11,401	Oliveira et al. (1995)
Brazil: Roraima	56	224,299	Oliveira et al. (2010)
French Guiana	69	83,846	Roubik (1989)
Brasil:Rondônia	93	237,576	This paper
Brasil:Ouro Preto do Oeste	82	3,150	This paper

Table II. Summary statistics for stingless bee species richness (r) within each meso-region in Rondônia state, Brazil.

Meso-region	Sample locations	Total r	Mean r	Median r	StdDev r	Min r	Max r
Campo Novo	5	43	18.2	16	7.40	11	27
Costa Marques	5	49	19.4	19	4.77	14	26
Extrema	5	52	21	20	7.87	10	30
Machadinho-Cujubim	10	61	21.1	20	10.86	5	37
São Miguel do Guaporé	6	54	18.8	17	10.26	5	36
Estação Ecológica Cuniã	14	35	8.9	8.5	3.75	3	15
Parque Estadual Guajará-Mirim	18	63	12.4	10.5	5.75	4	26
Reserva Extrativista do Rio Cautário	7	41	16.3	19	5.41	7	21
Reserva Extrativista do Rio Ouro Preto	15	56	12.9	13	7.96	2	30
Chupinguaia	8	37	12.1	12	7.62	4	22
Linha D	6	47	14.5	17	8.60	1	25
Ouro Preto	73	82	13.9	13	7.77	1	35
Pimenteiras	4	31	11.3	11.5	8.22	2	20
Porto Velho BR-364	3	22	9.7	9	9.02	1	19
Rolim de Moura	8	47	13.3	15	5.15	6	21

Light shading=newer settlement; dark shading=area of preservation; no shading=older settlements.

Table III. List of species appearing most negatively correlated to deforestation. "X" marks appearance of species in RDA bi-plots of corresponding figures.

Species name	Fig. 3	Fig. 6	Fig. 8
Dolichotrigona longitarsis	X	X	X
Frieseomelitta silvestrii	X		
Leurotrigona muelleri		X	
Melipona brachychaeta	X	X	
Melipona schwarzi	X	X	
Nannotrigona melanocera		X	
Partamona vicina	X		X
Plebeia aff. *minima*	X	X	X
Plebeia kerri	X		
Plebeia margaritae	X		
Plebeia sp. 1	X	X	X
Plebeia sp. 2	X	X	X
Plebeia variicolor			X
Scaptotrigona sp. 2		X	
Schwarzula timida	X		
Tetragona dorsalis		X	
Tetragona sp. n.	X		
Trigona crassipes		X	X
Trigona sp. n.			X
Trigonisca graeffei	X		
Trigonisca hirticornis	X		
Trigonisca sp. 2		X	
Trigonisca sp. 3		X	

Fig 1.

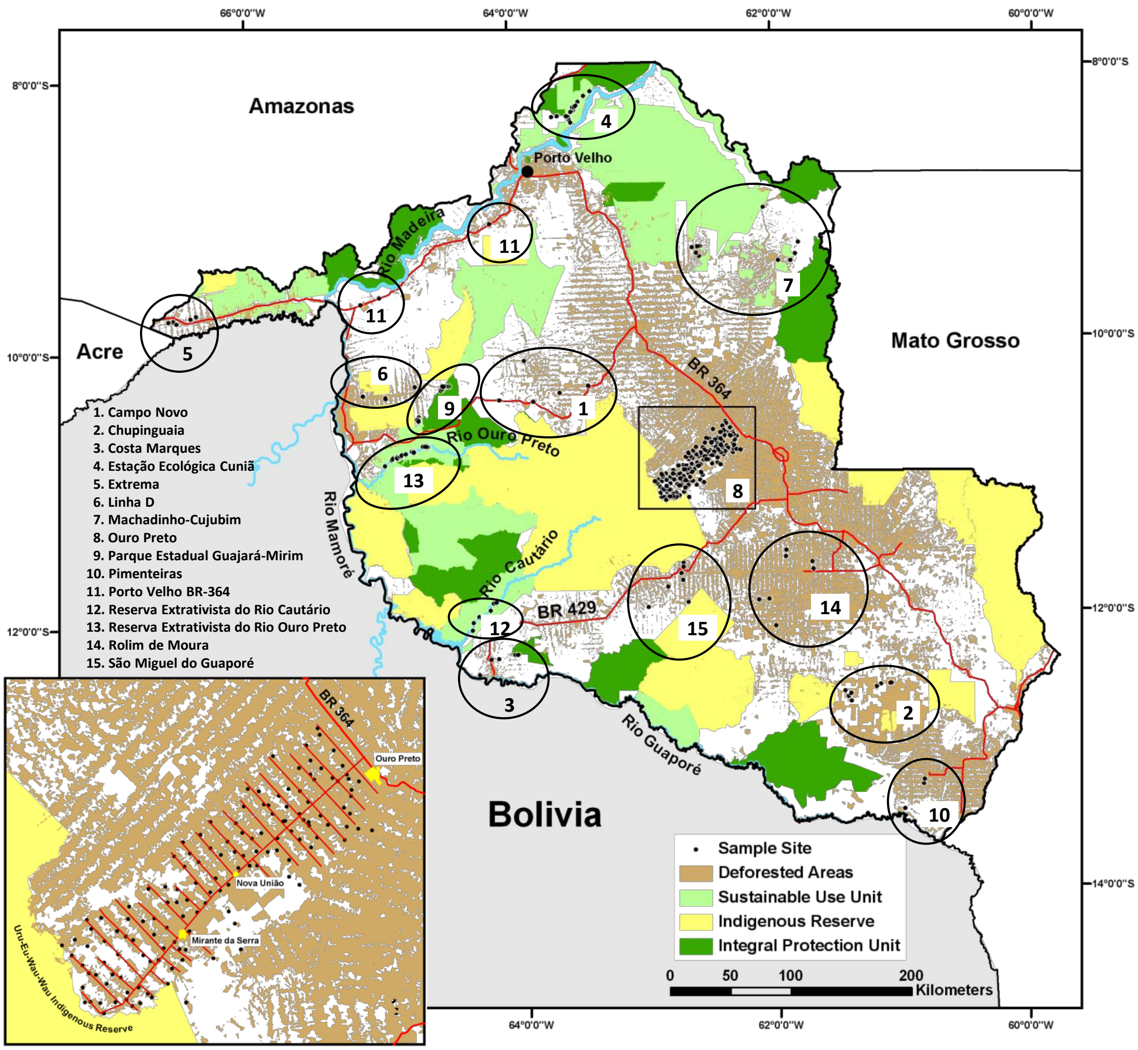

66°0'0"W
64°0'0"W
62°0'0"W
60°0'0"W
8°0'0"S
10°0'0"S
12°0'0"S
14°0'0"S
Amazonas
Porto Velho
Mato Grosso
Acre
Bolivia
Rio Madeira
Rio Ouro Preto
Rio Mamoré
Rio Cautário
Rio Guaporé
BR 364
BR 429
1. Campo Novo
2. Chupinguaia
3. Costa Marques
4. Estação Ecológica Cuniã
5. Extrema
6. Linha D
7. Machadinho-Cujubim
8. Ouro Preto
9. Parque Estadual Guajará-Mirim
10. Pimenteiras
11. Porto Velho BR-364
12. Reserva Extrativista do Rio Cautário
13. Reserva Extrativista do Rio Ouro Preto
14. Rolim de Moura
15. São Miguel do Guaporé
Sample Site
Deforested Areas
Sustainable Use Unit
Indigenous Reserve
Integral Protection Unit
0 50 100 200
Kilometers
Ouro Preto
Nova União
Mirante da Serra
Uru-Eu-Wau-Wau Indigenous Reserve

Fig 2.

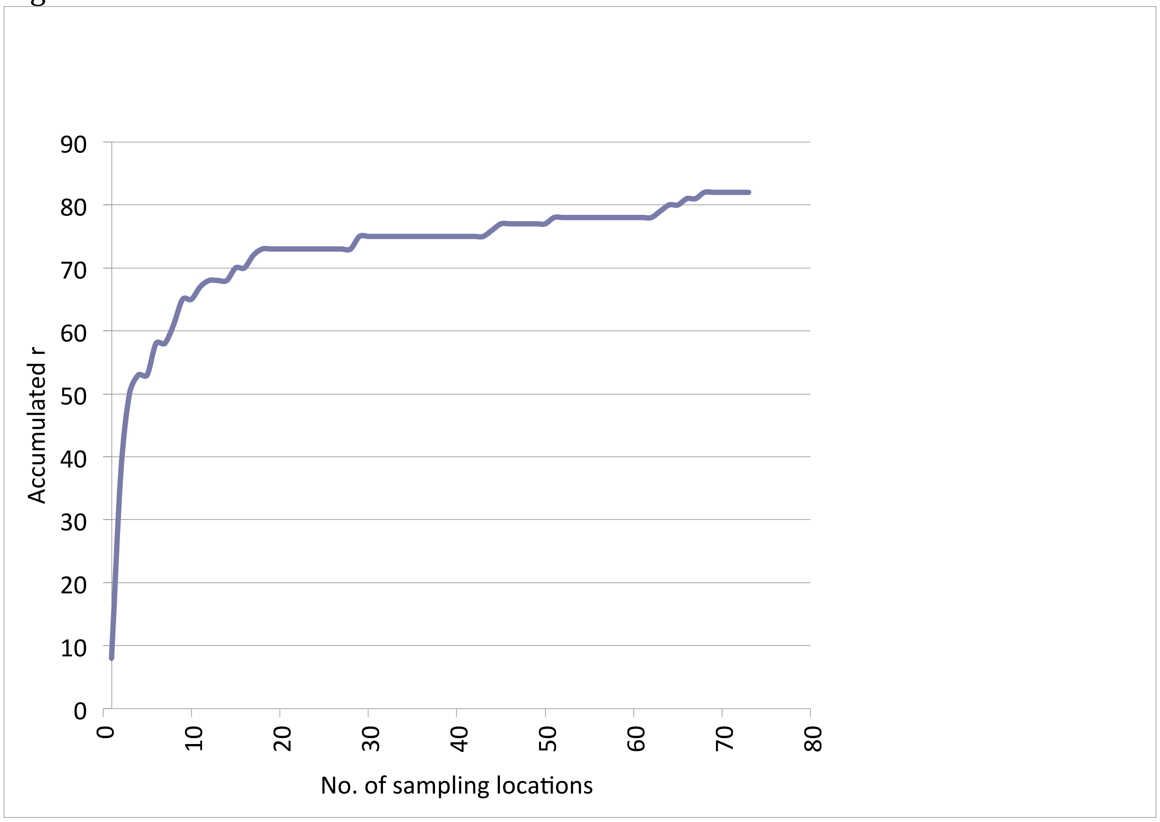
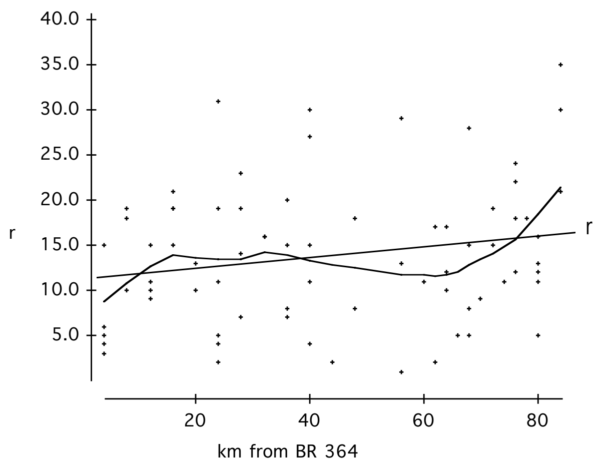
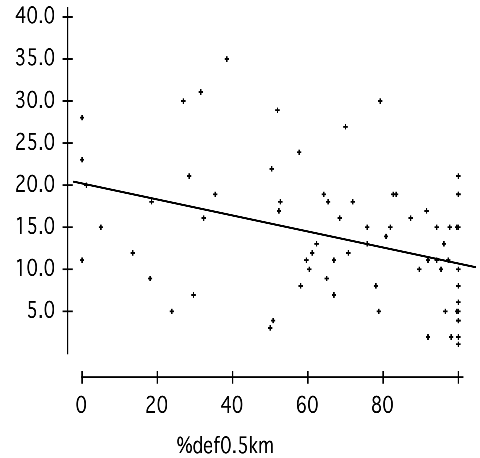

Accumulated r
No. of sampling locations
0
10
20
30
40
50
60
70
80
90

Fig 3.

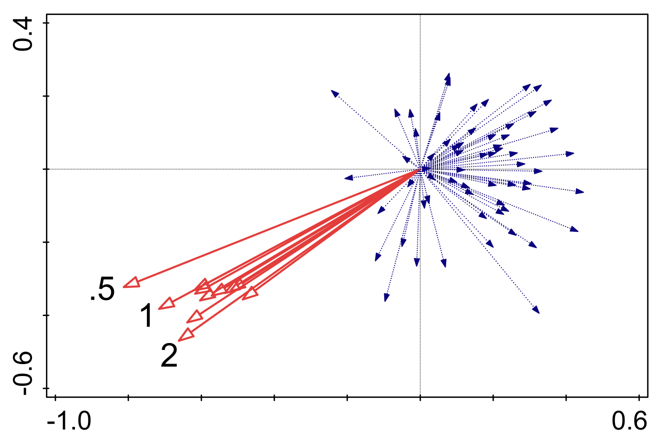
a


40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
r
r
20
40
60
80
km from BR 364

b


40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0
20
40
60
80
%def0.5km

c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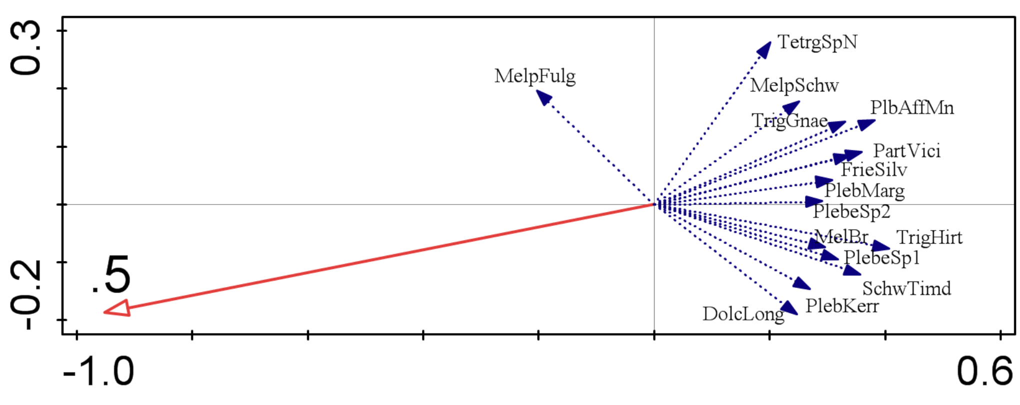
-0.6
-1.0
0.6
.5
1
2

d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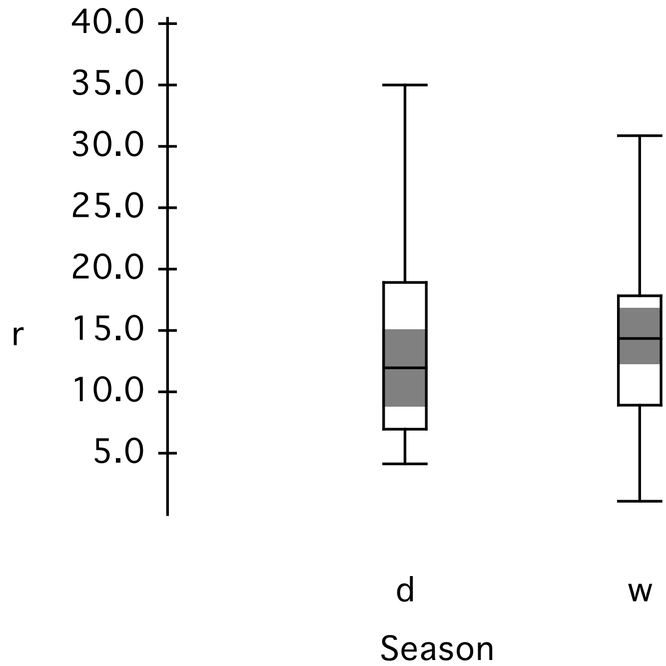
-1.0
0.6
.5
TetrgSpN
MelpFulg
MelpSchw
PlbAffMn
TrigGnae
PartVici
FrieSilv
PlebMarg
PlebeSp2
MelBr
TrigHirt
PlebeSp1
SchwTimd
PlebKerr
DolcLong

Fig 4.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35.0
30.0
25.0
20.0
15.0
10.0
5.0
r
d
w
Season

Fig 5.

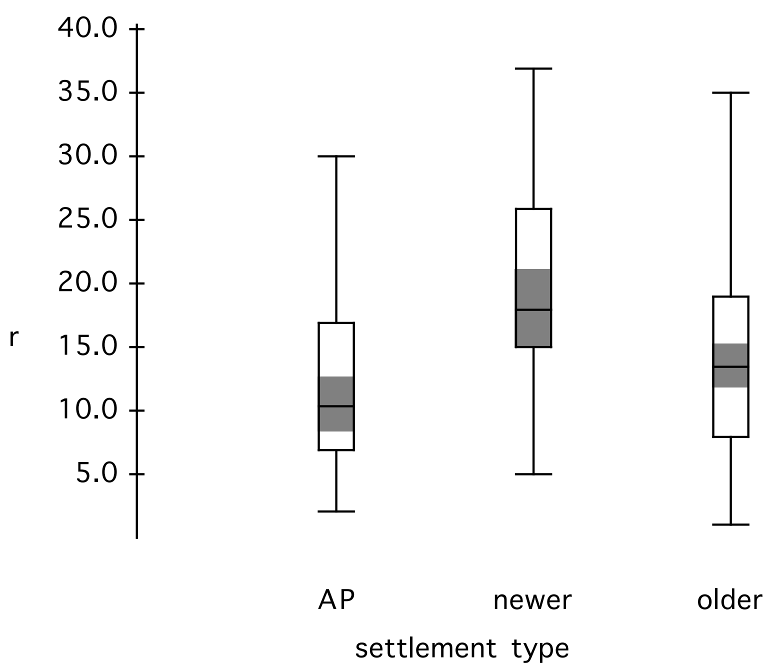
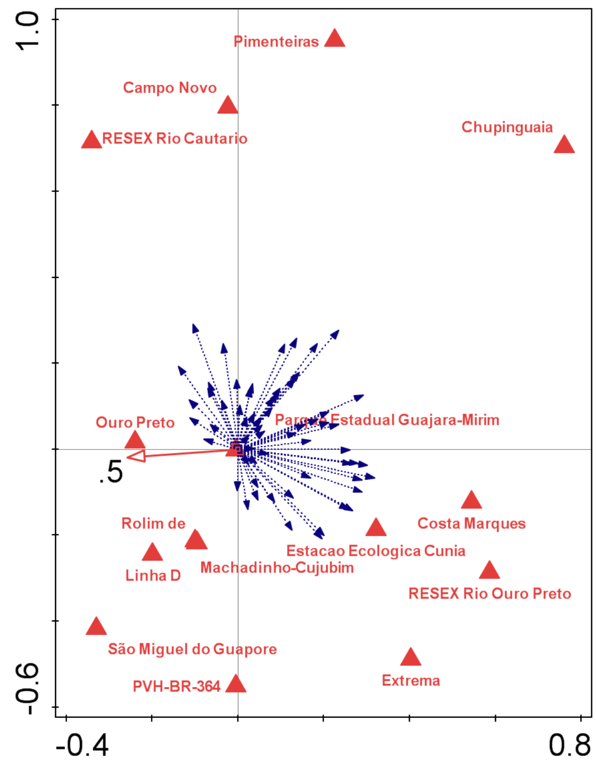

40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
r
AP
newer
older
settlement type

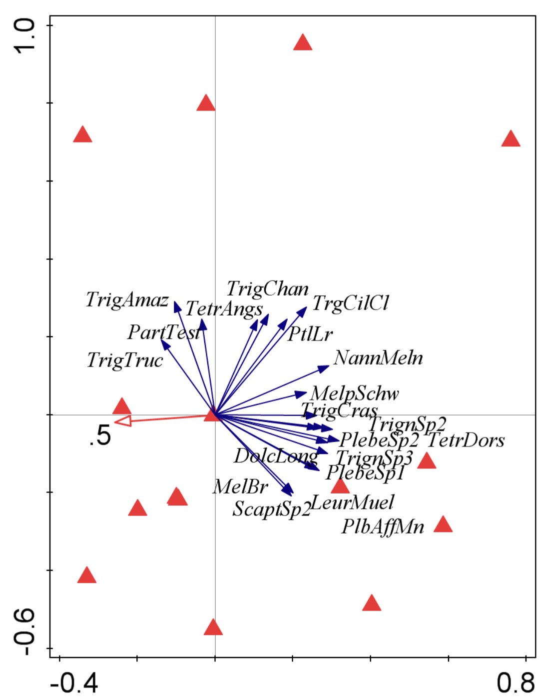
Fig 6.

a



1.0
-0.6
-0.4
0.8
.5
Pimenteiras
Campo Novo
RESEX Rio Cautario
Chupinguaia
Ouro Preto
Parque Estadual Guajara-Mirim
Rolim de
Linha D
Machadinho-Cujubim
Estacao Ecologica Cunia
Costa Marques
RESEX Rio Ouro Preto
São Miguel do Guapore
PVH-BR-364
Extrema

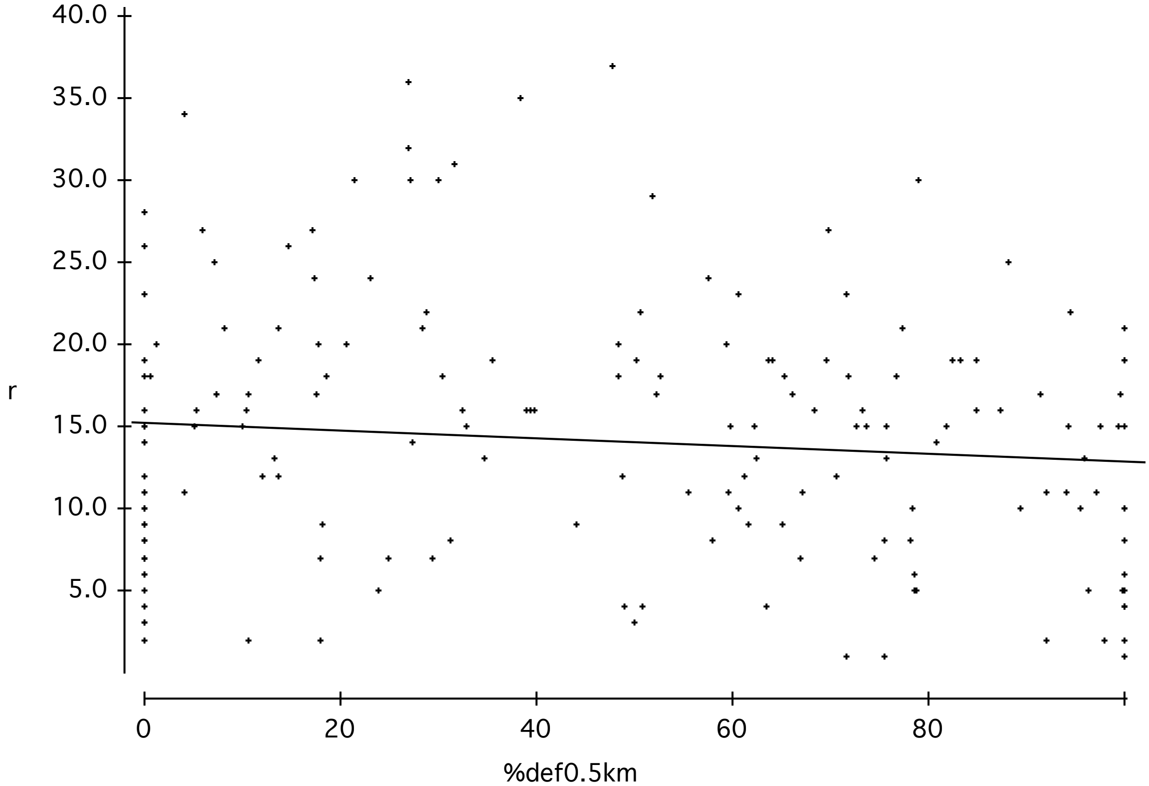
b



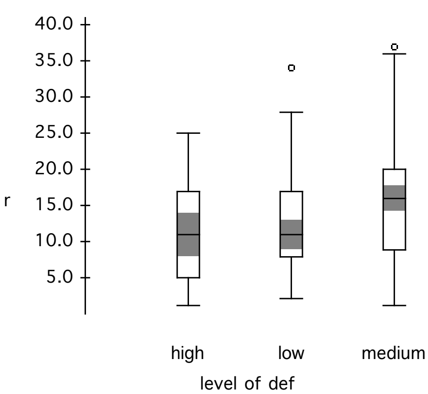
1.0
-0.6
-0.4
0.8
.5
TrigAmaz
TetrAngs
TrigChan
TrgCilCl
PartTest
PtlLr
TrigTruc
NannMeln
MelpSchw
TrigCras
TrignSp2
PlebeSp2
TetrDors
DolcLong
TrignSp3
PlebeSp1
MelBr
ScaptSp2
LeurMuel
PlbAffMn

Fig 7.

a



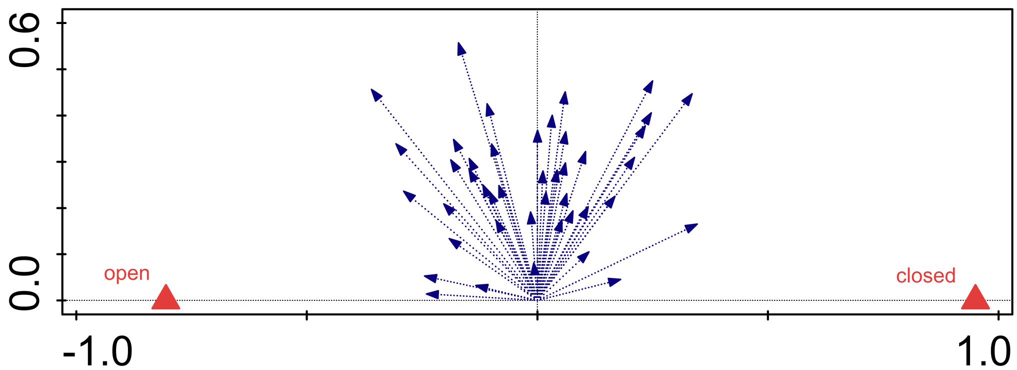
b



Group	Count	Mean	Median	StdDev	Min	Max
high	39	11.69	11	6.52588	1	25
low	50	12.90	11	7.14643	2	34
medium	98	15.86	16	8.24871	1	37

Fig 8.

a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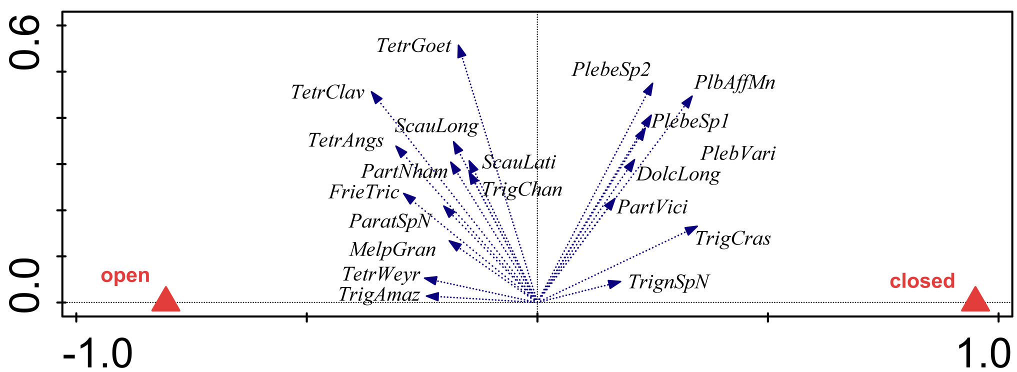
0.0
open
closed
-1.0
1.0

b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0.0
TetrGoet
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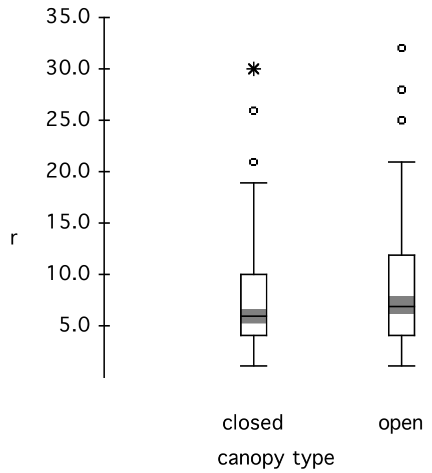
ScauLong
TetrAngs
PartNham
ScauLati
FrieTric
TrigChan
ParatSpN
MelpGran
TetrWeyr
TrigAmaz
PlebeSp2
PlbAffMn
PlebeSp1
PlebVari
DolcLong
PartVici
TrigCras
TrignSpN
open
closed
-1.0
1.0

Fig 9.



Group	Count	Mean	Median	StdDev	Min	Max
closed	184	7.52	6	5.22	1	30
open	217	8.55	7	5.78	1	32

Supplementary materials

Table A. Number of stingless bee individuals by species captured in the state of Rondônia, Brazil, by the substrate or method of capture.

Species	w	m	f	fec	fl	eu	h	n	o	r	s	Total	%
***Aparatrigona impunctata* (Ducke, 1916)**					8		3				1	12	0.13
***Celetrigona hirsuticornis* Camargo & Pedro, 2009**					1	1	5				7	14	0.15
***Celetrigona longicornis* (Moure, 1950)**					4		5				6	15	0.16
***Cephalotrigona femorata* (Smith, 1854)**					71	109	2				1	183	1.92
***Dolichotrigona browni* Camargo & Pedro, 2005**					3		3				21	27	0.28
***Dolichotrigona longitarsis* (Friese, 1903)**					1	2	3				62	68	0.71
***Dolichotrigona mendersoni* Camargo & Pedro, 2005**					1						1	2	0.02
***Dolichotrigona rondoni* Camargo & Pedro, 2005**						1	1				20	22	0.23
Duckeola ghilianii (Spinola, 1853)					**1**				**1**			**2**	**0.02**
Frieseomelitta flavicornis (Fabricius, 1798)					**2**							**2**	**0.02**
Frieseomelitta portoi (Friese, 1900)					**1**		**2**					**3**	**0.03**
Frieseomelitta silvestrii (Friese, 1902)					**16**	**1**	**3**				**1**	**21**	**0.22**
Frieseomelitta trichocerata (Moure, 1990)	**1**	**3**			**45**	**9**	**24**	**4**	**6**		**26**	**118**	**1.23**
***Geotrigona kwyrakai* Camargo & Moure, 1996**			3		2						8	13	0.14
***Geotrigona mattogrossensis* (Ducke, 1925)**		4			4	1	9					18	0.19
***Lestrimelitta limao* (Smith, 1863)**								6				6	0.06
***Leurotrigona gracilis* Pedro & Camargo, 2009**					1		2		1		4	8	0.08
***Leurotrigona muelleri* (Friese, 1900)**							9				42	51	0.53
***Melipona brachychaeta* Moure, 1950**	3	29	3	1	32	8	42	21	10	7	14	170	1.78
***Melipona illustris* Schwarz, 1932**			5						2			7	0.07
***Melipona crinita* Moure & Kerr, 1950**		6				4	1					11	0.12
Melipona fuliginosa Lepeletier, 1836					**6**	**5**	**1**	**24**	**6**			**42**	**0.44**
***Melipona grandis* Guerin, 1834**	5	13	3		60	9	9		8			107	1.12
***Melipona melanoventer* Schwarz, 1932**	1	9	1		20	12	11	4	10	1	1	70	0.73
***Melipona schwarzi* Moure, 1963**		15	3		10	1	38		1		7	75	0.78
***Melipona seminigra abunensis* Cockerell, 1912**	3	35	8	1	125	52	42	31	17	12	2	328	3.43
***Melipona seminigra* sp. forma Tefé**		11					1				1	13	0.14
***Melipona* sp. n.**		4				2	1		6		1	14	0.15
Nannotrigona melanocera (Schwarz, 1938)		**1**			**51**	**7**	**39**	**8**	**4**		**46**	**156**	**1.63**
Nannotrigona schultzei (Friese, 1901)					**1**	**1**	**12**				**4**	**18**	**0.19**
***Oxytrigona flaveola* (Friese, 1900)**					16	8	4		19		1	48	0.50
***Oxytrigona obscura* (Friese, 1900)**					26	1	33		1		2	63	0.66
Paratrigona* aff. *haeckeli											1	1	0.01
***Paratrigona haeckeli* (Friese, 1900)**					2						3	5	0.05
***Paratrigona myrmecophila* Moure, 1989**					1							1	0.01
***Paratrigona pacifica* (Schwarz, 1943)**							1					1	0.01
***Paratrigona prosopiformis* (Gribodo, 1893)**					9	1						10	0.10
Paratrigona* sp. n. aff. *lineata					54	2	23				4	83	0.87
***Partamona ailyae* Camargo, 1980**	2			2	22	28	66	3	3		94	220	2.30
***Partamona combinata* Pedro & Camargo, 2003**		3			7	13	23	9	3		39	97	1.02

***Partamona nhambiquara* Pedro & Camargo, 2003**		6			31	20	32	14			37	140	1.47
***Partamona testacea* (Klug, 1807)**		1	2		76	69	233	9	1	4	176	571	5.98
***Partamona vicina* Camargo, 1980**	1	1			7	9	143	32	5	2	73	273	2.86
Plebeia* aff. *minima					10	3	30		9		167	219	2.29
***Plebeia kerri* Moure, 1950**					19	3	80		2		36	140	1.47
***Plebeia margaritae* Moure, 1962**					2	2	34				39	77	0.81
***Plebeia variicolor* (Ducke, 1916)**					8	3	71				43	125	1.31
***Plebeia* sp. 1**				1	20	5	217		1		127	371	3.88
***Plebeia* sp. 2**				1	7	16	46		13		226	309	3.23
***Ptilotrigona lurida* (Smith, 1854)**					275	63	121	43	5	9	11	527	5.52
***Scaptotrigona affabra* (Moure, 1989)**											1	1	0.01
Scaptotrigona depilis (Moure, 1952)		**14**			**1**			**9**			**1**	**25**	**0.26**
***Scaptotrigona polysticta* (Latreille, 1807)**		2	3		8	1		5			2	21	0.22
***Scaptotrigona tricolorata* Camargo, 1988**		34	1		6		2	12	1			56	0.59
***Scaptotrigona* sp. 1**		63	2		20		1	11			1	98	1.03
***Scaptotrigona* sp. 2**		23	8		14		1	40			2	88	0.92
***Scaura latitarsis* (Friese, 1900)**					45	7	39		7		68	166	1.74
Scaura longula (Lepeletier, 1836)	**1**				**20**	**1**	**7**		**1**		**13**	**43**	**0.45**
Scaura tenuis (Ducke, 1916)					**24**	**1**	**22**	**13**	**11**		**61**	**132**	**1.38**
***Schwarzula coccidophila* Camargo & Pedro, 2002**							1				20	21	0.22
***Schwarzula timida* (Silvestri, 1902)**					3		6		8		27	44	0.46
Tetragona clavipes (Fabricius, 1804)	**3**	**1**		**2**	**241**	**23**	**138**	**14**	**12**	**5**	**41**	**480**	**5.02**
Tetragona dorsalis (Smith, 1854)					**36**	**41**	**48**				**15**	**140**	**1.47**
Tetragona essequiboensis (Schwarz, 1940)						**1**						**1**	**0.01**
***Tetragona goettei* (Friese, 1900)**					119	21	110	17	9	2	25	303	3.17
Tetragona handlirschii (Friese, 1900)					**1**		**1**				**3**	**5**	**0.05**
***Tetragona truncata* Moure, 1971**				4	6	1	2					13	0.14
***Tetragona* sp. n.**					16	1	57				27	101	1.06
***Tetragonisca angustula* (Latreille, 1811)**	1				244	2	60	37	4		12	360	3.77
***Tetragonisca weyrauchi* (Schwarz, 1943)**		1			63	2	10				9	85	0.89
***Trigona albipennis* Almeida, 1995**	1			1	28	14			12	5	7	68	0.71
***Trigona amazonensis* (Ducke, 1916)**	2	5	2	4	111	31	67	5	4	3	7	241	2.52
***Trigona branneri* Cockerell, 1912**				2	60	28	110	5	2	7	6	220	2.30
***Trigona chanchamayoensis* Schwarz, 1948**				3	117	8	131	10		4	4	277	2.90
***Trigona cilipes* (Fabricius, 1804)**					12	6	2		1			21	0.22
***Trigona crassipes* (Fabricus, 1793)**						4	215	11			4	234	2.45
***Trigona dallatorreana* Friese, 1900**			1		29	6	1		6		4	47	0.49
***Trigona dimidiata* Smith, 1854**					2	2	1		1	4		10	0.10
***Trigona fulviventris* Guerin, 1835**		1			113	33	113	8	2	2	50	322	3.37
***Trigona hypogea* Silvestri, 1902**					2		12		1			15	0.16
***Trigona pallens* (Fabricus, 1798)**					9	23	13	13		1	13	72	0.75
***Trigona pellucida* Cockerell, 1912**					32	1	1					34	0.36
***Trigona permodica* Almeida, 1995**					8	3	21				2	34	0.36
***Trigona recursa* Smith, 1863**		8		4	20	6	64	14	4	2	30	152	1.59
***Trigona truculenta* Almeida, 1984**	1			2	64	20	60	18	10	11	4	190	1.99
***Trigona williana* Friese, 1900**		1	1	3	112	29	52	14	12	9	13	246	2.57

***Trigona* sp. n.**		1			7	11	65		4		3	91	0.95
***Trigonisca bidentata* Albuquerque & Camargo, 2007**							2		1		23	26	0.27
***Trigonisca fraissei* (Friese, 1901)**									1		20	21	0.22
Trigonisca graeffei (Friese, 1901)					**3**						**13**	**16**	**0.17**
***Trigonisca hirticornis* Albuquerque & Camargo, 2007**					1		9				15	25	0.26
***Trigonisca variegatifrons* Albuquerque & Camargo, 2007**											1	1	0.01
***Trigonisca* sp. 1**					2		5				4	11	0.12
***Trigonisca* sp. 2**					1		4		2		62	69	0.72
***Trigonisca* sp. 3**							1		2		30	33	0.35
***Trigonisca* sp. 4**											4	4	0.04
***Trigonisca* sp. 6**							2				10	12	0.13
***Trigonisca* sp. 7**							1				2	3	0.03
No. of species by substrate	13	27	15	14	78	61	79	31	47	18	79	9555	100

w=water, m=mud, f=flesh, fec=feces, fl=flower, eu=euglossine bait, h=honey bait, n=nest, o=other, r=resin, s=skin. Species listed in bold are new records for the state of Rondônia.

Table B. List of stingless bee species according to the meso-region in which they were found in Rondônia state, Brazil. An "X" indicates at least one individual found in the meso-region.

Species name	CN	CM	EX	MC	SM	CÃ	PEGM	RESEX RCAU	RESEX ROP	CH	LD	OP	PM	PVH-BR-364	RM	Count of regions
Partamona ailyae	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	15
Tetragona clavipes	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	15
Trigona fulviventris	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	15
Melipona grandis	.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	14
Melipona seminigra abunensis	X	X	X	X	X	X	X	X	X	X	X	X	X	.	X	14
Plebeia aff. *minima*	X	X	X	X	X	X	X	X	X	X	X	X	.	X	X	14
Ptilotrigona lurida	X	X	X	X	X	X	X	X	X	X	X	X	.	X	X	14
Tetragona dorsalis	X	X	X	X	X	.	X	X	X	X	X	X	X	X	X	14
Tetragona goettei	.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	14
Trigona albipennis	X	X	X	X	X	X	X	.	X	X	X	X	X	X	X	14
Melipona brachychaeta	X	X	X	X	X	X	X	X	X	X	X	X	.	.	X	13
Partamona vicina	X	X	X	X	X	X	X	X	X	.	X	X	.	X	X	13
Partamona combinata	X	X	X	X	X	X	X	X	X	.	X	X	.	X	X	13
Partamona nhambiquara	X	X	X	X	X	X	X	X	X	X	X	X	.	.	X	13
Plebeia kerri	X	X	X	X	X	.	X	X	X	X	X	X	.	X	X	13
Plebeia sp. 1	X	X	.	X	X	X	X	X	X	X	X	X	.	X	X	13
Plebeia sp. 2	X	X	X	X	X	X	X	X	X	X	X	X	.	.	X	13
Trigona branneri	X	X	X	X	X	X	X	X	X	.	X	X	.	X	X	13
Trigona recursa	X	X	X	X	X	X	X	X	X	X	X	X	X	.	.	13
Trigona williana	X	X	X	X	X	X	X	X	X	X	.	X	X	.	X	13

Cephalotrigona femorata	X	X	.	X	X	X	.	X	.	X	X	X	X	X	X	12
Melipona schwarzi	X	X	X	X	X	X	X	X	.	.	X	X	.	X	X	12
Partamona testacea	X	X	X	X	X	.	X	.	.	X	X	X	X	X	X	12
Scaura tenuis	X	X	X	X	X	X	X	.	X	X	X	X	.	.	X	12
Trigona amazonensis	.	X	X	X	X	X	X	.	X	X	.	X	X	X	X	12
Trigona chanchamayoensis	X	X	X	X	X	.	X	.	X	.	X	X	X	X	X	12
Trigona truculenta	.	X	X	X	X	X	X	X	X	X	.	X	.	X	X	12
Frieseomelitta trichocerata	X	X	.	X	X	.	X	X	X	X	X	X	.	.	X	11
Melipona melanoventer	X	X	.	X	X	.	X	X	X	.	.	X	X	X	X	11
Tetragona sp. n.	X	X	.	X	X	X	X	X	X	.	X	X	X	.	.	11
Trigona pallens	.	X	X	X	X	X	X	X	X	X	.	X	.	X	.	11
Trigonisca sp. 2	X	X	.	X	X	.	X	X	X	.	X	X	.	X	X	11
Dolichotrigona longitarsis	X	.	X	X	X	X	X	X	X	.	.	X	.	X	.	10
Nannotrigona melanocera	X	.	X	X	X	.	X	X	X	X	X	X	.	.	.	10
Plebeia margaritae	X	X	X	X	X	.	X	X	X	.	.	X	.	.	X	10
Scaura latitarsis	.	X	X	X	X	.	X	X	X	X	.	X	.	.	X	10
Tetragonisca angustula	.	X	.	X	.	.	X	.	X	X	X	X	X	X	X	10
Trigona crassipes	X	X	X	X	.	X	X	X	X	.	X	X	.	.	.	10
Oxytrigona obscura	.	X	X	X	X	.	X	.	.	X	X	X	.	.	X	9
Dolichotrigona browni	X	.	X	X	X	.	X	.	.	.	X	X	.	.	X	8
Frieseomelitta silvestrii	X	X	X	X	X	.	.	.	.	.	.	X	X	.	X	8
Trigona sp. n.	X	.	X	X	X	X	X	.	.	.	.	X	.	.	X	8
Trigonisca graeffei	.	.	X	X	X	.	X	.	X	.	X	X	.	.	X	8
Paratrigona sp. n. aff. *lineata*	.	.	X	X	X	.	.	.	.	.	X	X	X	.	X	7
Plebeia variicolor	X	.	X	X	.	.	X	.	X	.	X	X	.	.	.	7
Scaptotrigona sp. 2	X	X	.	.	.	.	X	X	X	.	X	.	X	.	.	7
Scaura longula	.	X	.	X	.	.	X	.	X	X	.	X	.	X	.	7
Trigona hypogea	.	.	X	X	X	X	.	.	X	.	.	X	.	.	X	7
Celetrigona hirsuticornis	.	.	.	X	.	.	X	.	X	.	X	X	.	X	.	6
Dolichotrigona rondoni	.	X	.	X	X	.	.	.	X	.	X	X	.	.	.	6
Leurotrigona muelleri	X	.	.	X	.	.	X	.	X	.	X	X	.	.	.	6
Oxytrigona flaveola	X	X	.	.	.	.	.	X	.	X	.	X	.	.	X	6
Scaptotrigona polysticta	.	X	.	.	X	.	X	X	.	X	.	X	.	.	.	6
Schwarzula timida	.	X	.	X	.	.	.	.	X	X	X	X	.	.	.	6
Tetragonisca weyrauchi	.	.	.	.	X	.	X	.	.	X	.	X	.	X	X	6
Trigona permodica	X	.	.	X	X	.	X	.	.	.	X	X	.	.	.	6
Trigonisca fraissei	.	.	X	X	.	.	X	.	X	.	X	X	.	.	.	6
Trigonisca sp. 3	X	.	.	X	.	.	.	X	X	.	X	X	.	.	.	6
Aparatrigona impunctata	X	X	.	.	X	.	.	.	.	.	.	X	.	.	X	5
Geotrigona mattogrossensis	.	.	.	X	.	.	.	.	.	X	X	X	.	X	.	5
Melipona fuliginosa	.	X	.	.	X	.	X	.	X	.	.	X	.	.	.	5
Scaptotrigona tricolorata	X	X	.	.	X	.	X	.	.	.	.	X	.	.	.	5
Scaptotrigona sp. 1	.	.	.	.	X	.	X	.	X	.	X	X	.	.	.	5

Trigona pellucida	.	.	.	.	.	.	.	.	.	X	.	X	X	X	X	5
Trigona dallatorreana	.	.	.	.	X	.	X	X	.	X	.	X	.	.	.	5
Trigona dimidiata	.	X	X	.	.	.	.	.	.	X	.	X	.	X	.	5
Trigonisca sp. 1	.	.	X	X	.	.	X	.	.	.	X	.	.	.	X	5
Celetrigona longicornis	.	.	X	X	.	.	.	.	X	.	.	X	.	.	.	4
Leurotrigona gracilis	.	X	.	.	.	.	X	.	X	.	.	X	.	.	.	4
Scaptotrigona depilis	.	.	.	.	X	.	X	.	X	.	.	X	.	.	.	4
Trigona cilipes	.	.	.	X	.	.	X	.	.	.	.	X	.	.	X	4
Trigonisca sp. 6	X	.	.	.	.	X	.	.	X	.	.	X	.	.	.	4
Geotrigona kwyrakai	.	.	.	.	.	.	X	.	.	.	.	X	.	.	X	3
Melipona crinita	.	.	X	X	.	.	.	.	.	.	.	X	.	.	.	3
Nannotrigona schultzei	.	.	X	X	.	.	.	X	.	.	.	.	.	.	.	3
Paratrigona haeckeli	.	.	.	.	.	.	.	.	X	.	X	X	.	.	.	3
Paratrigona prosopiformis	.	.	.	.	.	X	.	.	.	.	.	X	X	.	.	3
Tetragona truncata	.	.	X	.	X	.	.	.	.	.	.	X	.	.	.	3
Trigonisca bidentata	.	.	.	.	.	.	X	.	X	.	.	X	.	.	.	3
Trigonisca hirticornis	.	.	.	X	.	.	.	.	X	.	.	X	.	.	.	3
Duckeola ghilianii	.	.	.	.	.	.	.	X	.	.	.	.	.	.	X	2
Frieseomelitta portoi	.	.	X	.	.	.	.	.	.	.	.	X	.	.	.	2
Melipona illustris	.	.	.	.	.	.	X	X	.	.	.	.	.	.	.	2
Tetragona handlirschii	.	.	X	.	.	X	.	.	.	.	.	.	.	.	.	2
Trigonisca sp. 4	.	.	.	.	.	.	X	.	.	.	.	X	.	.	.	2
Dolichotrigona mendersoni	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	1
Frieseomelitta flavicornis	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	1
Lestrimelitta limao	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	1
Melipona seminigra sp. forma Tefé	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	1
Melipona sp. n.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	1
Paratrigona aff. *haeckeli*	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	1
Paratrigona myrmecophila	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	1
Paratrigona pacifica	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	1
Scaptotrigona affabra	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	1
Schwarzula coccidophila	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	1
Tetragona essequiboensis	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	1
Trigonisca sp. 7	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	1
Trigonisca variegatifrons	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	1
Total richness in meso-region	43	49	52	61	54	35	63	41	56	37	47	82	22	31	47	
Locations sampled in meso-region	5	5	5	10	6	14	18	7	15	8	6	73	4	3	8	

CN-Campo Novo; CM-Costa Marques; EX-Extrema; MC-Machadinho-Cujubim; SM-São Miguel do Guaporé; CÃ-Estação Ecológica Cuniã; PEGM-Parque Estadual Guajará-Mirim; RESEX RCAU-Reserva Extrativista do Rio Cautário; RESEX ROP-Reserva Extrativista do Rio Ouro Preto; CH-Chupinguaia; LD-Linha D; OP-Ouro Preto do Oeste; PM-Pimenteiras; PVH-BR-364-Porto Velho BR-364; RM-Rolim de Moura. Light shading=newer settlement; dark shading=area of preservation; no shading=older settlements.

Table C. Count of times each stingless bee species was found in each location according to the level of deforestation within 0.5 km of sample location in Rondônia state, Brazil.

Species name	0 to <10% (50)	10 to <45% (43)	45 to <80% (55)	80 to 100% (39)	Sum
Melipona sp. n.	5	.	.	.	5
Frieseomelitta flavicornis	1	.	.	.	1
Lestrimelitta limao	1	.	.	.	1
Paratrigona aff. *haeckeli*	1	.	.	.	1
Trigonisca variegatifrons	1	.	.	.	1
Nannotrigona schultzei	3	5	.	.	8
Leurotrigona gracilis	5	3	.	.	8
Trigonisca bidentata	1	3	.	.	4
Trigonisca sp. 7	.	2	.	.	2
Melipona illustris	1	2	.	.	3
Dolichotrigona mendersoni	.	1	.	.	1
Paratrigona myrmecophila	.	1	.	.	1
Paratrigona pacifica	.	1	.	.	1
Trigonisca sp. 4	2	1	.	.	3
Tetragona handlirschii	1	1	.	.	2
Plebeia margaritae	8	6	6	.	20
Trigona hypogea	3	2	6	.	11
Aparatrigona impunctata	1	3	4	.	8
Paratrigona prosopiformis	1	.	2	.	3
Scaptotrigona polysticta	2	6	2	.	10
Celetrigona longicornis	1	4	2	.	7
Celetrigona hirsuticornis	5	2	2	.	9
Trigonisca sp. 1	3	2	2	.	7
Frieseomelitta portoi	.	1	2	.	3
Tetragona essequiboensis	.	.	1	.	1
Melipona seminigra sp. forma Tefé	.	3	1	.	4
Duckeola ghilianii	.	1	1	.	2
Tetragonisca angustula	8	17	26	25	76
Trigona fulviventris	31	25	31	21	108
Partamona testacea	17	20	31	21	89
Ptilotrigona lurida	21	26	31	20	98
Melipona seminigra abunensis	20	22	30	18	90
Trigona amazonensis	8	16	24	17	65
Trigona branneri	11	20	17	16	64
Trigona chanchamayoensis	9	9	17	16	51
Tetragona clavipes	16	30	39	15	100
Tetragona goettei	17	30	26	14	87
Cephalotrigona femorata	12	15	19	14	60
Partamona nhambiquara	8	17	16	14	55
Trigona williana	22	17	25	13	77
Partamona ailyae	17	21	26	11	75

Paratrigona sp. n. aff. *lineata*	1	4	11	11	27
Frieseomelitta trichocerata	6	13	15	10	44
Tetragonisca weyrauchi	1	6	15	10	32
Melipona grandis	5	12	14	10	41
Tetragona dorsalis	10	23	17	9	59
Plebeia sp. 1	25	18	14	9	66
Trigona truculenta	13	15	18	8	54
Nannotrigona melanocera	9	11	13	8	41
Scaura tenuis	14	13	10	8	45
Plebeia kerri	9	11	7	8	35
Melipona brachychaeta	20	25	15	7	67
Plebeia sp. 2	24	17	14	7	62
Trigona crassipes	22	10	11	7	50
Melipona melanoventer	7	12	14	6	39
Trigona albipennis	8	9	11	6	34
Plebeia aff. *minima*	27	17	16	5	65
Partamona vicina	22	18	14	5	59
Trigona recursa	17	16	11	5	49
Partamona combinata	5	15	9	5	34
Plebeia variicolor	7	7	8	5	27
Tetragona sp. n.	14	9	2	5	30
Scaura longula	5	7	6	4	22
Trigona cilipes	1	3	4	4	12
Trigona permodica	6	2	2	4	14
Trigona sp. n.	8	7	15	3	33
Trigona dallatorreana	3	3	7	3	16
Geotrigona mattogrossensis	.	.	6	3	9
Scaptotrigona sp. 1	2	3	6	3	14
Melipona fuliginosa	2	1	6	3	12
Oxytrigona obscura	1	7	5	3	16
Oxytrigona flaveola	2	3	5	3	13
Trigonisca sp. 3	5	5	2	3	15
Trigona pellucida	1	2	8	2	13
Scaura latitarsis	5	10	6	2	23
Dolichotrigona rondoni	.	4	6	2	12
Dolichotrigona browni	3	3	5	2	13
Schwarzula coccidophila	.	2	2	2	6
Leurotrigona muelleri	10	2	2	2	16
Scaptotrigona affabra	.	.	.	1	1
Scaptotrigona depilis	1	3	.	1	5
Geotrigona kwyrakai	2	1	.	1	4
Melipona schwarzi	5	9	7	1	22
Trigonisca sp. 2	8	11	6	1	26
Trigona pallens	7	9	5	1	22

Dolichotrigona longitarsis	10	8	4	1	23
Trigonisca graeffei	4	5	3	1	13
Frieseomelitta silvestrii	3	4	3	1	11
Trigona dimidiata	.	2	3	1	6
Schwarzula timida	3	7	2	1	13
Scaptotrigona sp. 2	3	5	2	1	11
Melipona crinita	.	4	2	1	7
Tetragona truncata	.	4	2	1	7
Scaptotrigona tricolorata	3	2	2	1	8
Trigonisca sp. 6	4	1	2	1	8
Trigonisca hirticornis	5	5	1	1	12
Trigonisca fraissei	4	5	1	1	11
Paratrigona haeckeli	.	2	1	1	4

Number of locations sampled at corresponding deforestation level in parentheses. Dark shading=species found only in locations of lower deforestation levels (<80%); light shading=species found in all locations, regardless of deforestation level; no shading=other.

Table D. List of stingless bee species and number of locations in which they were found, grouped by whether found in open or closed canopy vegetation sub-locations in Rondônia state, Brazil.

Species	Open	Closed	Total
Aparatrigona impunctata	6	2	8
Celetrigona hirsuticornis	3	6	9
Celetrigona longicornis	7	1	8
Cephalotrigona femorata	30	41	71
Dolichotrigona browni	13	2	15
Dolichotrigona longitarsis	3	21	24
Dolichotrigona mendersoni	2	.	2
Dolichotrigona rondoni	5	8	13
Duckeola ghilianii	2	.	2
Frieseomelitta flavicornis	1	.	1
Frieseomelitta portoi	1	2	3
Frieseomelitta silvestrii	10	1	11
Frieseomelitta trichocerata	49	5	54
Geotrigona mattogrossensis	9	.	9
Geotrigona kwyrakai	2	2	4
Lestrimelitta limao	.	1	1
Leurotrigona gracilis	6	2	8
Leurotrigona muelleri	4	12	16
Melipona crinita	4	5	9
Melipona fuliginosa	9	3	12
Melipona grandis	39	10	49
Melipona illustris	1	2	3
Melipona melanoventer	18	24	42
Melipona brachychaeta	40	43	83

Melipona schwarzi	14	13	27
Melipona seminigra abunensis	72	47	119
Melipona seminigra sp. forma Tefé	4	3	7
Melipona sp. n.	.	6	6
Nannotrigona melanocera	27	27	54
Nannotrigona schultzei	1	7	8
Oxytrigona flaveola	11	2	13
Oxytrigona obscura	16	2	18
Paratrigona aff. *haeckeli*	.	1	1
Paratrigona haeckeli	2	2	4
Paratrigona myrmecophila	1	.	1
Paratrigona pacifica	.	1	1
Paratrigona prosopiformis	2	1	3
Paratrigona sp. n. aff. *lineata*	29	4	33
Partamona ailyae	46	49	95
Partamona combinata	27	13	40
Partamona nhambiquara	49	16	65
Partamona vicina	27	47	74
Partamona testacea	87	53	140
Plebeia aff. *minima*	14	60	74
Plebeia kerri	18	22	40
Plebeia margaritae	9	12	21
Plebeia sp. 1	24	57	81
Plebeia sp. 2	22	55	77
Plebeia variicolor	5	28	33
Ptilotrigona lurida	85	53	138
Scaptotrigona affabra	1	.	1
Scaptotrigona depilis	1	4	5
Scaptotrigona polysticta	8	2	10
Scaptotrigona sp. 1	11	3	14
Scaptotrigona sp. 2	6	5	11
Scaptotrigona tricolorata	4	4	8
Scaura latitarsis	24	6	30
Scaura longula	23	3	26
Scaura tenuis	33	16	49
Schwarzula coccidophila	4	2	6
Schwarzula timida	10	5	15
Tetragona clavipes	110	30	140
Tetragona dorsalis	40	34	74
Tetragona essequiboensis	.	1	1
Tetragona goettei	80	39	119
Tetragona handlirschii	1	2	3
Tetragona sp. n.	16	18	34
Tetragona truncata	8	.	8

Tetragonisca angustula	80	19	99
Tetragonisca weyrauchi	32	2	34
Trigona albipennis	21	17	38
Trigona amazonensis	65	19	84
Trigona branneri	51	28	79
Trigona chanchamayoensis	43	17	60
Trigona cilipes	8	4	12
Trigona pellucida	13	.	13
Trigona crassipes	7	51	58
Trigona dallatorreana	14	2	16
Trigona dimidiata	5	1	6
Trigona fulviventris	70	78	148
Trigona hypogea	4	7	11
Trigona pallens	9	18	27
Trigona permodica	7	7	14
Trigona recursa	29	27	56
Trigona sp. n.	10	28	38
Trigona truculenta	45	20	65
Trigona williana	51	41	92
Trigonisca bidentata	3	1	4
Trigonisca fraissei	10	1	11
Trigonisca graeffei	11	2	13
Trigonisca hirticornis	4	9	13
Trigonisca sp. 1	2	5	7
Trigonisca sp. 2	12	16	28
Trigonisca sp. 3	11	5	16
Trigonisca sp. 4	2	1	3
Trigonisca sp. 6	.	8	8
Trigonisca sp. 7	1	1	2
Trigonisca variegatifrons	.	1	1

Light shading=found only in open canopy vegetation; dark shading=found only in closed canopy vegetation; no shading=found in both.

Table E. Stingless bee species found in nests, grouped by sample sub-location type (open or closed canopy) in Rondônia state, Brazil.

Species	Open	Closed	Total
Frieseomelitta trichocerata	1		1
Lestrimelitta limao		1	1
Melipona fuliginosa	2	1	3
Melipona melanoventer		2	2
Melipona brachychaeta	1	2	3
Melipona seminigra abunensis	3	2	5

Nannotrigona melanocera		1	1
Partamona ailyae		1	1
Partamona combinata		1	1
Partamona nhambiquara		2	2
Partamona vicina		4	4
Partamona testacea	1		1
Ptilotrigona lurida	2	3	5
Scaptotrigona depilis		2	2
Scaptotrigona polysticta	1		1
Scaptotrigona sp. 1		1	1
Scaptotrigona sp. 2		2	2
Scaptotrigona tricolorata	1		1
Scaura tenuis	2	1	3
Tetragona clavipes		2	2
Tetragona goettei	2	1	3
Tetragonisca angustula	6	2	8
Trigona amazonensis		1	1
Trigona branneri	1		1
Trigona chanchamayoensis	2		2
Trigona crassipes		2	2
Trigona fulviventris	1	1	2
Trigona pallens		2	2
Trigona recursa		3	3
Trigona truculenta		2	2
Trigona williana	2		2
Total	**28**	**42**	**70**

Light shading=found only in open canopy; dark shading=found only in closed canopy; no shading=found in both open and closed canopy.

Potential taxonomic issues regarding list of species

There are a few taxonomic issues in the species list we generated. According to Camargo and Pedro (2007), the status of *Oxytrigona flaveola* (Friese, 1900) remains unclear; it could be comprised of as many as three species, considering that the type series is composed of individuals from Brazil (Espírito Santo), Colombia and Guatemala. The situation of *Trigona fulviventris* Guerin, 1835 is also complicated; Camargo and Pedro (2007) assume that this species extends from Mexico to western Ecuador, and that there are many undescribed species in the group. Moreover, they note that *T. guianae* Cockerell, 1910 and *T. braueri* Friese, 1900 have been treated in the literature as *T. fulviventris*. So, it is possible that the bees identified as *T. fulviventris* in the present study are really *T. guianae*, since this occurs in Rondônia and *T. braueri* does not.