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The Influence of the Loss of Brazilian Savanna Vegetation on the Occurrence of Stingless Bees Nests (Hymenoptera: Apidae: Meliponini)

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Abstract
The vegetation of the Cerrado, also known as the Brazilian savanna, is rapidly being replaced by agricultural and urban areas. The scope of this study was to evaluate the relationship between the reduction in savanna vegetation and the occurrence of nests of stingless bees (Apidae: Meliponini), particularly those of the genus *Melipona* Illiger. We mapped 33 surveys of stingless bees nests located in Cerrado areas (25 sampled by us and 8 from literature) on Landsat images and assessed the proportions of vegetated, urban and rural areas within a radius of 3 km from each nest. We performed two-step cluster analyses separately for common and rare Meliponini species and *Melipona* species and assessed the proportion of vegetation in the resulting clusters. Common species such as *Trigona spinipes* Fabricius and *Tetragonisca angustula* Latreille were frequent in areas surrounded by vegetation as well as in degraded surround areas. Some species, such as *Oxytrigona tataira* Smith, occurred predominantly in degraded areas. Most *Melipona* species were uncommon or absent in the degraded areas. It is possible that isolated trees in rural landscapes provide functional connectivity for opportunistic species of stingless bees but not for susceptible species such as species of *Melipona*. This study is one of the first to attempt to understand the effects of the loss of Cerrado vegetation on the occurrence of stingless bees' nests.

Introduction

Stingless bees (Apidae: Meliponini) are highly social bees considered by several authors as generalists, both in relation to floral resources and in relation to their choice of nesting substrate. Their nests are found primarily in tree cavities, but, as *Apis mellifera* Linnaeus, they may also occupy different types of natural cavities (Roubik, 1989), and some species may also use artificial cavities (e.g. Zanette et al., 2005). Unlike *A. mellifera*, however, their physiogastric queens are unable to fly, which has two major implications: first, they are unable to move the colony to another cavity if the nest site suffers a disturbance; second, the reproduction of the colony is made after the workers from the mother nest find a new cavity and prepare it to receive the new queen. After the new queen is established in the new nest, workers from the mother nest look after it up to six months (Roubik, 2006). Thus, as stingless bees are unable to migrate their colonies and to establish a new nest too far from the mother nest, they are potentially sensitive to habitat degradation. To ensure the viability of stingless bees populations, the area around the nests must provide appropriate resources, as food and nesting sites.

Despite some species are able to live and to find resources in urban places, the environmental anthropization may have a deleterious effect on the community (Zanette et al., 2005). Besides the effects of deforestation, which is not yet known how it can affect bee populations (e.g. edge effect, increase of temperature and decrease of relative humidity), a direct and obvious problem is the reduction of available nesting sites, since most species nest in tree cavities. For many species, the availability of nesting sites may be a crucial factor limiting colonies reproduction (Inoue et al., 1993). For sensitive species, however, not only quantity but mainly

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quality of potential nesting sites is of greater importance. In some Brazilian dry forests and savanna, most of the stingless bees nests were found in a few species of trees, despite the presence of many tree species with available cavities (Antonini & Martins, 2003; Martins et al., 2004).

Among Brazilian biomes, the cerrado is one of the most affected by deforestation. The biome is one of the largest savanna formations in the world and occupied an original area of approximately two million square kilometres (Ab'Saber, 1981). Approximately half of the original area of the cerrado, however, has been converted to pastures and crops, primarily large monocultures of soybean, sugarcane and eucalyptus. A large portion has also been converted to urban land uses. Only 33,000 km² is protected by a series of discontinuous protected areas (Mittermeier et al., 1999; Klink & Machado, 2005).

Even so disturbed, the cerrado is considered a biodiversity hotspot. From the 33 neotropical genus of stingless bees, 23 are represented in the cerrado (Camargo & Pedro, 2013). Bees also represent the most important group of Cerrado pollinators (Biesmeijer et al., 2005; Gottsberger & Silberbauer-Gottsberger, 2006), and stingless bees may represent the highest biomass of insects that visit flowers in areas where they occur due to their large colonies, consisting of many workers that can be recruited to gather resources (Michener, 1979). Thus, stingless bees are very important to maintain genetic variability of the remnant flora of the cerrado.

Despite the high rate of devastation of Brazilian environments, especially the cerrado, the effects of human landscape disturbances on the populations of most species of stingless bees are still poorly understood. Most empirical studies of bees have generally focused on floral visitations, comparing the fauna in environments with different levels of anthropogenic disturbance within the same locality (e.g. Antonini & Martins, 2003; Araujo et al., 2006; Carvalho et al., 2007).

Surveys of flower visitors are important for characterising the current fauna but may mask the true status of stingless bee populations. First, the foraging area of stingless bees varies according to the size of the workers, and workers of some species, such as *Melipona compressipes* Smith*,* may forage more than 2 km from the colony (Araujo et al., 2004). This maximum distance results in a foraging area of more than 2,500 ha, whereas the area sampled in surveys is usually not more than 100 ha (one hectare: 10,000 m²). Thus, transient foraging visitors may be sampled in an area even though the foragers' colony actually resides in an area with an entirely different vegetation composition. Therefore, a study focused on the effects of human disturbances on the occurrence of stingless bee nests in a given area can provide a more precise understanding of the effects of these disturbances on bee populations.

Among stingless bees species, those of *Melipona* genus have been considered particularly sensitive to habitat loss. One of the reasons for this susceptibility is because many species of *Melipona* require large cavities for nesting, usually in large trees (Roubik, 2006), which are preferred targets for commercial exploitation and what make these bees susceptible to deforestation. Brown & Albercht (2001), for example, found that Amazonian *Melipona* bees are sensitive to deforestation, showing a population decrease even where some forest remnants were kept in the surroundings. *Melipona* species are on the list of endangered species in several Brazilian states, including populations located in cerrado environment (Machado et al., 1998), despite the studies have only included data from floral visitors surveys.

Given the great importance of stingless bees for pollination across the cerrado, understanding the effects of human disturbances on stingless bees nests is essential for ensuring the conservation of these bees and, consequently, the remnants of native cerrado vegetation. To evaluate the influence of the loss of cerrado vegetation on the occurrence of stingless bees nests, we surveyed bee nests in two areas of cerrado in the state of São Paulo and 23 areas of cerrado in the state of Maranhão and evaluated the degree of anthropogenic change in the landscape, analysing the data together with those from other nest surveys in the cerrado. The goal of this study was to understand if there was a relationship between loss of cerrado vegetation and the occurrence of the stingless bees nests found in the nest surveys, to answer the following questions: (1) does the presence of stingless bees nests decrease with loss of cerrado vegetation? (2) how does the frequency of nests of different species changes with the loss of cerrado vegetation? and (3) how does the frequency of *Melipona* nests responds to the loss of cerrado vegetation?

Material and Methods

Study areas and nest surveys

Meliponini nest surveys were conducted in 25 natural, vegetated areas of Brazilian savanna: 23 areas of 4 ha in northeastern Brazil and two areas of 5 ha in southeastern Brazil. Nests were actively searched for until each area was completely examined. All trees and abandoned termite and ant nests were inspected. Location for each nest found was recorded using GPS. Bee workers were collected at nest entrances for further identification and sent to specialists when necessary. Bees collected in the southeastern areas are deposited in the Paulo Nogueira-Neto Entomological Collection, Bee Laboratory, Institute of Biosciences of the University of São Paulo – USP (CEPANN) and those collected in the northeastern areas are deposited in the Entomological Collection of the Federal University of Maranhão.

The data collected were analysed together with data from previous nest surveys reported on literature, selected based on the following criteria: (1) the surveys had been conducted in an area of Brazilian Cerrado; (2) they contained data from surveys of nests of different species of stingless bees; (3) the surveys were conducted following the same method used in this study; and (4) they included geographic coordinates or information that could be used to determine the exact location of the study area. An initial selection of 31 studies was identified, including two theses, a work of graduate course completion, and 28 articles, including two popular science articles (supplementary material available on line). Based on the selection criteria, only eight of the 31 studies were retained (Table 1). Samples were collected in five geographic regions: São Paulo, Minas Gerais, Mato Grosso, southwestern and northeastern Maranhão (Fig 1).

Characterisation of environmental variables

Sampled areas of each survey were located on georeferenced LANDSAT satellite images, obtained through the website of the Brazilian Environmental Institute (http://siscom.ibama.gov.br/monitorabiomas/cerrado/ - last accessed 10/25/2012). To verify the amount of remnant savanna vegetation surround the sampled areas, we drawn a circle with a 3 km radius around each one using the buffer function of the program ArcGis 9.2 ®. This area size was selected based on the average maximum foraging radius of the stingless bees (Araújo et al., 2004) inhabiting a nest located at the edge of the largest area sampled in the selected surveys. We thus tried to assess the scale of the landscape likely to be used by most of the stingless bees inhabiting the nests found in the studies.

Table 1. Locations of the included nest surveys. Landsat: point-orbit of the Landsat satellite where the surveys were located. % Vegetation: amount of remnant Cerrado vegetation in each survey. Coordinates in UTM – SAD69. References in supplementary material available online.

Survey name	Landsat	Longitude	Latitude	% Vegetation	Reference
Araguari	221-073	155049	7923805	69.8	Siqueira *et al.* 2007
Arizona	221-065	346637	9223868	55.4	This work
Bacaba	224-070	354877	8375344	41.2	Pereira 2004
Bacabinha	222-065	230705	9253082	73.5	This work
Balsas	221-065	368933	9146931	95.7	Rego *et al.* 2008
Bom Lugar	222-064	239513	9415091	61.4	This work
Buriti	219-063	712945	9494380	94.5	This work
Caj. Winnits	222-064	326864	9334741	84.7	This work
Carmo	219-063	713144	9537956	93.7	This work
Castiça	219-064	698053	9392620	95.0	This work
Chapadinha	220-063	666549	9548548	86.2	Rego et al. 1998
Cocalinho	220-064	676565	9377561	79.4	This work
EEI	220-075	199103	7541617	38.4	This work
Extrema	222-065	276484	9169159	99.3	This work
Faz. São Pedro	221-065	312959	9153858	98.4	This work
Faz. Walter	222-065	236598	9205941	95.4	This work
Feio	222-064	236312	9330425	48.7	This work
Formosa	221-065	367645	9273900	89.5	This work
Gleba Cajueiro	222-065	299478	9237677	91.7	This work
IAB	220-075	203483	7545030	29.9	This work
Jatoba	220-064	585754	9357013	75.0	This work
Macaco	220-064	576991	9334800	77.7	This work
Normasa	220-064	668536	9380055	55.0	This work
Panga	221-073	141662	7875233	39.3	Nogueira-Ferreira & Siqueira 2008
São Lourenço	219-064	710963	9426135	98.1	This work
São Luizinho	220-064	582344	9404812	79.3	This work
São Francisco	221-064	328443	9302114	88.0	This work
Sipauba	220-063	639155	9478107	91.9	This work
Santa Teresa	220-075	204430	7650779	11.6	Alvarenga 2008
Tabocal	219-064	678591	9312946	97.7	This work
Urb. Santos	220-062	677454	9645344	75.3	Serra *et al.* 2009
Urubu	219-064	712108	9418736	90.8	This work
USP Ribeirão	220-075	203224	7657088	11.1	Freitas *et al.* 2009

The images were manually classified by drawing polygons that delineated cover types: Brazilian savanna vegetation (regardless of size or condition of the vegetation), rural areas (identified based on regular designs with a predominance of crops or bare soil), and urban areas. The area of open water visible at a resolution of 1:30000 was subtracted from the total. When in doubt, the classification of the LANDSAT images was verified using images from Google Earth®. The areas of the polygons were calculated and the areas of polygons of the same cover type were summed and converted into a percentage to obtain the proportion of remnant savanna area in the landscape. To evaluate the effect of landscape on the distribution of species, the number of nests of each species in each survey was transformed into presence-absence and subjected to a principal coordinate analysis (PCO). These analyses were performed in PAST 2.07 (Hammer et al., 2001).

Data analysis

Due to the variation in the sizes of the areas sampled during the literature surveys and the few number of nests found in most of our surveys, the number of nests of each species in each study was transformed into presence or absence data. A two-step cluster analysis without a predefined number of clusters was used to investigate the relationship between species composition and the proportions of surround remnant savanna vegetation. We performed three separate analyses: one considering the species occurring in five or more surveys ("frequent species"); the second considering species with occurrences in four or fewer surveys ("rare species"); and the third considering only species of the genus *Melipona*, regardless of the number of surveys in which they occurred. We performed these separate analysis to evaluate the effect of loss of cerrado

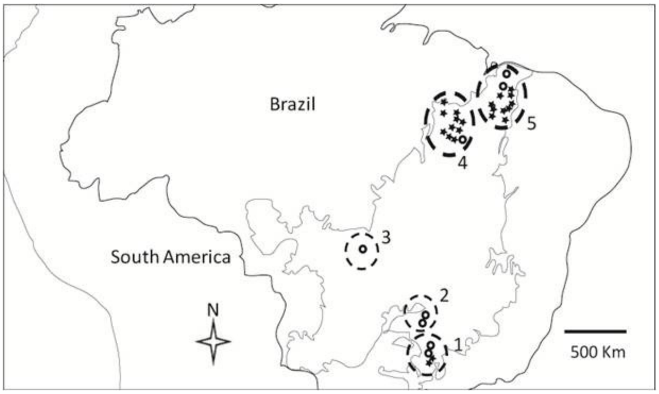

Fig 1. Overview of survey locations. Stars: this study. Circles: Surveys from literature. Surveys: 1: São Paulo state surveys (EEI, IAB, Santa Teresa and USP Ribeirão); 2: Minas Gerais state surveys (Araguari and Panga); 3: Mato Grosso survey (Bacaba); 4 and 5: Maranhão state surveys, being 4: Arizona, Bacabinha, Balsas, Bom Lugar, Cajueiro Winnits, Extrema, Fazenda São Pedro, Fazenda Walter, Feio, Formosa, Gleba Cajueiro, and São Francisco; 5: Arizona, Buriti, Carmo, Castiça, Cocalinho, Jatoba, Macaco, Normasa, São Lourenço, São Luizinho, Sipauba, Tabocal, Urbano Santos, and Urubu. The light delimited area corresponds to Cerrado.

areas to the occurrence of each kind of species (common species, usually found in antropic environments; rare species, detected in few surveys; and *Melipona* bees, reported in literature as sensitive to deforestation). To evaluate the effect of the variable order on the cluster arrangement, the position of common species was randomised using a Monte-Carlo method with 10,000 iterations, and its significance within the clusters was tested by a Chi-square test. The significance of the environmental variables in the species composition of the clusters was assessed using a Mann-Whitney test. Analyses were performed using the program SPSS 13.0.

Results

The surveys compiled for the present study comprised a total of 1135 nests belonging to 19 genera and 63 species, of which 10 were unidentified (supplementary material available on line).

The first axis of the PCO of surveys from the species presence-absence data explained only 20% of the variation. The spread of the ordination coefficients along the first two axes showed that geographically closer surveys tended to have more similar species compositions, as expected for a large landscape scale (Fig 2).

Frequency of occurrence of stingless bees species versus the reduction in Cerrado vegetation

Fourteen species occurred in at least five sites (Table 2). These "frequent species" formed tree natural clusters (A, B and C). Cluster A had significantly less vegetation (43% ± 31%) than cluster B (82% ± 17%; Z=-2.419, α=0,014) and than cluster C (80% ± 17%; Z=-2.538, α=0,008), but cluster B and C are similar with respect to the amount of vegetation (Z=-0.539, α= 0,614). Cluster A showed 39% of the occurrences of the "frequent species", and clusters B and C, together, showed 61% of the occurrences. Of the 14 species, eight had significant results regarding the frequency in each cluster: *Frieseomelitta longipes* Smith, *Lestrimelitta limao* Smith, *Oxytrigona tataira* Smith, *Tetragona clavipes* Fabricius, *Trigona fulviventris* Guérin, *Trigona pallens* Fabricius, and *Trigona spinipes* Fabricius. The other six species exhibited random frequencies between clusters. Excluding these random species, cluster A showed 51% of the occurrences and clusters B and C, together, showed 49% of the occurrences (Fig 3).

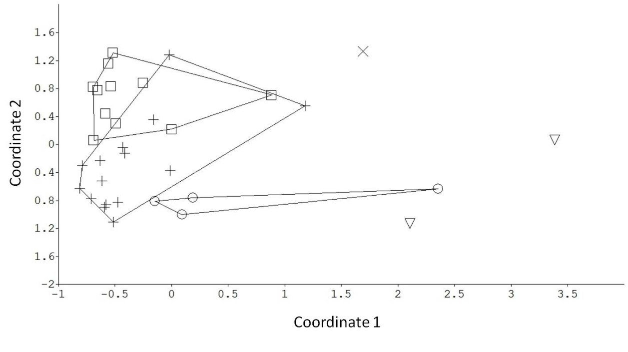

Fig 2. PCO analysis (1st coordinate X 2nd coordinate) of the ordination of sites by the presence-absence species data. Circle: São Paulo; triangle: Minas Gerais; x: Mato Grosso; square: SW of Maranhão; cross: NE of Maranhão.

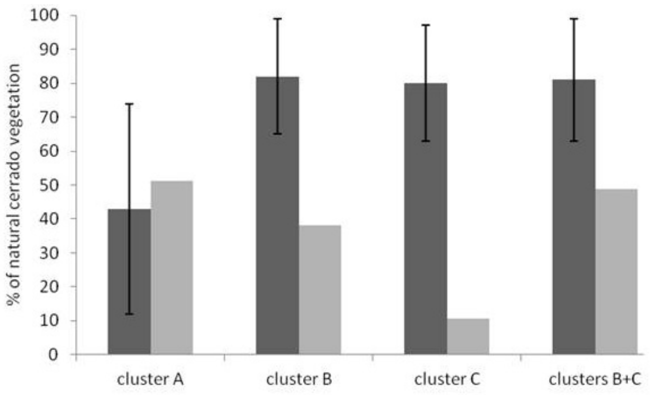

Fig 3. Percentage and standard deviation of natural cerrado vegetation in cluster A, B, C and B+C (dark gray) and percentage of occurrence of non-random clustered common species (light gray).

From the eight non-random species clustered, four occurred mainly in cluster A (most degraded): *O. tataira* (100% of the species occurrence), *L. limao* (80% of the species occurrence), *Tetragonisca angustula* Latreille (62%) and *T. clavipes* (58%). *T. pallens* showed 50% of occurrence in cluster A and in cluster B+C. The other three species were less frequent or absent in most degraded cluster A (*T. fulviventris*, 43%; *T. spinipes*, 42%; and *F. longipes*, 0%).

The 38 species with a frequency of four or fewer sites (supplementary material available on line) were grouped into two clusters (D and E) that not differed with respect to the amount of vegetation (z=-1.542, α= 0.13); 69% of the occurrence of the "rare species" was found in cluster C, against 31% of occurrences in cluster D. The significance of the position of each species in each cluster could not be determined because of their low frequencies of occurrence.

Table 2. Species that were found in five or more surveys. Nº of nests: total of nests found in all surveys; occurrences: number of surveys where species are found; State: Brazilian state where species were found. MA: Maranhão state; MG: Minas Gerais state; MT: Mato Grosso state; SP: São Paulo state.

Species	Nº of nests	Occurrences	State
Scaptotrigona postica Moure	38	17	MA, MT, SP
Tetragona clavipes Fabricius	75	13	MA, MG, MT, SP
Tetragonisca angustula Latreille	149	12	MA, MG, MT, SP
Trigona pallens Fabricius	22	12	MA, MT
Trigona spinipes Fabricius	82	12	MA, MG, MT, SP
Melipona fasciculata Smith	16	10	MA
Frieseomelitta flavicornis Fabricius	51	9	MA
Frieseomelitta longipes Smith	12	9	MA
Melipona flavolineata Friese	13	9	MA
Trigona branneri Cockerell	10	7	MA
Trigona fulviventris Guérin	8	7	MA, MG
Oxytrigona tataira Smith	26	6	MA, MG, MT
Lestrimelitta limao Smith	12	5	MA, MG, MT, SP
Trigona truculenta Almeida	5	5	MA, MG

*Frequency of occurrence of **Melipona** species versus the reduction in Cerrado vegetation*

Melipona species were grouped into two clusters (F and G), and none of the species occurred in more than one cluster. Cluster F showed significantly less vegetation (63% ± 19%) than cluster G (vegetation: 85% ± 13%; Z= -2.261, α=0.022). Cluster F showed only 17% of *Melipona* occurrences, against 83% of occurrences for cluster G (Fig 4).

Of the six species of *Melipona* identified in the surveys, three showed non-random position in clustering: *Melipona fasciculata* Smith, *Melipona flavolineata* Friese and *Melipona seminigra* Friese. 100% of the occurrence of these species was in cluster G.

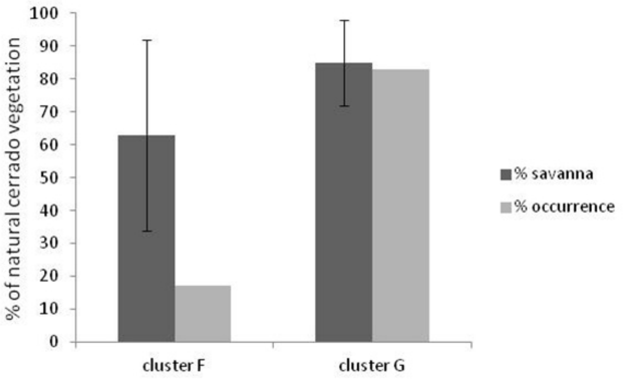

Fig 4. Percentage and standard deviation of natural cerrado vegetation in cluster F and G (dark gray) and percentage of occurrence of *Melipona* species (light gray).

Discussion

From the results obtained, we found that the loss of Cerrado vegetation may have a negative effect on the occurrence of nests of most species of stingless bees, mainly those from *Melipona* genus. This effect, however, is not the same for all species, which makes it difficult to establish a general pattern of response for Meliponini in relation to the degradation of vegetation. Although not all stingless bees species are capable of nesting in the areas with most degraded surroundings, as observed in the cluster analysis, some species are more frequent in these areas. Moreover, species composition may differ among surveys surrounded by degraded or preserved areas, as seen in the cluster analysis.

Frequency of occurrence of Meliponini species versus the reduction in Cerrado vegetation

We could not establish a relationship between the frequency of rare species and the amount of vegetation. Their clustering should be more related to geographic proximity, as shown in the PCO (Fig 2), than by the amount of vegetation. This was expected, since most of them occurred in the Maranhão surveys (supplementary material available on line), that also concentrate the most vegetated areas.

The 14 more frequent species found in the surveys showed a spread occurrence among the clusters, despite the amount of vegetation in them. In fact, from the eight frequent, non-random clustered species, the most degraded cluster showed the higher frequencies of four species and at least 40% of occurrence for three species. *F. longipes* was the unique of the frequent species not found in the more degraded cluster.

The apparent insensitivity of these common species to the reduction in native vegetation may be related to the behavioural plasticity of each species. While many Meliponini species are selective about their choice of nesting site (Antonini & Martins, 2003; Macías-Macías et al., 2014), most of the species frequent in degraded cluster are opportunistic and are commonly reported in surveys made in anthropical and urban environments. Bees such as *T. angustula*, for example, are extreme generalists in their choice of nesting site, and can occupy both natural and artificial cavities and may even be more numerous in artificial cavities (Sousa et al., 2002), being also able to take over nests of other species. *L. limao* is also a known parasitic bee, attacking other stingless bees nests. Other, as *O. tataira* and *Trigona* bees are aggressive foragers, being efficient in acquiring resources, including resource monopolization (e.g. Breed et al., 1999, Nieh et al., 2004; 2005).

Thus, the loss of cerrado vegetation and its replacement by a matrix of cropland and pastures is not enough to represent a loss of habitat connectivity to these common species. Connectivity indicates the aggregation of similar landscape elements. Connectivity at landscape level is considered structural, but there is a second type of connectivity, functional connectivity. In this case, the structure of the matrix and the landscape corridors may allow the movement of a particular taxon but be prohibitive to another, i.e. a given fragment can be isolated for an animal but connected by matrix elements that function as corridors (Goodwin, 2003). Thereby, structural fragmentation does not always reflect the loss of functional connectivity because this loss will depend on the mobility of each organism and the extent to which the fragmentation of the landscape represents a real loss of habitat (d'Eon et al., 2002; Goodwin, 2003; Manning et al., 2004). Thus, the loss of natural areas may have a greater effect on some species of stingless bees that are more sensitive to the reduction in these areas than on the most frequent species reported in this study.

Another factor to consider is the type of environment considered in this study, which was predominantly savanna. Previous studies have shown that the richness of stingless bees decreases with increasing distance of forest fragments from native forest (Brosi et al., 2007; 2008), as well as the sensitivity of many species to deforestation (Brosi, 2009). These studies, however, were conducted in tropical forest areas, where there is a stark contrast between vegetation and agricultural areas. For the present study, we considered environments whose phytophysiognomies are characteristically more open, featuring mostly shrubby vegetation with a few isolated trees. In the works selected for this study, although the proportion of rural areas was high in some sites, none featured a fragment of native vegetation completely isolated by agricultural fields. Thus, the agricultural matrix interspersed with fragments of field type phytophysiognomies may not differ significantly from the natural phytophysiognomies from the perspective of habitat use by stingless bees as a whole. That is, the degradation of native vegetation may represent a loss of structural, but not functional, connectivity, especially for species that are less restrictive in their choice of nesting site. The species most frequently recorded in surveys are common species of stingless bees, some reared by man and others common in anthropogenic environments. Moreover, for many species, a single isolated tree can support more than five nests of stingless bees, including multiple species (Martins et al., 2004). Thus, even if the proportion of native vegetation decreases, the matrix between fragments may provide functional connectivity to the most opportunistic species.

*The frequency of occurrence of **Melipona** species versus the reduction in Cerrado vegetation*

Unlike found for the frequent species, the decrease of native cerrado vegetation may imply in a loss of habitat connectivity to *Melipona* bees. The absence of the non-random clustered species of *Melipona* from the cluster with the greatest reduction in native vegetation confirms the sensitivity of these bees to habitat reduction.

One of the reasons may be the loss of available nest sites in areas with low cerrado vegetation. Except for *Melipona quinquefasciata* Lepeletier, which builds nests in cavities in the soil (Martins et al., 2004) and was not found in any of the selected works, bees of the genus *Melipona* require large cavities for nesting, which are found in large trees. Therefore, the absence of large trees may cause the absence of this type of bee from a given region.

Furthermore, the occurrence of some species at low frequencies in locations with a lower proportion of native vegetation may be a result of nests that have persisted from a pre-degradation stage because high longevity and low fecundity are characteristic of stingless bees (Eltz et al., 2003) and colonies may remain active for more than a decade. In contrast, the replacement of natural areas and agricultural areas can be rapid (CSR-IBAMA, 2009). Thus, species that are uncommon today in degraded areas may disappear from areas where they are unable to establish new nests in the long term.

Despite many *Melipona* species are kept in artificial nests by beekeepers, there are no reports on spontaneous nesting in artificial cavities, as for *T. angustula*, for example. Surveys on urban or anthropogenic environments usually do not report *Melipona* bees, even where large trees are still remaining. Thus, not only the loss of nest sites as the quality of the environment may represent a problem to *Melipona* bees. Therefore, the conservation of natural environments may represent an important step towards the viability of *Melipona* species populations, either in forest environments (Brown & Albrecht, 2001) or in the Brazilian savanna.

Study limitations

In most of our surveys there was a few number of nests (one to five), and each survey presented a different size of the sampled area. These issues have become a problem for some analyses as direct relationships between the amount of vegetation and parameters as nest density, species diversity or richness, even for those based on rarefaction techniques. Thus, we chose to run a robust analysis through the exploratory technique of two-step cluster analysis between species frequency of occurrence and the amount of vegetation.

Interpretations of the results of the present study should take into account three major limitations. First, there is a lack of peer-reviewed scientific journal articles that present data from nest surveys, especially for the cerrado. This deficiency is worrisome because the advancement of human disturbances across the remaining areas of cerrado is outpacing scientific studies. Second, the absence of nest surveys in the central areas of the cerrado leaves a large gap in the present study. Thirdly, the sampled areas of different sizes needed retrospective standardisation, limiting the interpretation of the results.

Conclusions

Even with the appropriate caveats, the present study is one of the first attempts to understand the effects of human disturbances of the cerrado on the nests of stingless bees, showing that the loss of native vegetation of the cerrado may have a deleterious effect on *Melipona* species. Our results produced the following answers to our initial questions regarding the reduction in the native cerrado: (1) Does the presence of stingless bees nests decrease with the loss of cerrado vegetation? Yes to *Melipona* bees, but not to common, opportunistic stingless bees species; (2) How does the frequency of nests of different species changes with the loss of cerrado vegetation? Common, opportunistic bee species are frequent either in degraded as in preserved areas, being sometimes more frequent in more degraded areas; frequency of rare species may not be related to the amount of vegetation in their area of occurrence, being their distribution in this study probably a reflection of geographical location; (3) How does the frequency of *Melipona* nests respond to the loss of cerrado vegetation? Nests of *Melipona* bees are significantly less frequent in lesser vegetated areas, being absent of them when it is considered only non-random clustered species.

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