

Nesting sites and abundance of Meliponini (Hymenoptera: Apidae) in heterogeneous habitats of the Atlantic Rain Forest, Bahia, Brazil

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Abstract

This work compares the nest distributions of the six most abundant species of stingless bees among three habitat types (structured, recovering and depleted forest) within a fragment of Atlantic Rain Forest: *Tetragonisca angustula*, *Nannotrigona punctata*, *Partamona helleri*, *Scaptotrigona xanthotricha*, *Plebeia* sp.n. and *Scaptotrigona tubiba*. The nests of these species represented, respectively, 31%, 12%, 9%, 7%, 6% and 5% of all stingless bees' nests (n=137) found within an area of 11,3 ha. The frequency of nests found in each habitat and substratum type varied significantly among the six species. *S. xanthotricha* and *S. tubiba* were found to nest only in tree holes within structured forest, while *T. angustula*, *P. helleri* and *Plebeia* sp.n. were found in all three habitats. *P. helleri* was abundant in depleted forest, where it build partially exposed nests in manmade structures, frequently in association with termites. *T. angustula* and *Plebeia* sp. n. were the most abundant species in the recovering forest, nesting in tight association with the fast growing and dominant tree *Tapirira guianensis*. Simplification of forest structure in the recovering habitat clearly favors the population expansion of *T. angustula*. *N. punctata* occupies living trees in structured forest and artificial cavities in depleted habitat, where it is the most abundant nesting species. The unexpected absence of *N. punctata* in the recovering forest was partially attributed to exploitative competition with *T. angustula*.

Keywords: Stingless bees, Nesting sites, Nest density, Endemic species, Atlantic Rain Forest, *Tetragonisca angustula*.

Introduction

The stingless bees (Hymenoptera, Apidae, Meliponini) often need large preexisting cavities to shelter their populous colonies. The majority of species nest in tree holes; however, some occupy other substrata such as abandoned ant and termite nests, underground cavities within tree roots, etc. (Camargo, 1970; Darchen, 1972; Hubell & Johnson, 1977, Roubik, 1989).

The Meliponini represent the largest biomass of bees within tropical rain forests (Roubik, 1993), where they are thought to be limited by the availability of nesting sites (Hubbell & Johnson, 1977). However, this hypothesis has not been tested in the field yet. Physical factors as temperature may also influence the choice of nesting sites by different species, because they show limited and varying nest thermoregulation capacities (Darchen, 1972). Finally, minimum size threshold of potential nest cavities is also likely related to both the colony

population and the species' body size (Hubbell & Johnson, 1977).

This work compares the distribution of the six most abundant stingless bee species in a small fragment of Northern Atlantic Rain Forest, and examines 1) how they use the available substrata within local heterogeneous habitats; 2) which is the degree of specialization or generalization in using nesting sites; 3) how habitat types and availability of nest substrata affect local distribution and abundance of the species; 4) whether or not the species abundance is related to degree of generalization in colonizing habitat types and/or nesting substrata and 5) what is the apparent role of species interactions.

Material and Methods

Field surveys were conducted in a fragment of Northern Atlantic Rain Forest in the Joanes - Ipitanga rivers valley, an Environmental Protection Area (APA) on the outskirts of the city of Salvador (Bahia, 12°53 S 38°23 W). The area is at sea level, and the weather is hot and humid, with an annual average temperature of 25°C. There is no dry season, and the annual rainfall is approximately 1700 mm (Radambrasil, 1981).

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Nesting sites were intensively sampled in an area of 11,3 hectares containing three habitat types representing different stages of forest disturbance: structured forest (forest with developed canopy and understory), intermediary-recovering forest (successional stage with small trees and shrubs, open canopy and high dominance of the tree species *Tapirira guianensis*), and depleted forest (grass-shrub stage with manmade structures). Individual bees were sampled from each nest to be identified.

Similarities between habitats and substrata used by species pairs of stingless bees were analyzed. A cluster analysis using the UPGMA algorithm was performed with Bray Curtis dissimilarities (e.g. Valentin, 2000). The Bray Curtis dissimilarities vary between 0 (complete similarity) to 1 (total dissimilarity). Fisher’s Exact Test (e.g. Zar, 1999) was applied to contingency tables of species *versus* habitats and species *versus* substrata types to test for dependence. This test may be applied to 2x2 contingency tables, and is indicated for tables with very low cell-countings, including those with zeroes.

Results and Discussion

The six most abundant stingless bee species in the area were: *Tetragonisca angustula angustula* (Latreille, 1811), *Nannotrigona punctata* (Smith, 1854), *Partamona helleri* (Friese, 1900), *Scaptotrigona xanthotricha* (Moure, 1950), *Plebeia* sp.n., and *Scaptotrigona tubiba* (Smith, 1863). The nests of these species represented, respectively, 30.7%, 12.4%, 9.5%, 7.3%, 6.6% and 5.1% of all nests (n = 137) of 16 stingless bees species found within this small forest fragment.

Tetragonisca angustula is widely distributed in the Neotropics, from Mexico to Northern Argentina (Nogueira-Neto, 1970). Published data and personal field observations suggest that *S. xanthotricha*, *P. helleri*, *N. punctata*, and *S.*

tubiba are all endemic to the Atlantic Rain Forest (Moure, 1950; Camargo, 1988; Batista & Ramalho, 2003).

The structured forest was found to contain the largest numbers of nests and abundant species, followed by the depleted forest habitat (Figure 1). The recovering forest contained the smallest numbers of nests and species and showed the highest dominance by a single species. The species diversity (Batista et al., 2003) and the number of nests sampled in each habitat type are related with the diversity of substrata available for nest building (Tables 1 and 2). The structured forest habitat was found to offer a wide variety of cavity sizes, primarily within living and dead trees (trunks). The depleted habitat offered many artificial cavities, but very few tree holes. The recovering forest was found to be the most homogeneous habitat type, offering mainly small tree holes in a dominant pioneering tree species (*Tapirira guianensis* Aubl.).

The frequency of nests per habitat and substratum type varied among the six stingless bee species (Figure 1; Table 2). In general, the UPGMA cluster analyses indicated (at the 0.4 dissimilarity level) that the two *Scaptotrigona* species prefer similar habitat and substratum types (Figure 2). The similarities between the two *Scaptotrigona* species are actually greater than among the other bee groups. *N. punctata* appears to prefer the same habitats as *P. helleri*, and the same substrata as *Plebeia* sp. n. *T. angustula* was the most divergent species, followed by *P. helleri*. Therefore, both the generalized (in the first case) and specialized (in the second case) nesting behavior produce high dissimilarities in using habitat types or nesting sites within a stingless bee community.

The exposed nests of *P. helleri* were often associated with termites and/or epiphytic Bromeliaceae rosettes. This specificity explains the significant differences between *P. helleri* and the other stingless bees (Figure 2b). This is a very aggressive species with cryptic, populous, and over-spaced

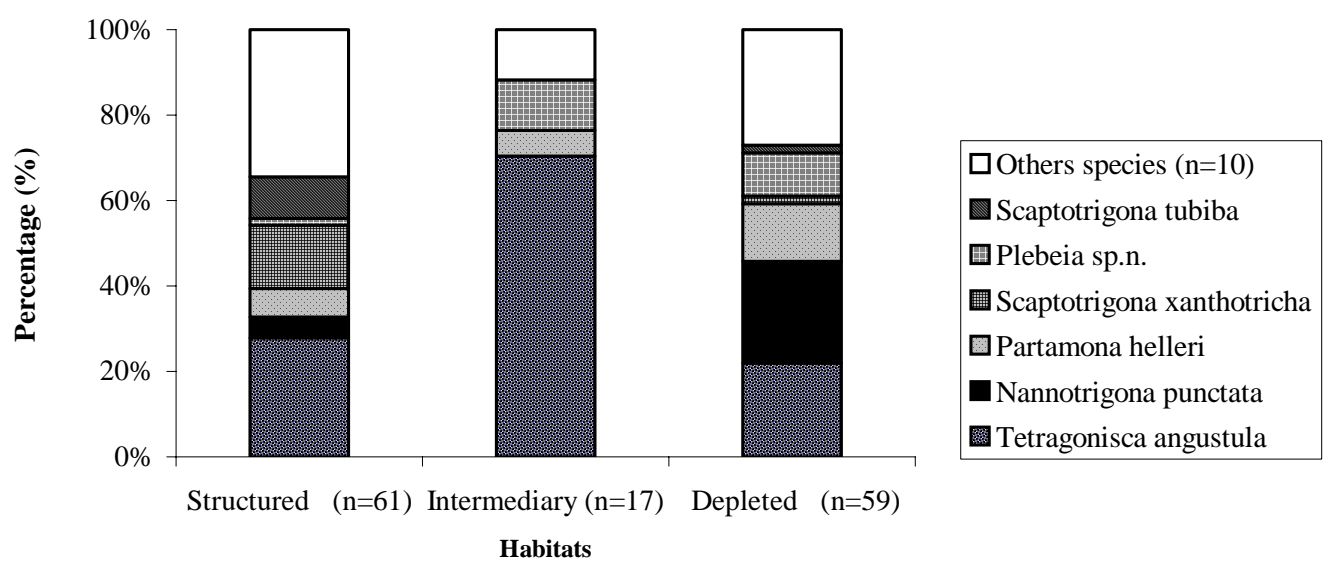


Figure 1 - Relative frequencies of stingless bees' nests in three habitat types in the Atlantic Rain Forest (n = 137).

colonies. Its regular nest spacing in the structured forest is a pattern also presented by very aggressive *Trigona* species (e. g. Hubbell & Johnson, 1977).

Tetragonisca angustula was the only species found to be abundant in all three habitats (Figure 1), and also to use all nesting sites successfully (Table 2). Ecological plasticity, allied with aggressive patrolling of potential nesting cavities within the colony’s territory and a high swarming rate (M. A. Batista in prep.) favor its fast spreading into disturbed forest habitats, in apparent detriment to other co-occurring very small stingless bee species.

Scaptotrigona xanthotricha and *S. tubiba* are medium-small bees (6-7mm), and were found to nest mainly in tree

holes within structured forest. *S. xanthotricha* appeared to be a generalist species with regard to nesting substrata, while *S. tubiba* occupied mainly large living tree-holes (Table 2). This difference is likely a result of divergent responses by co-generic species to the same selective effects of predators and robbers on nesting site selection (e.g., Roubik, 1989). *Scaptotrigona tubiba* is a timid and unaggressive species that constructs its nests in living trees, which provide protection and camouflage. *Scaptotrigona xanthotricha*, on the other hand, is able to use less protected cavities such as dead tree holes (trunks) and manmade cavities (e.g. wooden boxes) because of its high aggressiveness against intruders.

In the structured forest, the variety and abundance of tree-

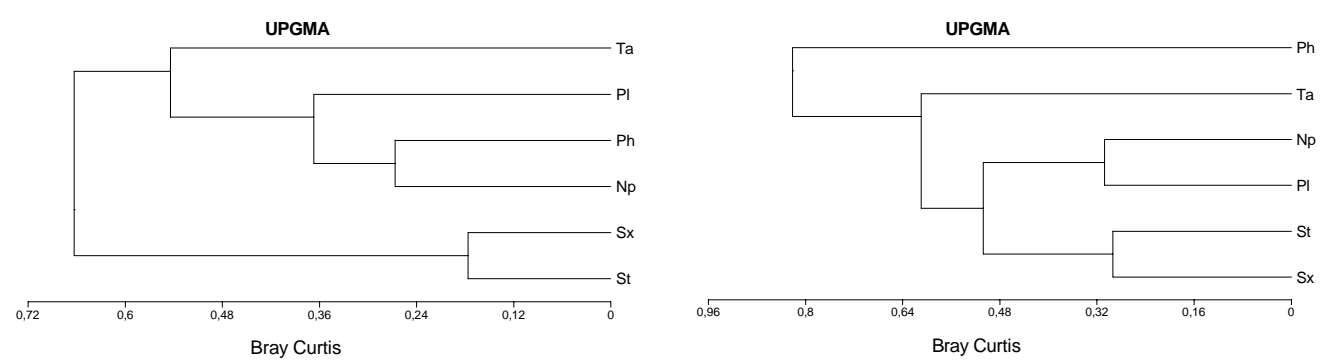


Figure 2 - Cluster analyses (UPGMA): a) Bee species versus habitat types; b) Bee species versus nesting sites. Np – *Nannotrigona punctata*; Ph – *Partamona helleri*; Pl – *Plebeia* sp. n.; St – *Scaptotrigona tubiba*; Sx – *Scaptotrigona xanthotricha*; Ta – *Tetragonisca angustula*.

Table 1 - Availability of potential nesting sites for stingless bees in three habitats in the Atlantic Rain Forest.

Nest sites	Habitat type (= Forest Degradation Stage)		
	Structured	Depleted	Recovering
	High	Medium	Low
	Types (trees, trunks, underground)	Medium (artificial holes, rare trees)	Low (small trees)

Table 2 - Frequency of nesting substrata used by the most abundant stingless bee species.

Species	Nest Sites (%)				
	Trees	*Trunks	Artificial Holes	Underground	Exposed
<i>Tetragonisca angustula</i> (n=42)	54,8	7,1	31,0	7,1	0
<i>Nannotrigona punctata</i> (n=17)	35,3	0,0	64,7	0,0	0
<i>Partamona helleri</i> (n=13)	0,0	7,7**	23,1	0,0	69,2***
<i>Scaptotrigona xanthotricha</i> (n=10)	50,0	40,0	10,0	0,0	0
<i>Plebeia</i> sp. n. (n=9)	44,4	0,0	55,6	0,0	0
<i>Scaptotrigona tubiba</i> (n=7)	85,7	14,3	0,0	0,0	0

hole sizes (Table 1) favors the coexistence of both *Scaptotrigona* species, which reached nest densities almost as high as *T. angustula* (Figure 1). They both differed from *N. punctata* and *Plebeia* sp. n. regarding preference of nesting sites (Table 2), cavity size and habitat (Figure 1). *Scaptotrigona* species were not found in the recovering forest, and were rare in the depleted forest, probably because this habitat types generally lack tree holes large enough to shelter their large colonies (e.g. Hubbell & Johnson, 1977).

Nannotrigona punctata were found at nest aggregations (Batista & Ramalho, 2003) with *Plebeia* spp., as well as with aggressive species such as *Frieseomelitta francoi* (Moure, 1946) and *P. helleri*. These inter-specific aggregations can improve overall nest protection and food foraging (Camargo, 1970; Hubbell & Johnson, 1977; Roubik, 1989). In contrast, *T. angustula* occurred mainly in monospecific aggregations, probably because it monopolizes aggregated cavities, thereby preventing the establishment of other very small, non-aggressive stingless bees in the vicinity of its colonies. This interference is likely intensified in the recovering forest due to its simplified vertical structure and high density of small

Tapirira guianensis trees, which constitute the major nesting substratum in this habitat.

N. punctata, *Plebeia* sp. n. and *T. angustula* are very small bees (< 5mm), and exhibited generalized behavior concerning both nesting sites and habitat colonization. *N. punctata* was found to nest only in living tree holes in the structured forest. However, it nested mainly in artificial cavities in the depleted forest (Figure 1), where it was the most abundant species. Its occurrence on a nearby continental island a few kilometers from the mainland forest (M. A. Batista, personal obs.) also suggests a high and large distance dispersal rate. In the depleted habitat, their nests were found in very small manmade cavities (volume smaller than one liter), which substrata are usually exposed to direct sunlight. Under these habitat conditions, *N. punctata* is more successful than *T. angustula*. However, in the recovering forest, the opposite was true, suggesting that minimum hole size and thermal characteristics of substrata might be the primary constraints upon colony-reproduction rates of both species.

The tests for dependence between several species pairs (Fisher’s Exact Test) were significant in a few particular

Table 3 - Significant results of Fisher’s Exact Test for dependence between species pairs (n = 27): Np – *Nannotrigona punctata*; Ph – *Partamona helleri*; Pl – *Plebeia* sp. n.; St – *Scaptotrigona tubiba*; Sx – *Scaptotrigona xanthotricha*; Ta – *Tetragonisca angustula*. * p < 0.05, ** p < 0.01, *** p < 0.005. Non-significant results between species pair (n = 168) are not listed.

HABITATS TYPES	SPECIES PAIRS	SIGNIFICANCE LEVEL
STRUCTURED x RECOVERING	Ta x Sx	*
STRUCTURED x RECOVERING	Sx x Pl	*
RECOVERING x DEPLETED	Ta x Np	**
STRUCTURED x DEPLETED	Ta x Np	*
STRUCTURED x DEPLETED	Np x Sx	***
STRUCTURED x DEPLETED	Np x St	**
STRUCTURED x DEPLETED	Ph x Sx	*
STRUCTURED x DEPLETED	Sx x Pl	**
STRUCTURED x DEPLETED	Pl x St	*
SUBSTRATA TYPES		
TREES x EXPOSED	Ta x Ph	***
TREES x EXPOSED	Np x Ph	***
TREES x EXPOSED	Ph x Sx	***
TREES x EXPOSED	Ph x Pl	**
TREES x EXPOSED	Ph x St	***
TREES x ARTIFICIAL CAVITIES	Np x St	*
TREES x ARTIFICIAL CAVITIES	Ph x Sx	*
TREES x ARTIFICIAL CAVITIES	Ph x St	*
TREES x ARTIFICIAL CAVITIES	Pl x St	*
TRUNKS x ARTIFICIAL CAVITIES	Ta x Sx	*
TRUNKS x ARTIFICIAL CAVITIES	Np x Sx	**
TRUNKS x ARTIFICIAL CAVITIES	Sx x Pl	*
TRUNKS x EXPOSED	Ta x Ph	*
TRUNKS x EXPOSED	Ph x Sx	**
UNDERGROUND x EXPOSED	Ta x Ph	**
ARTIFICIAL CAV. x EXPOSED	Ta x Ph	***
ARTIFICIAL CAV. x EXPOSED	Np x Ph	***
ARTIFICIAL CAV. x EXPOSED	Ph x Pl	**

situations ($n = 27$; Table 3). Comparisons between most of the species pairs ($n = 168$) did not achieve statistical significance, when neither habitat type nor nesting substrata utilization were concerned ($p < 0.05$).

Species interactions are potentially more relevant to the distribution of the abundant and generalized species that use similar nesting sites, such as *T. angustula*, *N. punctata* and *S. xanthotricha*, than to other species. In this situation, significant negative interactions (Table 3) may result from exploitative competition, if one assumes that nesting sites are limited.

Considering the overall dominance of *T. angustula*, its apparent negative interaction with *N. punctata* in the recovering and the depleted habitat types is significant (Table 3). This is so, especially because these species do not exhibit significant difference in the use of nesting substrata: they prefer different habitat types (Figure 1) but use similar nesting sites (Table 2). Both are very small bees (< 5 mm), have similar minimum cavity-size thresholds and use similar nesting sites ($p > 0.05$). Therefore, this spatial replacement of one species by the other in contiguous habitat types (Figure 1) suggests that antagonistic interaction also play a role in their spatial distribution and relative abundance within the forest fragment.

The tight association between *T. angustula* and *Tapirira guianensis* tree in the recovering forest (Batista & Ramalho, 2003) is likely a key factor in determining the local spatial distribution and abundance of other stingless bees. The simplified vertical structure of vegetation and the high dominance and small diameter of tree species in the recovering forest release the population expansion of *T. angustula* (Figure 1), with cascade mass effects (e.g., Cody, 1993) upon other surrounding habitats, including the structured forest. This spatial dynamics and comparable data on abundance of *T. angustula* within extensive regional pristine forest habitats (e.g., Wilms et al., 1997; Ramalho, 2003) suggest that this species may be used as an empirical tool to assess forest disturbance and/or regeneration stage in the Atlantic Rain Forest (Batista & Ramalho, in prep.).

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