Original Paper

ISSN 2175-7860 (online)

Diversity and nesting characteristics of stingless bees in an urban green area, the Botanical Garden of Rio de Janeiro

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Key words:
- Atlantic Forest
- biodiversity
- Meliponina
- stingless bees nesting habits
- urban afforestation

Abstract

Green urban areas act as refuges for the nests of stingless bees, during reproduction, in response to niche constraints. This study investigated the characteristics of natural colonization by stingless bees in the arboretum of the Botanical Garden of Rio de Janeiro, located within the city's urban fabric. A total of 94 nests belonging to 13 species were found in the following proportions: *Tetragonisca angustula* (37.3%), *Partamona helleri* (16%), *Nannotrigona testaceicornis* (12.8%), *Oxytrigona cagafogo* (8.5%), *Scaptotrigona xanthotricha*, *Paratrigona subnuda*, *Trigona spinipes*, and *Trigona hypogea* (each 4.2%), *Plebeia droryana* (3.2%), *Lestrimelitta tropica* (2.1%), *Melipona (Eomelipona) bicolor*, *Scaptotrigona bipunctata*, and *Trigona braueri* (each 1.1%). Most nests were built inside tree trunks or in the treetops, but some were also found in stone walls, in monuments, and in the ground. Nests were identified in 48 tree species across 21 botanical families, predominantly in Moraceae (19.44%) and Cupressaceae (15.28%). The colonized trees had an average diameter of 1.09 m, indicating mature trees, which favor the establishment of stingless bee nests. The height, density, spatial distribution and survival of the nests were evaluated. These results underscore the importance of conserving stingless bee nests in urban green areas.

Palavras-chave:
- Mata Atlântica
- biodiversidade
- Meliponina
- nidificação de abelhas sem ferrão
- arborização urbana

Resumo

Áreas verdes urbanas atuam como um refúgio para ninhos de abelhas sem ferrão em reprodução frente à restrição de seu nicho. As características de nidificação por espécies de abelhas sem ferrão no Jardim Botânico do Rio de Janeiro, localizado na malha urbana da cidade, foram estudadas. Um total de 94 ninhos pertencentes a treze espécies foram registrados nas seguintes proporções: *Tetragonista angustula* (37.3%), *Partamona helleri* (16%), *Nannotrigona testaceicornis* (12.8%), *Oxytrigona cagafogo* (8.5%), *Scaptotrigona xanthotricha*, *Paratrigona subnuda*, *Trigona spinipes* and *Trigona hypogea* (4.2%), *Plebeia droryana* (3.2%), *Lestrimelitta tropica* (2,1%), *Melipona (Eomelipona) bicolor*, *Scaptotrigona bipunctata* e *Trigona braueri* (1.1%). Grande parte dos ninhos foram construídos dentro de troncos de árvores, mas também nas copas, muros de pedras, monumentos e no solo. Quarenta e oito espécies pertencentes a 21 famílias botânicas foram colonizadas, com ênfase para Moraceae (19.44%) e Cupressaceae (15.28%). Árvores e palmeiras tinham um diâmetro médio na altura do peito de 1,09 m, portanto maduras, que favorece o estabelecimento dos ninhos de abelhas sem ferrão. Altura, densidade, distribuição espacial e sobrevivência dos ninhos foram avaliados. Os resultados apoiam as ações para conservação dos ninhos de abelhas sem ferrão em áreas verdes urbanas.

Original Paper

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Cite as: Teixeira MLF (2025) Diversity and nesting characteristics of stingless bees in an urban green area, the Botanical Garden of Rio de Janeiro. Rodriguésia 77: e01052024. DOI: 10.1590/2175-7860202677004

Area Editor: Dr. Leandro Freitas
Received on December 26, 2024. Accepted on September 11, 2025.

Rodriguésia
Revista do Instituto de Pesquisas Jardim Botânico do Rio de Janeiro
<http://rodriguesia.jbrj.gov.br>.

Introduction

In Brazilian Tropical Atlantic Rainforests, stingless bees account for approximately 70% of foraging bees (Ramalho 2004). Brazil is home to 244 described stingless bee species and about 89 undescribed species across 29 genera (Pedro 2014). Surveys have recorded 22 species of stingless bees in the state of Rio de Janeiro (Nogueira 2023); however, research focusing on stingless bees in urban green spaces within the state remains limited (Santos *et al.* 2020).

Stingless bees display significant diversity in morphology, colony size, nesting biology, associations with other insects, nest architecture, queen production, foraging strategies, and other traits. They nest in living trees, underground cavities, exposed branches or embankments, and in ant or termite nests (Roubik 2023). Their trophic resources include water, pollen, and nectar. Additionally they gather nest-building materials and defensive compounds, such as mud, oils, and resins (Roubik 1989). Depending on the species, colonies may range from 100 to over 10,000 individuals (Roubik 2023). Swarming is typically preceded by the preparation of a nesting site by the parental colony before the departure of the swarm with the new queen. Their colonies are typically long-lived and remain in the same location, as physogastric queens are unable to fly (Roubik 2023). Colonies spread gradually to nearby areas, making them highly reliant on stable habitats with specific characteristics. This dependence renders them particularly vulnerable to habitat alterations and disturbances (Toledo-Hernández *et al.* 2022).

The reduction of native vegetation has compelled stingless bees to migrate to urban zones, where they find potential nesting sites such as large, often hollow, old trees and artificial substrates, including stone walls. Nesting requirements vary by species (Knoll *et al.* 1994), and urban green areas often provide an abundance of floral resources and other necessary materials derived from both native and exotic trees and shrubs (Kleinert 2020). The richness of resources collected by stingless bees is closely influenced by the composition and proportion of the surrounding landscape (Machado *et al.* 2020). While some species of stingless bees in these environments are polylectic - collecting pollen from a variety of unrelated plants - others, which are more sensitive to environmental changes and have specific ecological demands, may also thrive. These sensitive species can act as bioindicators of environmental quality (Silva & Paz 2012).

The loss of natural habitats due to urbanization poses substantial challenges to bees by reducing natural sources of food and nesting sites, promoting habitat fragmentation, and increasing exposure to anthropogenic pressures such as pollutants (Paixão & Silva 2021), pesticides (Siviter *et al.* 2023), human traffic, construction activities (Zanette *et al.* 2005), predatory actions (Velez-Ruiz *et al.* 2013), and other stressors (Hernandez *et al.* 2009). Establishing, maintaining, and expanding ecological corridors are key strategies for preventing the extinction of native pollinators, including stingless bees (Giannini *et al.* 2015; Toledo- Hernández *et al.* 2022). The creation and adaptation of urban parks and gardens that feature a diversity of native flowers and trees, along with reliable water availability (Kaluza *et al.* 2016; Anderson *et al.* 2023), as well as the enhancement of ecological connectivity between forest fragments (Antonini *et al.* 2013), can promote the persistence of native bee populations in urban settings. These efforts are further strengthened by environmental education initiatives (Silveira *et al.* 2021), public policy measures (Santos *et al.* 2021), legal frameworks (Brasil 2020), and targeted research aimed at conserving these species (Santos *et al.* 2020).

The Botanical Garden, located within the urban area of Rio de Janeiro (RJ), has an arboretum with a high diversity of native and exotic botanical species. Founded in 1808, the living collection comprises many old trees with natural hollows and cavities. The area is actively managed and frequented by numerous visitors and employees, factors that can influence colony establishment and maintenance in various ways depending on the habitat and biology of each species.

The objective of this study was to investigate the stingless bees nesting in the arboretum of the Botanical Garden of Rio de Janeiro. Understanding the characteristics that enable the establishment and maintenance of nests of different stingless bee species in an urban visitation area can provide valuable insights for the management and conservation of similar environments.

Materials and Methods

The study was conducted from January 2015 to December 2022 at the Botanical Garden of Rio de Janeiro (JBRJ), both in the Cultural Corridor and in the arboretum itself, adjacent areas covering a total of 39.8 hectares. The arboretum is subdivided into 41 sections and numbered beds used for cultivating plant species. It is located adjacent to the urban area of Rio de Janeiro, within the coordinates -22°57′30″ to -22°58′40″S and -43°13′07″ to -43°13′45″W.

Each section of the arboretum was surveyed once a week between 9:00 a.m. and 12:00 p.m., resulting in eight complete surveys and 984 hours of monitoring for stingless bee nests over the entire study period. All trees, clumps, and palm trees were inspected within each section, resulting in the annual inspection of 100% of the arboretum's sections and specimens. With the aid of maps for each section, botanical specimens harboring stingless bee nests were identified with tomb numbers and geographical coordinates (JBRJ 2024). In addition, adjacent soil, buildings, and monuments were surveyed in search of stingless bee nests. Using a Garmin Map 78 GPS device, geographic coordinates of nests located in the soil and in artificial substrates were recorded.

For nests of unknown species, bee samples were collected with an entomological net, sent for identification, and deposited in the collection of the Plant Health Laboratory at the JBRJ. The height of each nest was measured from the tree trunk base to the entrance hole using a measuring tape (Wille & Michener 1973). For heights beyond the reach of the tape measure, a Hypsometer Laser Mileseey PF240 was employed. Tree diameters were measured at breast height (DBH).

To determine whether the distribution of nests among botanical families deviated significantly from a uniform distribution, a Chi-square goodness-of-fit test was applied, considering families with $N \geq 3$. Statistical significance was determined at a p-value of less than 0.05.

The spatial distribution of stingless bee nests was assessed to identify aggregation or randomness. For the total study area, observed distances between nests were compared to expected distances under a random distribution. The R index was calculated to classify the distribution as aggregated, random, or regular. A Monte Carlo simulation with 99 iterations generated random scenarios to compare with the actual nest distribution, producing a p-value. All statistical analyses were performed using R software, version 4.4.1, 2024.

Results and Discussion

Ninety-four nests belonging to thirteen species of stingless bees were identified, with the following proportions: *Tetragonista angustula* (Latreille, 1811) (37.3%), *Partamona helleri* (Friese, 1900) (16%), *Nannotrigona testaceicornis* (Lepeletier, 1836) (12.8%),

Oxytrigona cagafogo Müller 1874 (8.5%), *Scaptotrigona xanthotricha* Moure, 1950, *Paratrigona subnuda* Moure, 1947, *Trigona spinipes* (Fabricius, 1793), and *Trigona hypogea* Silvestri, 1902 (4.2%), *Plebeia droryana* (Friese, 1900) (3.2%), *Lestrimelitta tropica* Marchi & Melo, 2006 (2.1%), and *Melipona (Eomelipona) bicolor* Lepeletier, 1836, *Scaptotrigona bipunctata* (Lepeletier, 1836) and *Trigona braueri* Friese, 1900 (1.1%) (Figs. 1a-m; 2).

Among these species, *Tetragonista angustula* exhibits generalist habits and is highly efficient in pollinating tropical flora. Its ecological plasticity, combined with aggressive cavity patrolling within the colony's territory and high swarm rates, facilitates its rapid distribution in the Atlantic Forest (Batista *et al.* 2003). According to Santos *et al.* (2020), *T. spinipes* and *T. angustula* are the most frequently observed species in surveys of urban environments.

A significant proportion of the nests (76.6%) were located on trees, palm trees, and a bamboo clump, while 19.15% were on artificial substrates and 4.25% were in the soil (Fig. 3). Many stingless bee species prefer trees as nesting substrates in both natural (Werneck & Faria-Mucci 2014; Macedo *et al.* 2020; Cab-Baqueiro *et al.* 2022) and anthropized areas (Aidar *et al.* 2013; Albernaz *et al.* 2022), emphasizing the role of afforestation in biodiversity conservation and the preservation of social bees.

Tetragonista angustula and *N. testaceicornis* utilized substrates such as stone walls (Fig. 4a) and Wallace Cast Iron Fountains from the Val d'Osne Foundry (Fig. 4b-c). Nesting in buildings and monuments suggests that these bees can utilize artificial substrates in urban environments and associated green spaces, as seen in studies conducted at university campuses, plazas, and cemeteries (Nates-Parra *et al.* 2006; Martins *et al.* 2015; Vieira *et al.* 2016), a pattern that may be driven by the limited availability of natural substrates, such as trees with suitable cavities (Fig. 4d-g). The small size of their colonies enables these species to occupy limited spaces, providing access to a broader range of niches (Taura & Laroca 1991; Rocha-Filho *et al.* 2020). *N. testaceicornis* is known to visit tropical flora species in both natural and urbanized areas and contributes to the pollination of economically significant plants (Imperatriz-Fonseca *et al.* 2011; Silva *et al.* 2020).

Nest density was 2.36 ha^{-1}, which is intermediate compared to other studies in Brazilian green urban areas: 15.1 nests ha^{-1} across five species (Martins *et al.* 2015), 2.17 nests ha^{-1} across seven species (Aidar *et al.* 2013), 1.64 nests ha^{-1} across five species (Souza *et al.* 2005), and 0.52 nests ha^{-1} across seven species (Vieira *et al.* 2016). It is likely that not all nests in the arboretum were detected due to concealment in the tall, dense canopy or ground vegetation. In some areas, the soil is covered with perennial plants such as *Syngonium angustatum* Schott, *Epipremnum aureum* (Linden & André) G.S. Bunting, and *Spathiphyllum cannifolium* (Dryand. *ex* Sims) Schott, which can obscure nests located in the ground.

The species abundance observed at JBRJ - thirteen species - likely results from the arboretum's abundance of trunk cavities and its extensive collection of native and exotic plant species, comprising 6,960 specimens from 1,647 taxa (Almeida *et al.* 2024). In a monitoring study of 157

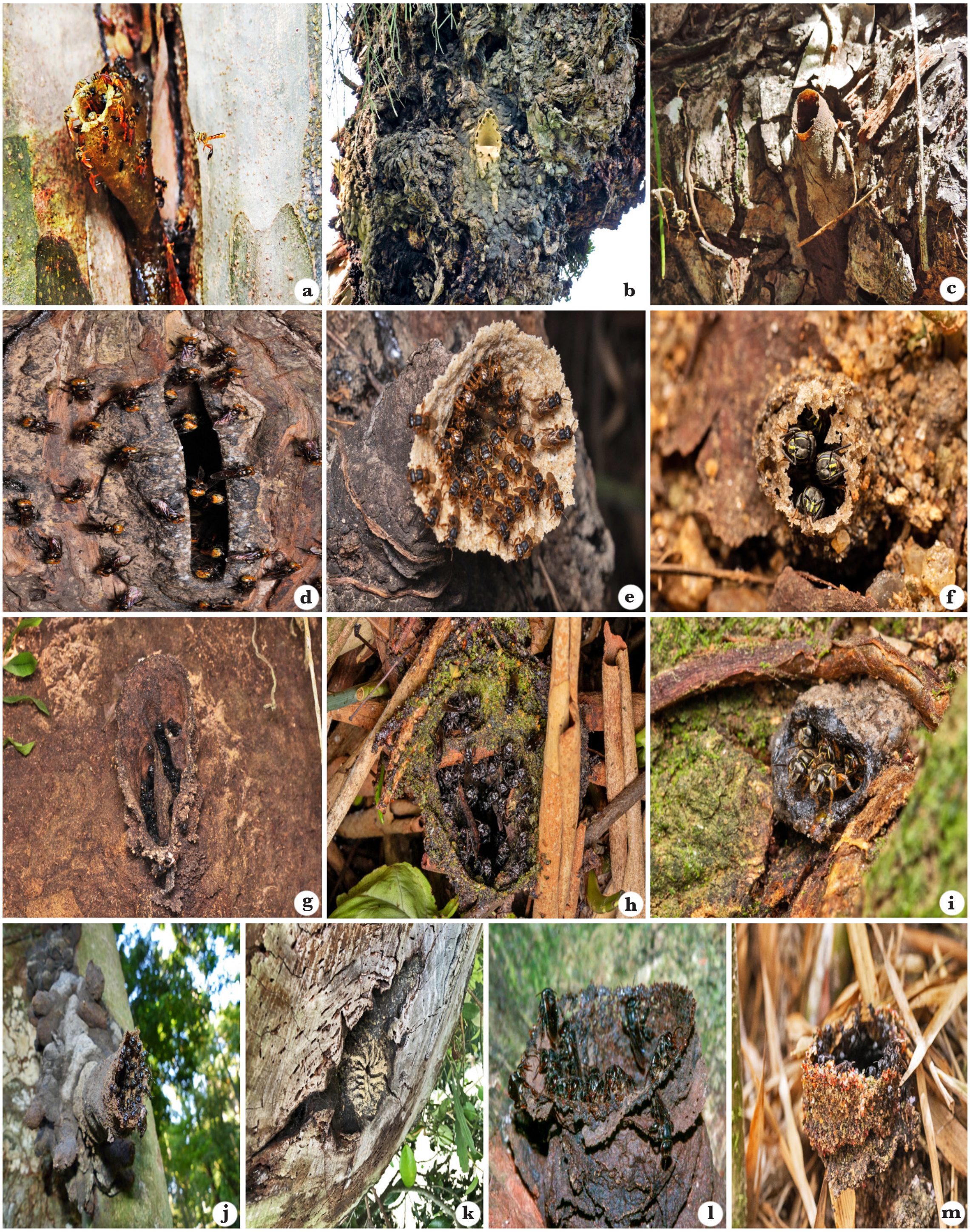

Figure 1 – a-m. Nest entrances of stingless bee species at the Botanical Garden of Rio de Janeiro, RJ, Brazil – a. *Tetragonisca angustula*; b. *Partamona helleri*; c. *Nannotrigona testaceicornis*; d. *Oxytrigona cagafogo*; e. *Scaptotrigona xanthotricha*; f. *Paratrigona subnuda*; g. *Trigona spinipes*; h. *Trigona hypogea*; i. *Plebeia droryana*; j. *Lestrimelitta tropica*; k. *Melipona (Eomelipona) bicolor*; l. *Scaptotrigona bipunctata*; m. *Trigona braueri*.

botanical species in the JBRJ arboretum, Gobatto *et al.* (2021) observed year- round flowering, high attractiveness to pollinators, and floral rewards such as pollen, nectar, oil, and resin. For nest construction, depending on the species, bees may also collect materials such as clay, mud, decaying wood, and fecal matter, in addition to resins and oils (Roubik 1989). The soils in the arboretum are generally of medium texture (EMBRAPA & IBAMA 1992), thus providing access to clay, as well as to resins found on branches and trunks.

Pollinator diversity and abundance are positively correlated with the connectivity of green areas across landscapes with varying degrees of urbanization (Graffigna *et al.* 2024). The arboretum is connected to a secondary Atlantic Forest, a recognized biodiversity hotspot, and adjoins other green spaces such as Parque Nacional da Tijuca. This enables it to function as both an ecological corridor and an urban refuge for pollinators (Gobatto *et al.* 2021). Together, these areas form one of the largest urban Atlantic Forest complexes globally.

In Meliponini, reduced genetic variability is influenced by several factors, including the queen's mating with a single male, the establishment of new colonies in close proximity to the mother colony, and the small effective population size (Nogueira-Neto 1997). In fragmented environments, this condition is exacerbated by the loss of genetic stock due to population isolation (Antonini *et al.* 2013). Bee body size is directly related to flight capacity and, in fragmented landscapes, may limit dispersal depending on distance (Araújo *et al.* 2004). In the arboretum, the connection to a forest fragment with high floristic diversity (JBRJ & IBAMA 1994) may favor gene flow in medium-sized species such as *T. hypogea*, capable of flying distances from 1,159 to 1,710 meters; in large-sized species such as *M. bicolor*, with flight capacity exceeding 2 kilometers; and even in small-sized species such as *P. droryana*, with a dispersal range of 621 to 951 meters (Araújo *et al.* 2004).

Over the course of eight years, there was an increase of 41 nests and a loss of 23 nests, resulting in a net gain of 33.96%. In surveys conducted in Juiz de Fora (MG), a 50% increase in the number of nests was recorded over the same period, attributed to urban expansion and the greater availability of artificial nesting niches for species such as *T. angustula* and *N. testaceicornis* (Vieira *et al.* 2016). However, urban sprawl, associated with pollution and deforestation, has led to significant declines in bee species diversity and abundance in urban areas of Curitiba (PR) (Taura & Laroca 2001). Despite the arboretum's exposure to urban pollution (Paixão & Silva 2021), the area remained stable throughout the study period, with no reduction in the vegetation or a significant increase in the urbanized area.

Efforts to relocate 17 nests from dead trees and branches to nearby trees in the case of *O. cagafogo*, *P. helleri*, and *T. spinipes* or to the stingless beekeeping site (meliponary) in the case of *T. angustula*, *N. testaceicornis*, *S. xanthotricha*, and *P. helleri* ensure their survival. This management prevents the destruction of the nests during and after tree felling, protecting them from exposure to predators and environmental stressors even when the nest itself has not been directly affected, as described by Eltz *et al.* (2003). However, colonies remain vulnerable to threats such as ants (Fig. 5), subterranean termite infestations (Roubik 1989) and the kleptobiotic species *L. tropica*, which attacks stingless bee nests to steal food and materials for its own nest construction (Nogueira-Neto 1997) (Fig. 1j).

The average nest heights of *T. angustula* and *N. testaceicornis* were 1.24 m and 1.84 m, respectively (Tab. 1). These values align with ranges reported in other studies in urban green areas, such as 2–2.7 m (Martins *et al.* 2015) and 1–1.57 m (Carvalho & Marchini 1999). The highest nest observed was for *P. helleri* at 35 m, located among the branches of *Araucaria bidwillii* Hook (Fig. 6a), while the lowest nest for this species was on *Encephalartos altensteinii* Lehm. at 1.80 m, attached

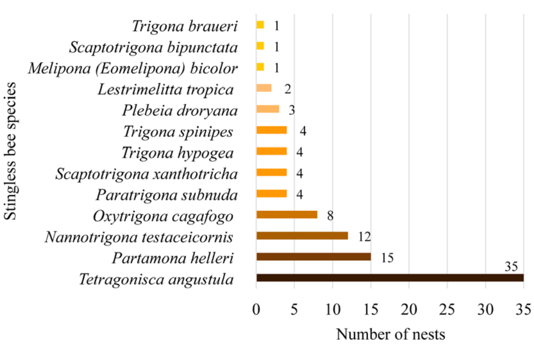

Figure 2 – Number of nests of stingless bee species at the Botanical Garden of Rio de Janeiro, RJ, Brazil.

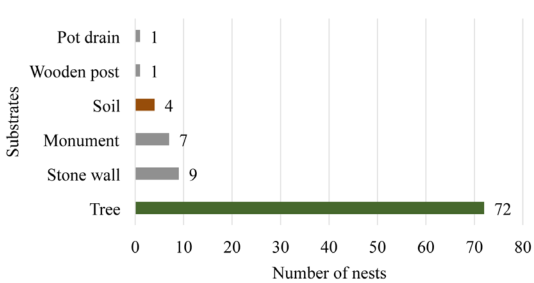

Figure 3 – Number of stingless bee nests in different substrates at the Botanical Garden of Rio de Janeiro, RJ, Brazil.

to the petioles of its leaves (Tab. 1; Fig. 6b). Nests of *P. helleri* and *T. spinipes* built on leaves or smooth trunks, such as those of *Roystonea oleracea* (Jacq.) O.F. Cook, were often susceptible to failure during heavy rain unless relocated (Fig. 6c-d). A single *P. helleri* nest relocated at a height of one meter was predated in the meliponary. The fauna at JBRJ is rich, and animals such as the Southern tamandua (*Tamandua tetradactyla*, Linnaeus 1758) and the South American raccoon (*Procyon cancrivorus*, G. Cuvier 1798) may predate exogenous nests located at accessible heights. Therefore, nests of *P. helleri* and *T. spinipes* are relocated to branches positioned at heights above 2.5 m.

Vieira *et al*. (2016) observed that *P. helleri* targeted artificial substrates for nesting and, at JBRJ, a single nest was located on a historical monument, the Portal of Belas Artes (Fig. 4d). Endemic to the Atlantic Forest, *P. helleri* adapts to open and urban areas when suitable materials for feeding and nest construction are available (Batista *et al.* 2003). Known for its efficiency as a pollen collector, the species shows both breadth and consistency in trophic resource selection (Carvalho *et al.* 1999; Ramalho 2004). At JBRJ, *P. helleri* nests were predominantly found on trees and palm trees, with 78.57% located near epiphytes, cacti, ferns, climbing plants, bromeliads and *Rhipsalis* species (Fig. 6e).

Figure 4 – a-g. Stingless bee nesting in artificial substrates at the Botanical Garden of Rio de Janeiro, RJ, Brazil – a. *Tetragonisca angustula* in a stone wall; b. *Tetragonisca angustula* in Wallace Fountain; c. *Nannotrigona testaceicornis* in Wallace Fountain; d. *Partamona helleri* in the Portal of Belas Artes; e. *Scaptotrigona xanthotricha* in the Statue of Nymph Eco; f. *Nannotrigona testaceicornis* in a wooden post; g. *Tetragonisca angustula* in a pot drain.

Figure 5 – The ant *Camponotus sericeiventris* (Guérin-Méneville 1838) on the entrance of a *Tetragonisca angustula* nest.

Over time, as nests grow, surrounding plants often colonize their exterior, intensifying the association (Wille 1983). However, plants were present at the entrances of only 21.73% of *T. angustula* nests and 12.5% of *N. testaceicornis* and *O. cagafogo* nests, with no records for other species.

The exogenous nests of *T. spinipes* were built on trunks at an average height of 16.2 m (Tab. 1). Similar findings were reported by Souza *et al.* (2005) and Aidar *et al.* (2013), who also observed *T. spinipes* nests placed high up, with Wille & Michener (1973) noting that nests of this species are typically found at a minimum height of 4 m above the ground. *T. spinipes* is a generalist and opportunistic pollinator, characterized by populous nests and wide dispersal capacity, earning it the designation of a "rescue pollinator" (Nogueira-Neto 1997; Jaffé *et al.* 2016).

For *Oxytrigona cagafogo*, the highest recorded nest was 2.4 m above the ground on a *Mangifera indica* L. tree, while the lowest was at 40 cm on the trunk of *Bridelia tomentosa* Blume (Tab. 1). *O. cagafogo* nests can contain up to 40,000 individuals, and the species produces caustic chemical secretions as a defense mechanism, enabling it to plunder the nests of other bees, including *Apis mellifera* Linnaeus, 1758. As a pollinator, *Oxytrigona tataira* (Smith, 1863) contributes to the reconstitution and conservation of tropical forests (Souza *et al.* 2007).

The exogenous species *P. helleri* and *T. spinipes* built the highest nests (Tab. 1). These findings may also reflect the difficulty of locating the nests of endogenous species, such as *T. angustula*, *N. testaceicornis*, and *P. droryana*, at higher elevations due to their small, inconspicuous entrances and short tubes (Fig. 1a,c,i) (Carvalho & Marchini 1999). Among the endogenous species, *S. xanthotricha*

Table 1 – Maximum, minimum, and average values (with standard error) for the height of stingless bee nest entrances in natural and artificial substrates, as well as the diameter at breast height (DBH) of trees, palm trees, and a bamboo clump used for nesting at the Botanical Garden of Rio de Janeiro, RJ, Brazil.

Stingless bee species	Height (m)			Diameter (DBH) (m)		
	Minimum	Average	Maximum	Minimum	Average	Maximum
Tetragonisca angustula	0	1.24 (± 0.03)	3.25	0.16	0.82 (± 0.02)	2.12
Partamona helleri	1.8	9.01 (± 2.29)	35	0.16	0.92 (± 0.19)	2.63
Nannotrigona testaceicornis	0.1	1.84 (± 0.27)	3.95	1.1	1.62 (± 0.15)	2.02
Oxytrigona cagafogo	0.4	1.56 (± 0,29)	2.4	0.48	0.92 (± 0.18)	2.1
Trigona hypogea	0	0	0	0.74	1.72 (±0.66)	3.7
Trigona spinipes	7.5	16.2 (±5.09)	30.93	0.4	0.88 (±0.20)	1.23
Scaptotrigona xanthotricha	4.8	7.83 (±1.92)	13.1	1.03	1.63 (±0.36)	2.3
Plebeia droryana	0.5	1.14 (±0.45)	1.6	1.38	1.56 (± 0.10)	1.69
Lestrimelitta tropica	0.2	2.9 (±2.70)	5.6	0.4	0.59 (± 0.19)	0.79
Scaptotrigona bipunctata	-	1.9	-	-	0.78	-
Melipona (Eomelipona) bicolor	-	6.7	-	-	1.56	-
Trigona braueri	0	0	0	-	2.77	-
Totals		**3.39 (± 0.6)**	**(n = 90)**		**1.09 (± 0.08)**	**(n = 72)**

stood out for its larger and more visible entrance tubes (Fig. 1e). According to Batista *et al.* (2003), this species can use less-protected cavities due to its aggressive defense against intruders.

Although *S. bipunctata* was the most common species in urban green areas of Poços de Caldas (MG) (Santos *et al.* 2023), only one endogenous nest was found at JBRJ, located in the trunk of *Guarea guidonia* (L.) Sleumer (Fig 1l; Tab. 2). This species is known for its numerous colonies, defensive behavior, and preference for large trees with entrance heights ranging from 0.38 to 1.5 m. It has been frequently recorded in urban green areas across southern and southeastern Brazil (Santos *et al.* 2020).

Melipona (Eomelipona) bicolor typically nests near the ground in cavities of mature hollow trees with large diameters (Nogueira-Neto 1997). However, at JBRJ, a single nest was recorded on the branch of a large *Dimocarpus longan* Lour. tree at 6.7 m above the ground. (Fig. 1k; Tab. 2). Witter *et al.* (2010) recorded that 50% of the nest entrances of *Melipona (Eomelipona) bicolor schencki* Gribodo, 1893 were located at heights below 28 cm, while the others were found at various elevations, including six nests above five meters, indicating that nest height may vary depending on the availability of suitable cavities for nesting. This species is polylectic and adapted to humid environments such as the Atlantic Forest (Hilário *et al.* 2000). It has been reported twice in forest remnants in the state of Minas Gerais (Antonini *et al.* 2013; Werneck & Faria-Mucci 2014; Santos *et al.* 2020) and does not commonly nest in anthropized areas, possibly due to its near-exclusive requirement for nesting in large-diameter trees (Hubbel & Johnson 1977; Eltz *et al.* 2003).

Stingless bees prefer trunks or branches of living trees with diameters exceeding 30 cm but can also nest in dead trees of various sizes (Kerr *et al.* 1996). At JBRJ, bees targeted living trees with an average trunk diameter of 1.09 m, as dead trees are removed upon dying (Tab. 1). According to Vieira *et al.* (2016), species such as *P. droryana*, *O. tataira*, and *S. bipunctata* build nests exclusively in tree hollows. The availability of these substrates, combined with the specific ecological requirements of each species, is a limiting factor for their survival in urban environments. The JBRJ has ancient trees that are preserved until they die, providing essential nesting habitats. In contrast, urban trees outside protected green areas are often pruned, rarely receive phytosanitary treatment, and are more likely to be removed.

The use of large fig trees for nesting resulted in a high average DBH for *N. testaceicornis* and *P. droryana*. However, the DBH values for *T. angustula*

Figure 6 – a-e. Nests of stingless bee at the Botanical Garden of Rio de Janeiro (RJ, Brazil) – a. *Partamona helleri* on *Araucaria bidwillii*; b. *Partamona helleri* on *Encephalartos altensteinii*; c. *Partamona helleri* on *Roystonea oleracea*; d. *Trigona spinipes* rescued from *Astrocaryum aculeatum*; e. *Partamona helleri* on epiphyte plants.

Table 2 – Plant species and their botanical families used for nesting by stingless bee species at the Botanical Garden of Rio de Janeiro (RJ, Brazil). Species abbreviations: Ta = *Tetragonisca angustula*; Ph = *Partamona helleri*; Nt = *Nannotrigona testaceicornis*; Oc = *Oxytrigona cagafogo*; Th = *Trigona hypogea*; Ts = *Trigona spinipes*; Pd = *Plebeia droryana*; Sx = *Scaptotrigona xanthotricha*; Lt = *Lestrimelitta tropica*; Mb = *Melipona (Eomelipona) bicolor*; Sb = *Scaptotrigona bipunctata* and Tb = *Trigona braueri*.

Plant species and botanical families	**Stingless bee species**												**Nest**	**Frequency**
	Ta	**Ph**	**Nt**	**Oc**	**Th**	**Ts**	**Pd**	**Sx**	**Lt**	**Mb**	**Sb**	**Tb**	**nº**	**%**
Moraceae													14	19.44
Ficus religiosa L.	1												1	1.39
Ficus gomelleira Kunth	1												1	1.39
Ficus virens Aiton	1		5				1						7	9.72
Ficus clusiifolia Schott	1		1										2	2.78
Ficus elastica Roxb. *ex* Hornem.		1											1	1.39
Artocarpus altilis (Parkinson) Fosberg				1									1	1.39
Ficus nymphaeifolia Mill.							1						1	1.39
Cupressaceae													11	15.28
Cupressus funebris Endl.	6			2									8	11.11
Chamaecyparis lawsoniana (A. Murray bis) Oerst.	1												1	1.39
Juniperus sp.	1												1	1.39
Taxodium distichum (L.) Rich.						1							1	1.39
Fabaceae													9	12.5
Machaerium scleroxylon Tul.	1												1	1.39
Libidibia ferrea (Mart. *ex* Tul.) L.P.Queiroz					1								1	1.39
Gliricidia sepium (Jacq.) Kunth			1				1						2	2.78
Tachigali paratyensis (Vell.) H.C. Lima				1									1	1.39
Erythrina sp.									1				1	1.39
Plathymenia reticulata Benth.								1					1	1.39
Cassia ferruginea (Schrad.) Schrad. *ex* DC.									1				1	1.39
Tipuana tipu (Benth.) Kuntze								1					1	1.39
Anacardiaceae													6	8.33
Mangifera indica L.	1	1		2									4	5.55
Spondias mombin L.					1								1	1.39
Astronium sp		1											1	1.39
Arecaceae													5	6.94
Syagrus romanzoffiana (Cham.) Glassman	1												1	1.39
Roystonea oleracea (Jacq.) O.F.Cook	1	1											2	2.78
Acrocomia aculeata (Jacq.) Lodd. *ex* Mart.		1											1	1.39
Astrocaryum aculeatum G.Mey.						1							1	1.39
Myrtaceae													5	6.94
Eugenia itaguahiensis Nied.	1												1	1.39
Eucalyptus sp.		1			1								2	2.78

Plant species and botanical families	**Stingless bee species**												**Nest**	**Frequency**
	Ta	**Ph**	**Nt**	**Oc**	**Th**	**Ts**	**Pd**	**Sx**	**Lt**	**Mb**	**Sb**	**Tb**	**nº**	**%**
Syzygium aromaticum (L.) Merr. & L.M.Perry		1											1	1.39
Eucalyptus globulus Labill.		1											1	1.39
Meliaceae													4	5.55
Carapa guianensis Aubl.			1										1	1.39
Guarea guidonia (L.) Sleumer	1										1		2	2.78
Khaya sp.						1							1	1.39
Sapindaceae													3	4.17
Dimocarpus longan Lour.	1							1		1			3	4.17
Sapotaceae													2	2.78
Pouteria caimito (Ruiz & Pav.) Radlk.		1											1	1.39
Mimusops balata (Aubl.) C.F. Gaerten.	1												1	1.39
Phyllanthaceae													1	1.39
Bridelia tomentosa Blume				1									1	1.39
Euphorbiaceae													1	1.39
Hura crepitans L.		1											1	1.39
Aquifoliaceae													1	1.39
Ilex x *altaclerensis* (London) Dallim.	1												1	1.39
Araucariaceae													1	1.39
Araucaria bidwillii Hook.		1											1	1.39
Bignoniaceae													1	1.39
Handroanthus chrysotrichus (Mart. *ex* DC.) Mattos		1											1	1.39
Elaeocarpaceae													1	1.39
Elaeocarpus angustifolius Blume					1								1	1.39
Pinaceae													1	1.39
Pinus sp.						1							1	1.39
Poaceae													1	1.39
Bambusa tuldoides Munro												1	1	1.39
Rhamnaceae													1	1.39
Sarcomphalus joazeiro (Mart.) Hauenschild				1									1	1.39
Salicaceae													1	1.39
Xylosma prockia (Turcz.) Turcz.	1												1	1.39
Sapindaceae													1	1.39
Litchi chinensis Sonn.	1												1	1.39
Zamiaceae													1	1.39
Encephalartos altensteinii Lehm.		1											1	1.39
Undetermined botanical family		1											1	1.39
Totals	23	14	8	8	4	4	3	3	2	1	1	1	72	100

were diluted due to its nests being distributed across various tree species and substrates (Tabs. 1-2). Despite their small size, *P. droryana* nests house populations ranging from 1,070 to 2,500 adults (Roldão-Sbordoni *et al.* 2018). Older trees with thicker trunks are more likely to be hollow, benefiting fast-growing nest-building species (Serra *et al.* 2009). For instance, *S. xanthotricha* often nests in hollows of thicker trunks (Tab. 1) and can form colonies of approximately 10,000 individuals with high honey productivity and multiplication potential (Carvalho-Zilse 2013). Notably, this species also built a nest inside a bronze statue, a replica of Nymph Eco by Mestre Valentim (Fig. 4e).

Stingless bees nested predominantly (90.28%) in botanical species with rough trunks. Exceptions included *T. angustula*, which nested on the smooth trunk of *Machaerium scleroxylon* Tul. (Fig. 1a), and *P. helleri*, which built two nests supported by branches of *Eucalyptus* sp. (Fig. 7a) and another one on bromeliads growing on the trunk of *R. oleracea* (Fig. 6c).

Trigona hypogea was found nesting near the ground, among the roots of four large trees with an average diameter of 1.72 m (Fig. 7b; Tabs. 1-2). This species, which has reduced corbiculae, collects protein-rich food from carcasses rather than pollen. It also produces honey from fruit juices and extrafloral nectaries (Noll *et al.* 1996). According to Camargo *et al.* (2023), this is the first recorded instance of *T. hypogea* in the state of Rio de Janeiro.

Although *Trigona braueri* can build aerial nests using tree trunks as support, at JBRJ, it nested in cavities at the base of a bamboo clump (*Bambusa tuldoides* Munro.), close to the ground (Fig. 7c). Found in preserved forests, this bee species from the Atlantic Forest Biome is a generalist, with recorded occurrences in coastal states (Silva *et al.* 2013). Similarly, *P. subnuda* is a generalist bee species from the Atlantic Forest, but it can also occur in poorly preserved forests and urban green areas (Mouga 2014). At JBRJ, *P. subnuda* nested in the soil, often in abandoned leaf-cutter ant nests on dirt paths and lawns (Fig. 1f). These nests were protected by fences to prevent trampling and lawn management interferences, as colonies typically do not survive such disturbances.

The conservation status of *T. angustula*, *P. helleri*, *N. testaceicornis*, *O. cagafogo*, *S. xanthotricha*, *P. subnuda*, *T. hypogea*, *P. droryana*, *M. (Eomelipona) bicolor*, and *S. bipunctata* is classified as "of least concern" according to SiBBr (2018). Data for *L. tropica* are considered "insufficient," and *T. spinipes* and *T. braueri* are not listed. None of the species appear on the Brazilian National List of Endangered Species (Brasil 2022).

Forty-eight tree species belonging to 21 botanical families hosted stingless bee nests, with Moraceae accounting for 19.44% and Cupressaceae for 15.28% of the nest sites (Tab. 2). The distribution of nests among botanical families was not uniform (Fig. 8), with a significant p-value of 0.043 indicating that nesting choices were not entirely random. Seven species of fig trees (Moraceae) were used for nesting, particularly *Ficus virens* Aiton, with seven trees bearing nests. Trees of the family Moraceae were colonized by *N. testaceicornis* (8.33%), *T. angustula* (5.55%), *P. droryana* (2.78%), *P. helleri* and *O. cagafogo* (1.39%) (Tab. 2). In a secondary forest fragment in Brazil, Moraceae trees housed 20% of stingless bee nests, 8% of which were on *Ficus* sp. (Correia *et al.* 2016). Similarly, surveys in Borneo (Eltz *et al.* 2003) and Jabuticabal, SP (Martins *et al.* 2015) found that *Ficus* sp. hosted nests of *N. testaceicornis*. The cavities and niches formed between the aerial roots of fig trees may facilitate the establishment of multiple small nests, as these trunks do not necessarily need to be hollow.

Stingless bee surveys frequently report multiple nests of different species in the same tree.

Figure 7 – a-c. Nests of stingless bee at the Botanical Garden of Rio de Janeiro (RJ, Brazil) – a. *Partamona helleri* on *Eucalyptus globulus*; b. *Trigona hypogea* on *Libidibia ferrea*; c. *Trigona braueri* on *Bambusa tuldoides*.

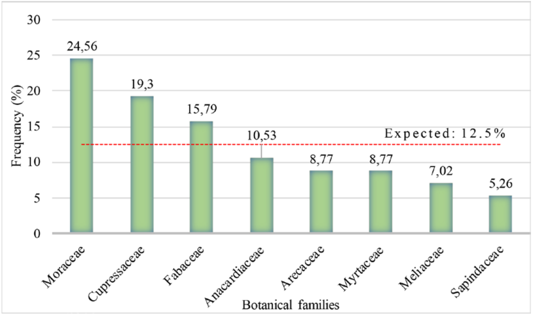

Figure 8 – Frequency distribution of stingless bee nests by botanical families (N ≥ 3) at the Botanical Garden of Rio de Janeiro. Chi-square goodness-of-fit test yielded a p-value of 0.043. The red line indicates the expected frequency of nests if distributed uniformly.

Eltz *et al.* (2003) recorded an average of 1.94 nests per tree, with up to eight nests belonging to three species in a single tree. They suggested that odors associated with existing nests may signal other bees that the tree is suitable for nesting. The defensive advantage of nesting near an aggressive colony combines with the use of large trees containing multiple suitable cavities, resulting in a tendency toward aggregation (Roubik 1989). For instance, a *Dimocarpus longan* tree at JBRJ housed nests of both *S. xanthotricha*, a very defensive species, and *M. bicolor* (Tab. 2). According to Roubik (1989), trees with adequate trunk diameter are frequently occupied by multiple colonies of *Scaptotrigona*, *Nannotrigona*, *Frieseomelitta*, *Tetragonisca*, and *Melipona*. Hubbell & Johnson (1977) suggested that colony spacing is regulated by pheromone marking of potential nest sites, worker recruitment, and aggression between workers from rival colonies. Slaa (2006) considered *N. testaceicornis*, *T. angustula*, and *P. droryana* to be non-aggressive species, which aligns with the present observation of multiple nests of these species on the same fig tree at JBRJ. The aggregation of colonies of docile species suggests that, in this case, nesting habits are not associated with defensive strategies (Roubik 1989).

Stingless bees distributed their 94 nests randomly across the study area. This pattern was also observed for the most frequent species - *T. angustula*, *P. helleri*, *N. testaceicornis*, and *O. cagafogo* - when analyzed separately. Although R indices below 1 suggested aggregated distributions, p-values above 0.05 indicated these patterns were not statistically significant, confirming randomness (Tab. 3; Fig. 9).

Among the 12 botanical families with nests of *T. angustula*, Cupressaceae accounted for 11.11% (Tab. 2). Many cypress trees at JBRJ have hollow trunks due to previous infestations by the underground termite *Coptotermes gestroi* (Wasmann), which have since been remedied. These hollows now provide suitable spaces for nesting (Taura & Laroca 1991). The cypress trees are old and resilient, with an average trunk DBH of 0.62 m. Most cypress species are resinous and some are aromatic (Earle 2024). These properties attract solitary bees, such as those of the genus *Xylocopa*, to build their nests while the aroma may repel bee parasites and offer protection (Blazer & Blazer 2013). Additionally, the resin, rich in diterpenes, is used by bees to produce Mediterranean propolis, a valuable product derived from *Cupressus sempervirens* L. (Bogdanov & Bancova 2016).

Partamona helleri colonized trees from 10 botanical families (Tab. 2). This host variety is likely due to its exogenous nests, which do not depend on hollows or niches in specific tree species.

Moraceae and Cupressaceae accounted for 3.92% and 1.23% of the tree specimens in the living collection, respectively (Almeida *et al.* 2024; JBRJ

Table 3 – Nearest neighbor analysis of stingless bee nest distribution patterns at the Botanical Garden of Rio de Janeiro (RJ, Brazil).

Stingless bee species	Nests	Distance		Index	Distribution	p-value	Classification
	nº	Observed	Expected				
Tetragonisca angustula	35	0.0004691	53.39	< 0.001	Aggregate	0.971	Random
Partamona helleri	15	0.0010274	81.55	< 0.001	Aggregate	1	Random
Nannotrigona testaceicornis	12	0.0004623	91.17	< 0.001	Aggregate	0.871	Random
Oxytrigona cagafogo	8	0.0018552	111.66	< 0.001	Aggregate	1	Random
All species	94	0.0002577	32.576	< 0.001	Aggregate	0.688	Random

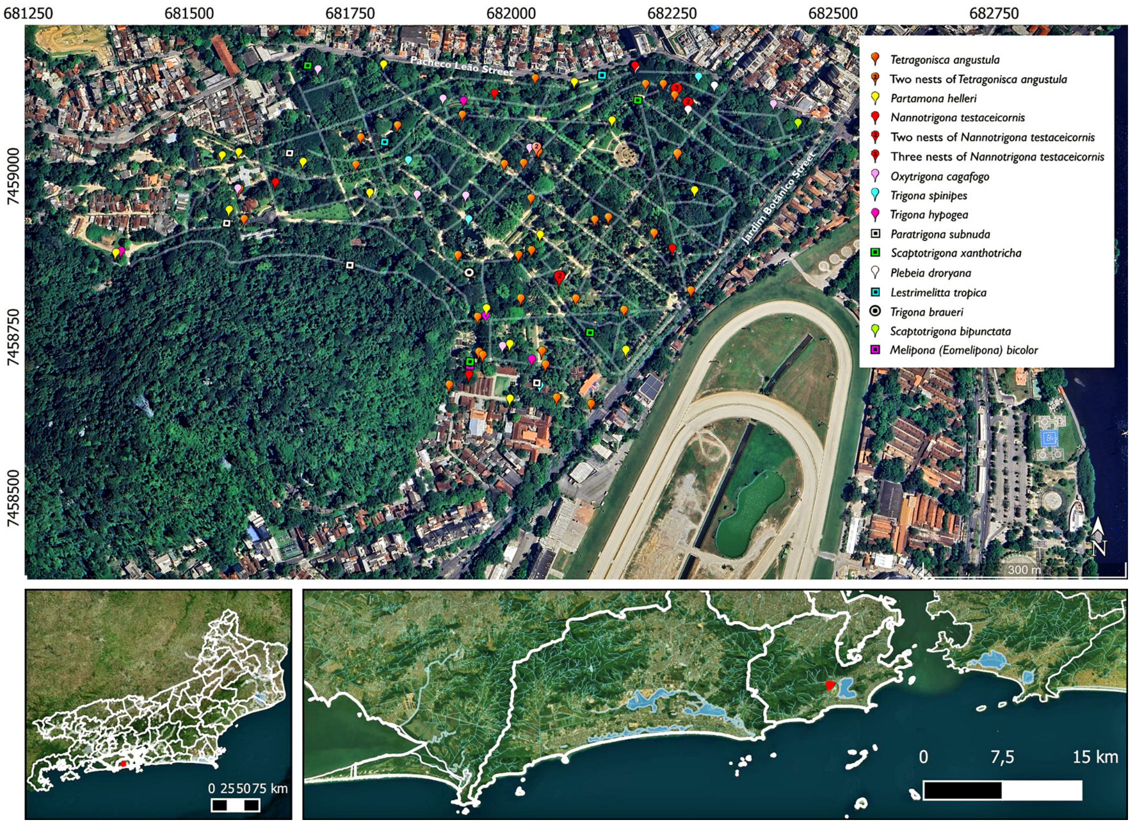

Figure 9 – Spatial distribution of 94 nests belonging to thirteen stingless bee species: *Tetragonisca angustula*, *Partamona helleri*, *Nannotrigona testaceicornis*, *Oxytrigona cagafogo*, *Trigona hypogea*, *Trigona spinipes*, *Plebeia droryana*, *Scaptotrigona xanthotricha*, *Paratrigona subnuda*, *Lestrimelitta tropica*, *Melipona (Eomelipona) bicolor*, *Scaptotrigona bipunctata*, and *Trigona braueri* at the Botanical Garden of Rio de Janeiro, RJ, Brazil.

2024). The preference of stingless bees for nesting in these families is significant and emphasizes the importance of preserving these specimens at JBRJ.

Nine botanical families hosted the 22 longest-lasting nests, with Cupressaceae and Fabaceae each accounting for 18.18% of these nests, Moraceae and Myrtaceae 13.63% each, and Meliaceae and Sapotaceae 9.09% each. The species *Cupressus funebris* Endl. hosted 11.11% of the nests, while *F. virens* hosted 9.72%. According to Roubik (1989), nest site selection is generally based on living trees and considers both the size of the cavity and the proximity to potential predators. Hubbell & Johnson (1977) proposed that the use of nesting cavities depends on their availability rather than specific tree species, while Laroca *et al.* (1982) concluded that the availability of nesting sites is a critical limiting factor for the establishment of bee species. According to Serra *et al.* (2009), the decision to nest in a particular tree species may be influenced by wood fiber density, as some tree species have highly resistant fibers that are less prone to forming cavities. The same authors suggested that the distribution of social bee nests may depend on a combination of factors, including the distribution and density of suitable nesting substrates, predation, anthropic interference, floral resource availability, and competition for food.

Apis mellifera builds exogenous nests but can also use cavities within or near the root systems of trees for nesting. For safety reasons, nests are removed and relocated to distant apiaries, thereby freeing nesting sites for stingless bees (Taura & Laroca 1991).

Despite increasing urbanization, pollution, noise, garden management practices, and other anthropogenic disturbances in the surrounding area, the variety of stingless bee species nesting in the arboretum remains notable. This diversity is likely supported by the connection to the secondary forest, availability of trophic resources and natural niches provided by the conservation of ancient trees. The management of exogenous nests that fall and endogenous nests in dead trees may also contribute to the thriving stingless bee population. Raising awareness and engaging field teams and maintenance staff responsible for buildings and monuments is essential to the effort of preserving nests. However, species that nest in the soil or between the roots of trees face challenges such as trampling, lawn management, and tree death. These factors require additional management efforts to ensure their survival.

Acknowledgements

The author would like to thank Diego Marinho (Museu Nacional/UFRJ), for identifying *T. hypogea*; Eduardo Andrade Botelho de Almeida (Universidade de São Paulo/USP), for identifying *S. bipunctata*, *S. xanthotricha* and *T. braueri*; Favízia Freitas de Oliveira (Universidade Federal da Bahia/UFBA), for identifying *L. tropica*; Ramon Lima Ramos (Universidade Federal da Bahia/UFBA), for identifying *O. cagafogo*; Alexandre Machado (JBRJ) (Figs. 1b,j,l; 4a-c,f-g; 6a-b; 7a,c); Ana Carolina Vilhena (JBRJ) (Figs. 1a,c; 6c); and João Felipe Herculano (Museu Nacional/UFRJ) (Figs. 1d-i,m; 4d-e; 7b), for providing photographs.

Data availability statement

In accordance with Open Science communication practices, the authors informs that the data are available at: <https://doi.org/10.5281/zenodo.17624085>.

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