

Urban nesting ecology of stingless bees (Apidae: Meliponini) and *Apis mellifera* in Santa Cruz de la Sierra, Bolivia

Ecología de nidificación urbana de las abejas sin aguijón (Apidae: Meliponini) y de *Apis mellifera* en Santa Cruz de la Sierra, Bolivia

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Abstract: Urbanization is rapidly transforming tropical landscapes, yet its effects on the nesting ecology of stingless bees remain poorly understood, particularly in South American cities. This study assessed the diversity, nesting ecology, and environmental drivers of nesting patterns of stingless bees (Meliponini) and *Apis mellifera* within the urban core of Santa Cruz de la Sierra, Bolivia. Bee nests were surveyed over a 36-month period throughout the city, recording nesting substrate, nest height, entrance orientation, surrounding vegetation cover, and co-occurrence among colonies within nesting substrates. Species richness was evaluated using rarefaction and extrapolation analyses, whereas species co-occurrence analyses were used to evaluate substrate sharing and Canonical Correspondence Analysis was used to identify associations between community composition and environmental variables. A total of 592 nests belonging to 13 bee species were recorded, including 12 stingless bee species and *Apis mellifera*. Species accumulation curves indicated that sampling captured most of the expected urban bee diversity. Nesting substrates, vegetation cover, and nest height significantly influenced community composition, whereas nest entrance orientation showed no detectable effect. Most stingless bees were associated with trees and termite nests, while *Apis mellifera* nested predominantly in concrete electric poles and other artificial structures. Species differed markedly in their tendency to aggregate within nesting substrates, although interspecific substrate sharing did not differ from random expectations. These findings demonstrate that highly urbanized tropical landscapes can support diverse stingless bee communities when suitable nesting substrates and vegetated habitats are maintained. Conserving heterogeneous urban habitats, including mature trees, termite nests, and green spaces, is likely to play an important role in sustaining native bee diversity in expanding tropical cities.

Key words: Environmental drivers, nesting substrates, pollinator conservation, species co-occurrence, vegetation cover.

Resumen: La urbanización está transformando rápidamente los paisajes tropicales; sin embargo, sus efectos sobre la ecología de nidificación de las abejas sin aguijón siguen siendo poco conocidos, particularmente en las ciudades sudamericanas. En este estudio se evaluó la diversidad, la ecología de nidificación y los factores ambientales asociados a los patrones de nidificación de las abejas sin aguijón (Meliponini) y de *Apis mellifera* en el área urbana de Santa Cruz de la Sierra, Bolivia. Los nidos fueron registrados

durante un período de 36 meses en toda la ciudad, documentando el sustrato de nidificación, la altura de la entrada del nido, la orientación de la entrada, la cobertura vegetal circundante y la coocurrencia de colonias dentro de los mismos sustratos de nidificación. La riqueza de especies se evaluó mediante análisis de rarefacción y extrapolación, mientras que los análisis de coocurrencia de especies se utilizaron para evaluar el uso compartido de sustratos y el Análisis Canónico de Correspondencia (CCA) para identificar asociaciones entre la composición de la comunidad y las variables ambientales. Se registraron un total de 592 nidos pertenecientes a 13 especies de abejas, incluyendo 12 especies de abejas sin aguijón y *Apis mellifera*. Las curvas de acumulación de especies indicaron que el muestreo capturó la mayor parte de la diversidad urbana esperada. El sustrato de nidificación, la cobertura vegetal y la altura del nido influyeron significativamente en la composición de la comunidad, mientras que la orientación de la entrada del nido no mostró un efecto detectable. La mayoría de las abejas sin aguijón se asociaron con árboles y termiteros, mientras que *Apis mellifera* nidificó predominantemente en postes de concreto y otras estructuras artificiales. Las especies difirieron marcadamente en su tendencia a agregarse dentro de un mismo sustrato de nidificación, aunque el uso compartido de sustratos entre especies no difirió de lo esperado por azar. Estos resultados demuestran que los paisajes tropicales altamente urbanizados pueden albergar comunidades diversas de abejas sin aguijón cuando se mantienen sustratos de nidificación adecuados y hábitats urbanos con vegetación. La conservación de hábitats urbanos heterogéneos, incluyendo árboles maduros, termiteros y áreas verdes, probablemente desempeñe un papel importante en el mantenimiento de la diversidad de abejas nativas en ciudades tropicales en expansión.

Palabras clave: factores ambientales, sustratos de nidificación, conservación de polinizadores, coocurrencia de especies, cobertura vegetal.

INTRODUCTION

Urbanization is one of the principal drivers of global habitat transformation, profoundly altering species composition, ecological interactions, and ecosystem functions (McKinney 2008, Aronson *et al.* 2014). Although urban expansion is generally associated with biodiversity loss, cities can also function as important refuges for wildlife when green infrastructure such as parks, gardens, street trees, and remnant vegetation is preserved and properly managed (Hall *et al.* 2017, Baldock 2020). Understanding how species respond to urban environments is therefore essential for designing management strategies that reconcile biodiversity conservation with urban development.

Bees are among the most important pollinators in both natural and urban ecosystems, providing essential pollination services that sustain plant reproduction and ecosystem functioning (Potts *et al.* 2010). Conserving bee diversity requires ecological knowledge of species distributions, nesting requirements, and habitat associations (Freitas *et al.* 2009). Stingless bees (Apidae: Meliponini) are particularly important throughout tropical and subtropical regions because of their remarkable diversity, eusocial behavior, and effectiveness as pollinators of both native and cultivated plants (Roubik 1989,

Michener 2013). Nevertheless, urbanization may reduce the availability of suitable nesting cavities, alter floral resource distribution, and increase interactions with introduced species, potentially reshaping the composition and structure of native bee communities.

Because colony persistence depends directly on the availability of suitable nesting sites, studies of nesting ecology provide one of the most informative approaches for understanding the status of stingless bee populations in both natural and human-modified landscapes (Cortopassi-Laurino *et al.* 2006). Previous research has shown that nesting patterns are influenced by multiple environmental factors, including substrate availability, vegetation cover, cavity characteristics, and landscape structure (Samejima *et al.* 2004, Kajoibe & Roubik 2006, Roubik 2023). The spatial arrangement of colonies also provides ecological information, as multiple colonies may occur within the same nesting substrate. Such aggregations can arise from species-specific nesting behavior, limited dispersal during colony reproduction, or the concentration of suitable nesting cavities (Camargo & Pedro 2003, Eltz *et al.* 2003, Roubik 2006). At finer spatial scales, characteristics of host trees, such as diameter at breast height (DBH), height, and species identity, have also been proposed as factors affecting cavity availability and nest establishment (Antonini & Martins 2003, Serra *et al.* 2009, Silva *et al.* 2013). Furthermore, evaluating the coexistence between native stingless bees and the introduced honey bee (*Apis mellifera*) is increasingly relevant because both groups may exploit similar floral resources and, under some conditions, compete for nesting cavities in urban landscapes (Cunningham *et al.* 2022, Iwasaki & Hogendoorn 2022, Casanelles-Abella *et al.* 2025).

Tropical cities are undergoing some of the fastest rates of urban expansion worldwide, yet they remain markedly underrepresented in urban ecology research relative to temperate systems, despite their disproportionate biodiversity and their value as early indicators of how ecosystems may respond to combined urbanization and climate change (Bonebrake *et al.* 2025). This gap is particularly evident for pollinators: although studies of urban bee communities have grown in number globally, information on the nesting ecology of stingless bees remains scarce in many tropical regions, particularly in Bolivia. Santa Cruz de la Sierra is the country's largest urban center with more than 82 % of the municipal population concentrated within the urban core, representing approximately 22,8 % of Bolivia's total population (INE 2025). Bolivia harbors at least 121 described species of stingless bees (Céspedes-Llave 2024), yet ecological studies have focused almost exclusively on natural or peri-urban environments. For example, Townsend (2016) and Saravia-Nava *et al.* (2018) investigated bee communities in the Potrerillos del Güendá Private Reserve, located approximately 30 km from the city, whereas no comprehensive assessment has been conducted within the urban core of Santa Cruz de la Sierra. Consequently, it remains unclear how urban environmental conditions influence the diversity, nesting strategies, and spatial organization of stingless bee communities in Santa Cruz de la Sierra.

To address this knowledge gap, the present study characterized the diversity and nesting ecology of stingless bees together with the introduced honey bee (*Apis mellifera*) within

the urban core of Santa Cruz de la Sierra, Bolivia. Five research questions were addressed: (1) What is the diversity and community structure of nesting stingless bees in the urban landscape? (2) Do stingless bee species differ in their tendency to aggregate within or share nesting substrates? (3) Which environmental variables, including nesting substrate, surrounding vegetation cover, nest height, and entrance orientation, best explain variation in nesting patterns across the city? (4) Do stingless bees and *Apis mellifera* exhibit contrasting nesting strategies within the urban environment? and (5) Within arboreal substrates, are nest occurrence and community composition associated with dendrometric characteristics such as DBH, tree height, or host tree species? Based on previous studies, vegetation cover and nesting substrate were expected to play a stronger role in structuring urban bee communities than nest entrance orientation because both influence habitat availability and nesting opportunities. Tree attributes associated with cavity availability, particularly DBH and tree height, were also expected to influence nesting within arboreal substrates, although the relative importance of these factors in highly urbanized tropical landscapes remains poorly understood (Baldock 2020).

MATERIALS AND METHODS

Study area

The study was conducted in the city of Santa Cruz de la Sierra (approximately 17°47'S, 63°11'W), located in the eastern lowlands of Bolivia at an elevation of 400–420 m.a.s.l. (Figure 1). This municipality is the principal urban center of eastern Bolivia and the most populated city in the country, with an estimated urban population of 1,6 million inhabitants (INE 2025). The urban area covers approximately 38,475 ha (GAMSCS 2023) and has experienced rapid expansion in recent decades, a process accompanied by a substantial reduction in natural vegetation. Between 1986 and 2019, approximately 36,947 ha of tree cover were lost within the municipal limits (Maillard *et al.* 2020).

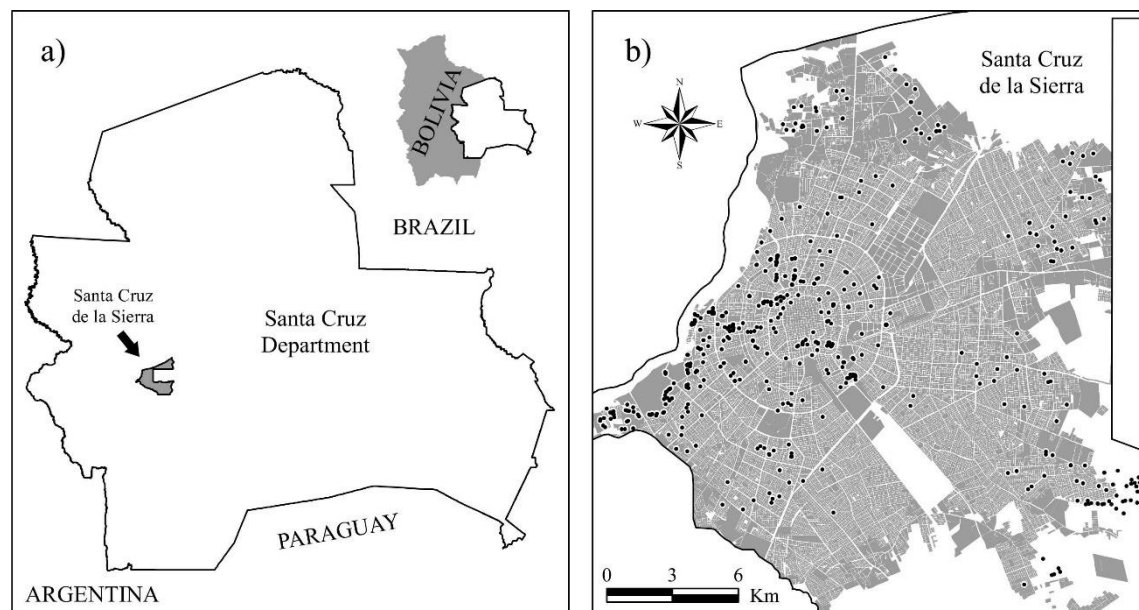


Figure 1. a) Location of Santa Cruz Department in Bolivia. b) Urban area of Santa Cruz de la Sierra showing the distribution of recorded bee nests.

According to the Köppen–Geiger classification, the climate is tropical savanna (Beck *et al.* 2023), with a mean annual precipitation of $1,540 \pm 216$ mm and an average annual temperature of 24.8°C during 2010–2023. Recorded temperatures range from 6.3°C to 41.0°C , and the region is periodically affected by cold southern air masses ("surazos") during the austral winter (ICE 2024).

Biogeographically, Santa Cruz de la Sierra is located at the transition between three major ecoregions: the southwestern Amazon, the Chiquitano Dry Forest, and the Gran Chaco (Ibisch *et al.* 2003). According to Navarro & Ferreira (2007), the municipality originally comprised Chiquitano forest on alluvial-aeolian sands, mesophytic-phreatophytic forest on alluvial plains, and riparian forests along the Piraí River dominated by *Erythrina dominguezii*–*Astronium urundeuva* and *Albizia niopoides*–*Gallesia integrifolia* associations. Urban expansion and habitat fragmentation have progressively transformed these ecosystems, leaving native vegetation largely restricted to parks, university campuses, riparian corridors, municipal reserves, and other isolated green spaces embedded within the urban matrix.

Data collection

Nest records were obtained through opportunistic sampling conducted between September 2021 and July 2025 along urban routes associated with daily activities. Sampling followed a cumulative inventory approach in which each nest was georeferenced and characterized only once, at the time of its first detection. A nest was considered active only when clear evidence of colony occupancy was observed, including the regular entrance and exit of foraging workers or active defensive behavior at the nest entrance. Consequently, although sampling extended over 36 months, the dataset represents a cumulative spatial inventory of active colonies rather than a temporal assessment of colony persistence.

Field surveys were conducted daily for 30–60 min during some periods and two to three times per week during others, averaging approximately ten sampling days per month. Surveys were performed between 09:00 and 17:00 h and focused primarily on parks, plazas, boulevards, sports fields, and other urban green areas, complemented by searches along sidewalks, streets, avenues, and accessible vacant lots.

Potential nesting substrates were classified as either natural (living trees, dead trees, terrestrial termite mounds, and arboreal termite mounds) or artificial (walls, concrete electric poles, power meter pillars, and other human-made structures). Each substrate was visually inspected from multiple angles, including the entire trunk and canopy when trees were examined.

For each active colony, geographic coordinates, nesting substrate, nest entrance height, and entrance orientation were recorded. For tree-nesting colonies, the host tree species, diameter at breast height (DBH), and total tree height were also measured. DBH was measured at 1.3 m above ground using a measuring tape (precision ± 5 cm), total height was visually estimated to the nearest 0.5 m, and entrance orientation was determined using a digital compass application and subsequently verified in Google Maps to ensure

consistency with true north. All records were photographically documented and stored using customized digital forms created in KoboToolbox and collected through KoBoCollect (versions 2021.2.4–2024.2.4) on Android devices.

To characterize the landscape surrounding each nest, vegetation cover was quantified within a 300 m radius buffer centered on each colony. This metric was estimated from a Sentinel-2A satellite image (10 m spatial resolution) acquired on 10 February 2026 using the Normalized Difference Vegetation Index (NDVI). Pixels with NDVI values > 0.30 were classified as vegetation, an approach validated for discriminating active green cover from urban artificial surfaces and bare soil backgrounds (Esau *et al.* 2016), ensuring an accurate extraction of urban vegetation abundance (Annatakarn *et al.* 2022).

Host trees were identified through comparison with taxonomic keys and botanical plates from the Flora Catalogue of Santa Cruz de la Sierra (GAMSCS 2017). Difficult identifications were confirmed through consultation with botanical specialists using photographs of leaves, bark, flowers, and fruits. Scientific names were subsequently verified using the International Plant Name Index (<https://www.ipni.org>) and The World Flora Online (<https://www.worldfloraonline.org>).

Bee identification was based on external morphology and nest entrance architecture without collecting voucher specimens. Photographs of the nest entrance and, when possible, of workers at the entrance were taken at each colony to support the identification and differentiation of morphospecies. *Apis mellifera* was identified directly because it is the only representative of its genus in the Americas. For stingless bees, identification combined nest entrance characteristics (shape, size, and coloration) with external worker morphology (body size, coloration, and pubescence). The designation "aff." (affinis) was applied to taxa whose morphology closely matched published descriptions in Townsend *et al.* (2021) and Morón *et al.* (2023) for genera in which no alternative regional species are currently known. Conversely, the designation "sp." was retained for genera such as *Partamona*, *Melipona*, and *Plebeia*, whose regional diversity or unresolved taxonomy prevented reliable species-level identification without examination of diagnostic morphological characters.

Data analysis

Species richness was evaluated using sample-based rarefaction curves based on the Mao Tau estimator implemented in the vegan package v2.7-1 (Chiarucci *et al.* 2008, Colwell *et al.* 2012, Oksanen *et al.* 2022). To account for undetected rare species, Chao1 and ACE richness estimators were also calculated (Chao 1984, Chao & Lee 1992). Inventory completeness was assessed using sample coverage implemented in the iNEXT package v3.0.2 (Hsieh *et al.* 2016). Community diversity was characterized using the Shannon (H'), Simpson (D'), and Pielou (J') indices.

Patterns of colony aggregation were evaluated for species represented by at least ten nests. Differences in the frequency of conspecific and interspecific co-occurrence within the same substrate were assessed using chi-square tests. Niche overlap in substrate use was quantified using Pianka's niche overlap index (O_{ij} ; Pianka 1973), and statistical significance was evaluated with null models based on 5,000 random permutations (Gotelli & Graves 1996, Gotelli 2000).

To identify the environmental factors associated with nesting patterns across the urban landscape, Canonical Correspondence Analysis (CCA) was performed using the *vegan* package (Oksanen *et al.* 2022). Community matrices (bee species $\times$ nesting substrate) were related to environmental variables including substrate type, vegetation cover, nest entrance height, and entrance orientation. For this analysis, substrate categories were consolidated to reduce the number of levels and avoid disproportionate representation among groups. The original classification was therefore simplified into four broader categories: Tree (including living and dead trees), Termite nest (including terrestrial and arboreal termite mounds), Concrete electric poles, and Other (including walls, power meter pillars, and other human-made structures). This grouping was applied exclusively for multivariate analyses and did not modify the detailed substrate classification used for descriptive analyses. To evaluate whether *Apis mellifera* influenced the observed community structure, the analysis was performed twice: first including *Apis mellifera* and subsequently excluding it to examine patterns within the stingless bee assemblage alone. An additional CCA was restricted to colonies nesting in trees to assess whether variation in arboreal community composition was associated with dendrometric variables, including DBH, total tree height, and host tree species identity. The significance of the overall models and individual explanatory variables was assessed using ANOVA-like permutation tests with 999 permutations. All analyses were performed in R v4.5.1 (R Core Team 2025), adopting a significance level of $\alpha = 0.05$.

RESULTS

Diversity and community structure

A total of 592 active bee nests were recorded throughout the urban area of Santa Cruz de la Sierra. Of these, 463 nests belonged to stingless bees (Apidae: Meliponini), representing eight genera and twelve species, whereas the remaining 129 nests corresponded to *Apis mellifera*. Among stingless bees, *Plebeia* was the most species-rich genus (three species), followed by *Scaptotrigona* and *Trigona* (two species each). The remaining genera (*Lestrimelitta*, *Melipona*, *Nannotrigona*, *Partamona*, and *Tetragonisca*) were each represented by a single species. Nest entrance morphology was distinctive for each taxon, allowing reliable field recognition (Figure 2).

The stingless bee community exhibited an uneven abundance distribution (Table 1). *Partamona* sp. was the most abundant species, followed by *Scaptotrigona* aff. *depilis*, *Tetragonisca* aff. *fiebrigi*, and *Plebeia* sp. 1. In contrast, *Plebeia* sp. 3, *Scaptotrigona* aff. *polysticta*, and *Nannotrigona* aff. *melanocera* were represented by relatively few nests, whereas *Melipona* sp. was recorded only once. Considering the complete eusocial bee community, *Apis mellifera* was the second most abundant species after *Partamona* sp. (Table 1).

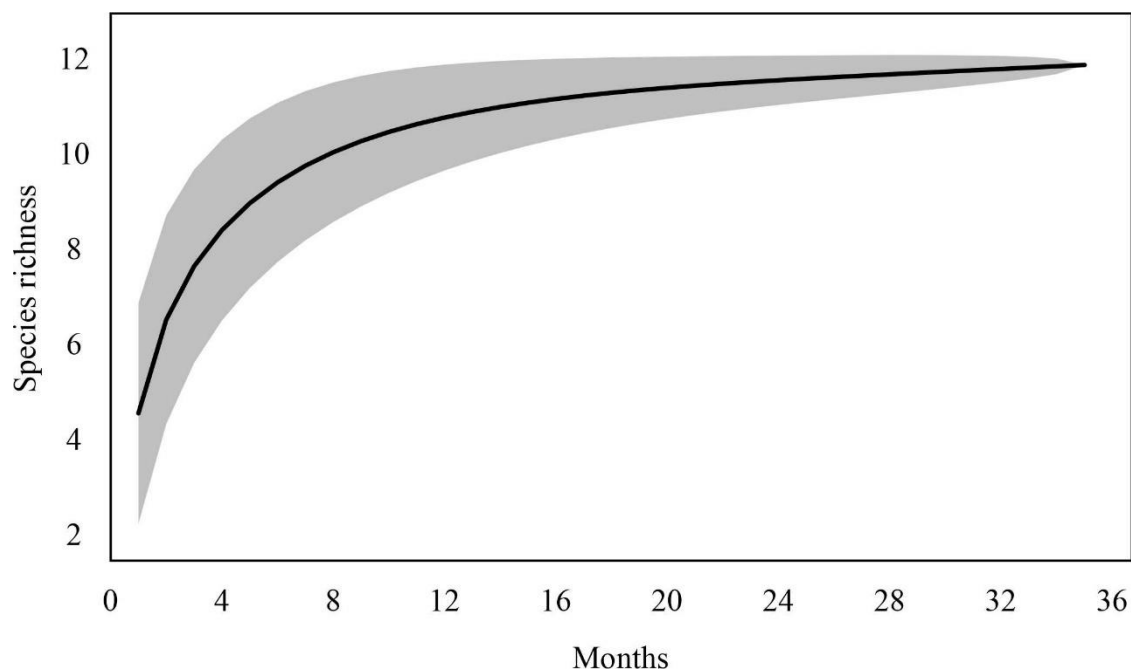
The species accumulation curve approached an asymptote (Figure 3). The Chao1 estimator closely matched the observed richness, estimating 12.0 species (95 % CI = 11.06–12.94), while the ACE estimator predicted 12.47 species. Sample completeness reached 98.71 %. The stingless bee community was characterized by a Shannon diversity index of $H' = 1.91$, a Simpson index of $D' = 0.82$, and a Pielou evenness index of $J' = 0.77$.



Figure 2. Nest entrances of stingless bees in Santa Cruz de la Sierra. a) *Lestrimelitta* sp., b) *Melipona* sp., c) *Nannotrigona* aff. *melanocera*, d) *Partamona* sp., e) *Plebeia* sp. 1, f) *Plebeia* sp. 2, g) *Plebeia* sp. 3, h) *Scaptotrigona* aff. *depilis*, i) *Scaptotrigona* aff. *polysticta*, j) *Tetragonisca* aff. *fiebrigi*, k) *Trigona* aff. *branneri*, l) *Trigona* aff. *chanchamayoensis*.

Table 1. Number of nests (N), relative frequency (F), and nesting substrates used by stingless bees and *Apis mellifera* in the urban core of Santa Cruz de la Sierra.

Species observed	Local name	N	F (%)	Substrate	
				Natural	Artificial
<i>Apis mellifera</i>	Extranjera	129	21.79	14 (11 %)	115 (89 %)
<i>Lestrimelitta</i> sp.	Limón	13	2.20	12 (92 %)	1 (8 %)
<i>Melipona</i> sp.	Erereú	1	0.17	1 (100 %)	0 (0 %)
<i>Nannotrigona</i> aff. <i>melanocera</i>	—	9	1.52	3 (33 %)	6 (67 %)
<i>Partamona</i> sp.	—	131	22.13	126 (96 %)	5 (4 %)
<i>Plebeia</i> sp. 1	Boca de vieja	72	12.16	69 (96 %)	3 (4 %)
<i>Plebeia</i> sp. 2	—	22	3.72	20 (91 %)	2 (9 %)
<i>Plebeia</i> sp. 3	—	4	0.68	0 (0 %)	4 (100 %)
<i>Scaptotrigona</i> aff. <i>depilis</i>	Obobosí	94	15.88	53 (56 %)	41 (44 %)
<i>Scaptotrigona</i> aff. <i>polysticta</i>	Suro	8	1.35	8 (100 %)	0 (0 %)
<i>Tetragonisca</i> aff. <i>fiebrigi</i>	Señorita	86	14.53	59 (69 %)	27 (31 %)
<i>Trigona</i> aff. <i>branneri</i>	Posetacú	12	2.03	11 (100 %)	0 (0 %)
<i>Trigona</i> aff. <i>chanchamayoensis</i>	Zarco	11	1.86	12 (100 %)	0 (0 %)
Total		592	100.00	388	204

**Figure 3.** Sample-based rarefaction curve showing observed stingless bee richness and its standard deviation in the urban core of Santa Cruz de la Sierra.

Nest aggregation and substrate sharing

A total of 504 nesting substrates were occupied by bees, comprising 311 natural and 193 artificial structures. Among natural substrates, trees were the most frequently occupied, accounting for 252 nests distributed across 204 individual trees belonging to 22 botanical families and 55 tree species (46 identified species, six unidentified trees, and nine dead trees). The tree species hosting the greatest numbers of nests were *Ficus elastica*, *Ficus pertusa*, *Neltuma chilensis*, *Chloroleucon tenuiflorum*, and *Cojoba arborea*, whereas *Tipuana tipu* supported the highest bee species richness, with nests of seven bee species recorded in ten individual trees (Appendix 1). Although most occupied substrates contained a single colony, multiple occupation was also recorded, occurring in 13,10 % of all occupied substrates. Ground termite mounds exhibited the highest frequency of multiple occupancy, followed by living trees, whereas no cases were recorded in arboreal termite mounds or dead trees (Table 2).

Table 2. Frequency of single and multiple nest occurrences per substrate type.

Substrate category	Substrate type	Number of nest per substrate					Total
		1 nest	2 nests	3 nests	4 nests	5 nests	
Natural	Living tree	162	22	9		2	195
	Dead tree	9					9
	Ground termite mound	73	18	2	1	1	95
	Arboreal termite mound	12					12
Artificial	Concrete electric pole	145	6				151
	Power meter pillar	14	2				16
	Wall	11	2				13
	Other	12	1				13
Total		438	51	11	1	3	504

Overall, 26.01 % of all recorded nests occurred in substrates shared with at least one additional colony. The frequency of conspecific aggregation differed significantly among species ($\chi^2 = 46.85$; $p < 0.001$). *Partamona* sp. showed the highest proportion of multiple colonies occupying the same substrate, followed by *Plebeia* sp. 1 and *Scaptotrigona* aff. *depilis*. In contrast, no cases of conspecific aggregation were recorded for *Apis mellifera*, *Lestrimelitta* sp., *Trigona* aff. *branneri*, or *Trigona* aff. *chanchamayoensis* (Table 3).

The frequency of interspecific substrate sharing also differed significantly among species ($\chi^2 = 62.97$; $p < 0.001$). *Plebeia* sp. 1 exhibited the highest proportion of shared substrates with other bee species, followed by *Lestrimelitta* sp., whereas *Apis mellifera* and *Partamona* sp. showed comparatively low frequencies of interspecific co-occurrence. No cases of interspecific substrate sharing were recorded for *Trigona* aff. *branneri* or *Trigona* aff. *chanchamayoensis*. The most frequent species combinations involved *Plebeia* sp. 1 with *Tetragonisca* aff. *fiebrigi*, *Lestrimelitta* sp., and *Plebeia* sp. 2. Despite these differences in observed frequencies, permutation tests detected no significant departures from random expectations ($p > 0.05$), indicating that interspecific co-occurrence did not differ from that expected under random substrate occupation (Table 3).

Table 3. Co-occurrence matrix of bee species occupying the same nesting substrate. Dark gray diagonal cells indicate multiple colonies of the same species within a single substrate, whereas light gray off-diagonal cells represent co-occurrence of different species. AM: *Apis mellifera*; Lsp: *Lestrimelitta* sp.; Msp: *Melipona* sp.; NM: *Nannotrigona* aff. *melanocera*; Psp: *Partamona* sp.; Pb1: *Plebeia* sp. 1; Pb2: *Plebeia* sp. 2; Pb3: *Plebeia* sp. 3; SD: *Scaptotrigona* aff. *depilis*; SP: *Scaptotrigona* aff. *polysticta*; TF: *Tetragonisca* aff. *fiebrigi*; TB: *Trigona* aff. *branneri*; TC: *Trigona* aff. *chanchamayoensis*.

	AM	Lsp	Msp	NM	Psp	Pb1	Pb2	Pb3	SD	SP	TF	TB	TC
AM													
Lsp													
Msp													
NM			1										
Psp					23								
Pb1	1	4			1	8							
Pb2	1					3	1						
Pb3													
SD	1	1				4	2		9				
SP									1	1			
TF	1				2	11	1		3		3		
TB													
TC													

Environmental drivers of nesting patterns

The Canonical Correspondence Analysis (CCA) revealed that environmental variables significantly explained variation in bee community composition across the urban landscape. Both the complete community model, including *Apis mellifera*, and the stingless bee model were significant according to permutation tests ($p = 0.001$). In the complete community analysis, the first two axes explained 13.63 % of the constrained variation (Axis 1 = 8.38 %; Axis 2 = 5.25 %), whereas the native community model explained 15.02 % (Axis 1 = 9.10 %; Axis 2 = 5.92 %).

Across both analyses, nesting substrate and nest height were the strongest predictors of community structure, showing significant effects in permutation tests ($F > 21.10$; $p = 0.001$). Vegetation cover also contributed significantly to explaining community composition, with a stronger effect in the complete community model ($F = 6.04$; $p = 0.001$) than in the stingless bee model ($F = 3.27$; $p = 0.002$). In contrast, nest entrance orientation did not significantly influence community composition in either analysis ($F \leq 1.23$; $p \geq 0.163$).

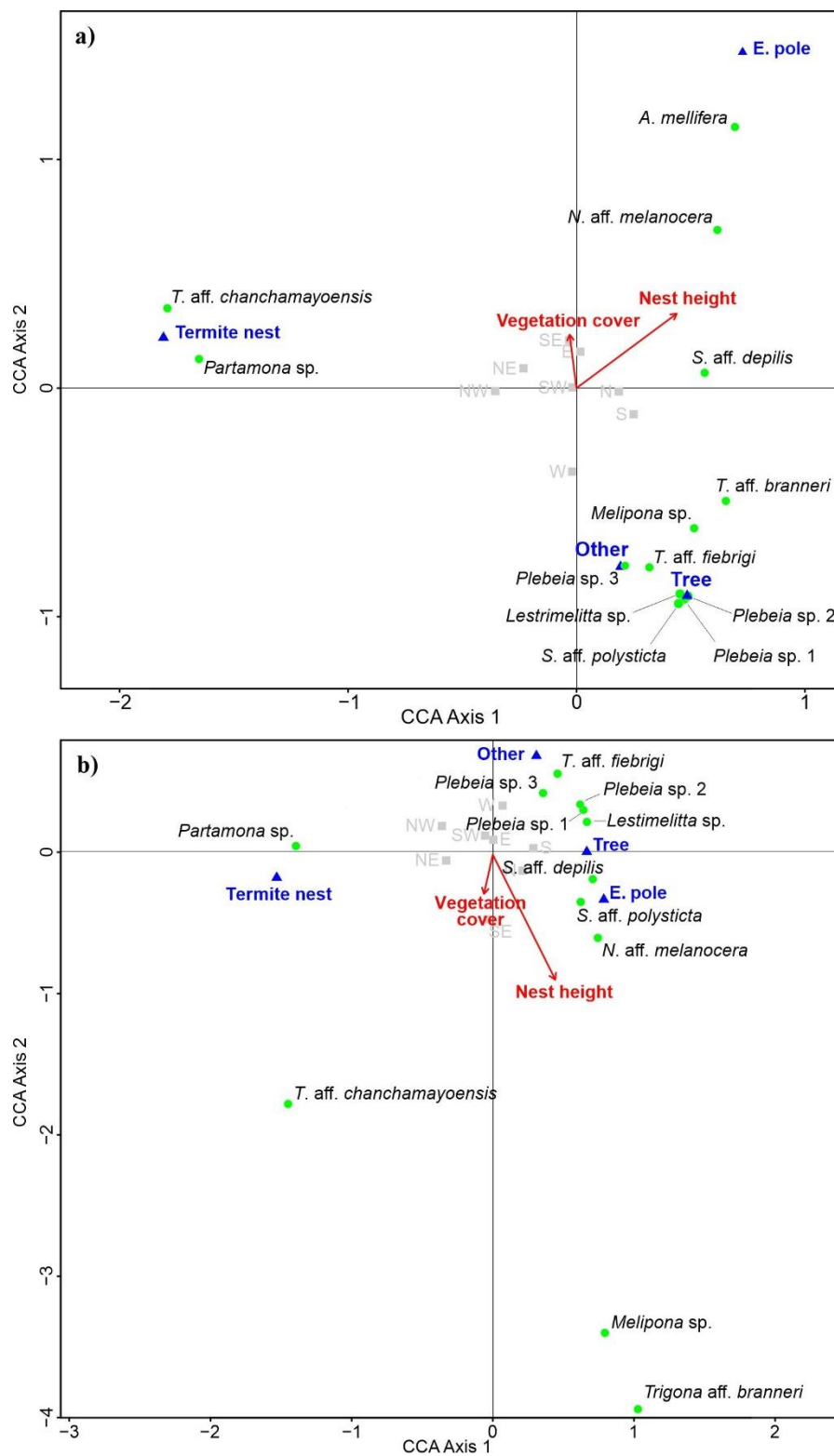


Figure 4. Canonical Correspondence Analysis (CCA) of the bee community across all substrate types: (a) total community including *Apis mellifera*, and (b) stingless bee species only. Green circles represent bee species, gray squares indicate cardinal orientation, and blue triangles denote substrate types. Solid red arrows represent significant landscape and microhabitat variables ($p < 0.05$), while dashed arrows represent non-significant variables ($p > 0.05$). Vector length and direction indicate the relative influence of each continuous predictor on community structure.

Species occupied distinct positions in the ordination space, and these relationships differed between the complete community and the stingless bee analyses (Figure 4). In the complete model (Figure 4a), *A. mellifera* was associated primarily with artificial substrates, particularly concrete electric poles, with greater nest height and high vegetation cover. In contrast, the stingless bee model (Figure 4b) revealed clearer species-environment relationships after excluding *A. mellifera*. *Melipona* sp., *Trigona* aff. *branneri*, *Trigona* aff. *chanchamayoensis*, and *Nannotrigona* aff. *melanocera* were associated with greater vegetation cover and higher nesting positions. Conversely, *Plebeia* spp., *Lestrimelitta* sp., and *Tetragonisca* aff. *fiebrigi* were associated with lower vegetation cover and reduced nest height, while maintaining positive relationships with tree substrates. *Partamona* sp. and *Trigona* aff. *chanchamayoensis* showed associations with termite mounds.

Environmental drivers within arboreal substrates

When the analysis was restricted to colonies nesting in trees, community structure remained significantly associated with local environmental conditions (permutation test, $p = 0.001$). The first two CCA axes explained 12.07 % of the constrained variation (Axis 1 = 7.30 %; Axis 2 = 4.77 %). Among the evaluated variables, nest height ($F = 5.64$; $p = 0.006$) and surrounding vegetation cover ($F = 2.36$; $p = 0.011$) significantly explained variation in community composition. In contrast, dendrometric characteristics, including DBH ($F = 0.70$; $p = 0.656$) and total tree height ($F = 0.96$; $p = 0.495$), did not significantly contribute to community ordination, although host tree species showed a marginal effect ($F = 1.39$; $p = 0.066$).

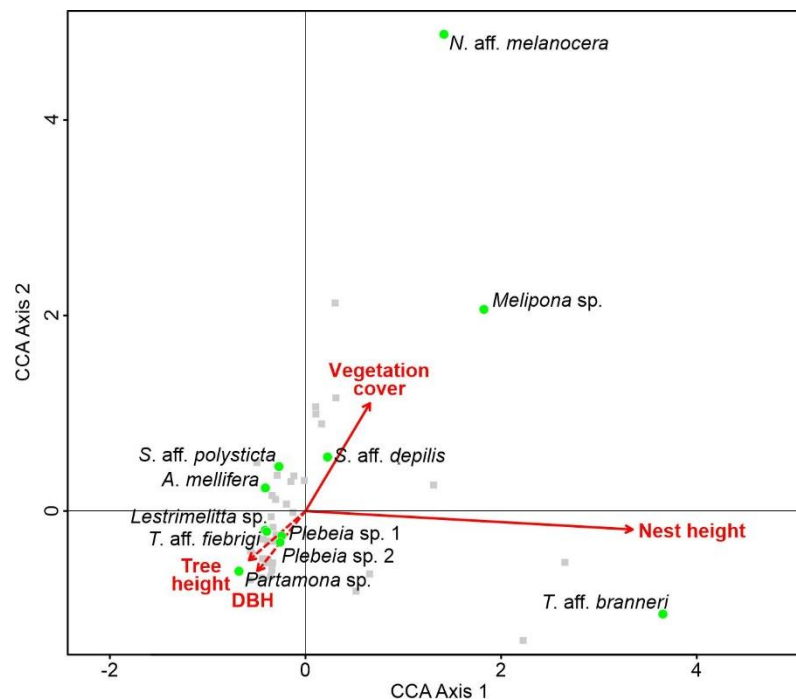


Figure 5. Canonical Correspondence Analysis (CCA) of the bee community nesting exclusively in trees. Green circles represent bee species and gray squares represent host tree species. Solid red arrows indicate significant environmental predictors ($p < 0.05$), whereas dashed arrows indicate non-significant variables. Vector length and direction represent the relative contribution of vegetation cover, nest height, DBH, and total tree height to community structure.

Species associations within arboreal substrates differed from those observed in the global analysis (Figure 5). *Scaptotrigona* aff. *depilis* and *Nannotrigona* aff. *melanocera* remained associated with areas of higher vegetation cover but occupied different positions along the nest height gradient. Conversely, *Plebeia* spp., *Lestrimelitta* sp., *Tetragonisca* aff. *fiebrigi*, and *Partamona* sp. clustered near the center of the ordination, showing relatively weak associations with the measured dendrometric variables. Within this restricted analysis, *Apis mellifera* shifted from its positive association with greater nest height observed in the global model to a negative association with this variable, while exhibiting only a weak relationship with surrounding vegetation cover.

DISCUSSION

The present study provides the first comprehensive assessment of the diversity and nesting ecology of stingless bees and the introduced honey bee (*Apis mellifera*) within the urban core of Santa Cruz de la Sierra, Bolivia. The results demonstrate that this highly urbanized landscape supports a diverse assemblage of stingless bees exhibiting distinct nesting strategies and habitat associations. Rather than responding uniformly to urbanization, species differed in their use of nesting substrates, spatial aggregation, and environmental conditions, highlighting the diversity of nesting habitats available within urban environments.

Urban diversity and community composition

The urban core of Santa Cruz de la Sierra supported a relatively diverse assemblage of stingless bees despite extensive urbanization. With twelve recorded species representing eight genera, and based on one of the longest sampling periods reported for an urban stingless bee survey (36 months), the present study documented a richer urban assemblage than most previous studies (Table 4). Although differences among studies should be interpreted cautiously because sampling effort, survey methods, and urban characteristics varied considerably, the compilation nevertheless indicates that Santa Cruz de la Sierra currently supports one of the richest urban stingless bee assemblages reported in the literature.

The comparatively high richness recorded in this study is likely explained by a combination of sampling effort and habitat characteristics. First, the prolonged sampling period and extensive spatial coverage of the present study increased the probability of detecting uncommon species. Second, Santa Cruz de la Sierra still retains numerous green areas, mature trees, and heterogeneous urban vegetation capable of providing nesting and floral resources for different bee species. Urban landscapes that preserve structurally diverse vegetation are increasingly recognized as important refuges for pollinators, particularly in tropical regions (Hall *et al.* 2017, Baldock 2020).

This heterogeneous mosaic of green spaces and nesting substrates, which provides opportunities for species with contrasting nesting requirements, likely also contributes to the uneven abundance observed across species, a pattern commonly reported in both natural and anthropogenic stingless bee communities (Batista *et al.* 2003, Siqueira *et al.* 2012, Silva *et al.* 2013) and generally attributed to interspecific differences in ecological tolerance and the capacity to exploit nesting opportunities within urban landscapes. The high sampling completeness and asymptotic rarefaction curve indicate that the observed dominance pattern is unlikely to be an artifact of incomplete sampling.

Table 4. Comparison of urban stingless bee nesting studies across different regions.

Country	City/Region	Study (Author, Year)	Sampling Months	Total Nests	No. of Species
Brazil	Curitiba, Paraná	(Taura & Laroca 1991)	5	38	5
Brazil	Juiz de Fora, Minas Gerais	(Sousa <i>et al.</i> 2002)	17	35	4
Brazil	Salvador, Bahia	(Souza <i>et al.</i> 2005)	3	94	4
Brazil	Uberlândia, Minas Gerais	(Aidar <i>et al.</i> 2013)	7	50	7
Brazil	São Paulo, São Paulo	(Sousa 2014)	27	21	5
Brazil	Juiz de Fora, Minas Gerais	(Vieira <i>et al.</i> 2016)	14	69	7
Brazil	Ubá, Minas Gerais	(Araújo <i>et al.</i> 2016)	11	28	4
Brazil	Governador Mangabeira, Bahia	(Silva <i>et al.</i> 2019)	12	39	5
Indonesia	Padang City, West Sumatra	(Herwina <i>et al.</i> 2022)	39	15	9
Mexico	San Francisco, Campeche	(Romero Rivero <i>et al.</i> 2023)	12	545	7
Brazil	Inconfidentes, Minas Gerais	(Menino <i>et al.</i> 2023)	5	13	5
Brazil	C. dos Goytacazes, Rio de Janeiro	(Alves 2023)	2	129	4
Brazil	Foz do Iguaçu, Paraná	(Ojeda 2023)	3	60	4
Brazil	Poços de Caldas, Minas Gerais	(Santos <i>et al.</i> 2023)	1	23	4
Brazil	Montes Claros, Minas Gerais	(Soares <i>et al.</i> 2025)	3	41	6
Costa Rica	Montes de Oca, San José	(Konicek <i>et al.</i> 2025)	4	86	5
Bolivia	Santa Cruz de la Sierra, Santa Cruz	Present study	36	463	12

The large number of feral colonies of *Apis mellifera* demonstrates that urban environments also provide favorable nesting conditions for this species. Previous studies have shown that cities frequently sustain persistent populations of wild honey bees because buildings and other artificial structures provide abundant nesting cavities while ornamental vegetation supplies floral resources throughout much of the year (Dubaić *et al.* 2021, Visick & Ratnieks 2023, Casanelles-Abella *et al.* 2025). Whether this coexistence reflects resource partitioning or competition cannot be determined from the present study, but previous work indicates that interactions between honey bees and native bees are strongly influenced by local habitat conditions and resource availability rather than following a single ecological pattern (Cunningham *et al.* 2022, Iwasaki & Hogendoorn 2022).

Nest aggregation and substrate sharing

Most nesting substrates contained only a single colony, suggesting that bee nests were generally dispersed throughout the urban landscape. Nevertheless, more than one quarter of all colonies occupied substrates shared with at least one additional colony, indicating that locally suitable nesting sites can be used simultaneously by multiple colonies. Similar patterns have been described in other stingless bee communities, where cavity availability is considered one of the principal factors influencing nest-site occupancy (Roubik 2006, Macedo *et al.* 2020).

Aggregation differed markedly among species. *Partamona* sp. exhibited the highest frequency of multiple colonies occupying the same substrate, consistent with the nesting biology of this genus, whose species commonly establish colonies within termite nests

capable of supporting several colonies simultaneously (Camargo & Pedro 2003, Barreto & Castro 2007). In contrast, *Apis mellifera* showed no evidence of conspecific aggregation despite being one of the most abundant species. Wild honey bee colonies typically occupy a single nest cavity per colony, and colony spacing is thought to be influenced largely by competition for floral resources because of their large colony sizes and extensive foraging ranges (Seeley & Morse 1976, Cunningham *et al.* 2022, Visick & Ratnieks 2023). A similar pattern may explain the absence of conspecific aggregation in *Trigona* aff. *branneri* and *Trigona* aff. *chanchamayoensis*. Species of *Trigona* are among the most aggressive stingless bees during foraging, and regular spacing between conspecific colonies has been interpreted as a consequence of intense intraspecific competition and territorial behavior that discourages the establishment of nearby colonies (Hubbell & Johnson 1977, Roubik 2006). This interpretation is consistent with the complete absence of both conspecific aggregation and interspecific substrate sharing observed for these two species in the present study.

Although interspecific substrate sharing occurred relatively frequently, particularly involving *Plebeia* sp. 1, permutation analyses indicated that these associations did not differ from random expectations. This suggests that different bee species converge on the same nesting substrates because they independently exploit suitable cavities rather than because they exhibit consistent positive or negative associations with one another. Together, these results indicate that nest-site availability, rather than interspecific attraction or avoidance, is the principal factor underlying substrate sharing within this urban bee assemblage, reinforcing the importance of nesting resources in structuring urban stingless bee communities.

Environmental drivers of nesting patterns

The CCA indicates that urban bee communities are structured primarily by the availability and characteristics of nesting habitats rather than by random occupation of the urban matrix. Nesting substrate, surrounding vegetation cover, and nest height consistently explained variation in community composition, whereas nest entrance orientation contributed little to species–habitat relationships. These results suggest that different bee species respond to distinct combinations of habitat attributes, reflecting differences in their nesting ecology rather than generalized responses to urbanization.

The influence of vegetation cover highlights the importance of urban green infrastructure in maintaining native bee communities. Vegetated areas not only provide floral resources but also create more stable microclimatic conditions and increase the availability of suitable nesting substrates, thereby supporting a greater diversity of cavity-nesting bees (Potts *et al.* 2010, Hall *et al.* 2017, Baldock 2020). Similar relationships between vegetation structure and stingless bee community composition have been reported in tropical landscapes, where habitat quality strongly influences nest density and species persistence (Samejima *et al.* 2004, Nates-Parra *et al.* 2008, Pérez-Morfi *et al.* 2024). Although the present study focused on nesting sites rather than foraging behavior, the observed associations suggest that urban vegetation contributes to the maintenance of suitable nesting environments for multiple species.

Nest height also emerged as an important component of community structure. Vertical stratification of nests may reflect differences among species in microclimatic requirements, exposure to disturbance, or access to suitable nesting cavities, all of which have been proposed as factors influencing nest-site selection in cavity-nesting bees (Roubik 2006, Wilson *et al.* 2020). Although nest entrance orientation can influence nest microclimate and thermal conditions in cavity-nesting bees (Wilson *et al.* 2020), the absence of a significant effect in the present study suggests that directional exposure plays a comparatively minor role within the heterogeneous urban environment, where local habitat characteristics and substrate availability may override potential thermal advantages associated with particular orientations. Similar patterns of weak or random orientation preferences have been reported for several stingless bee species (Kajobe 2007).

An additional factor that may influence the observed distribution of nest heights in urban environments is human intervention. During field surveys, occasional colonies of *Apis mellifera* established in concrete electric poles at low heights were found with their nest entrances deliberately sealed, apparently to prevent colony re-establishment and reduce the risk of stinging incidents for pedestrians (Figure 6). Similar management practices have been reported in urban environments by Taura & Laroca (1991). Although these observations were not quantified, they suggest that anthropogenic disturbance may contribute to the lower frequency of honey bee colonies at accessible heights and should be considered as a potential source of bias when interpreting vertical nesting patterns in cities.

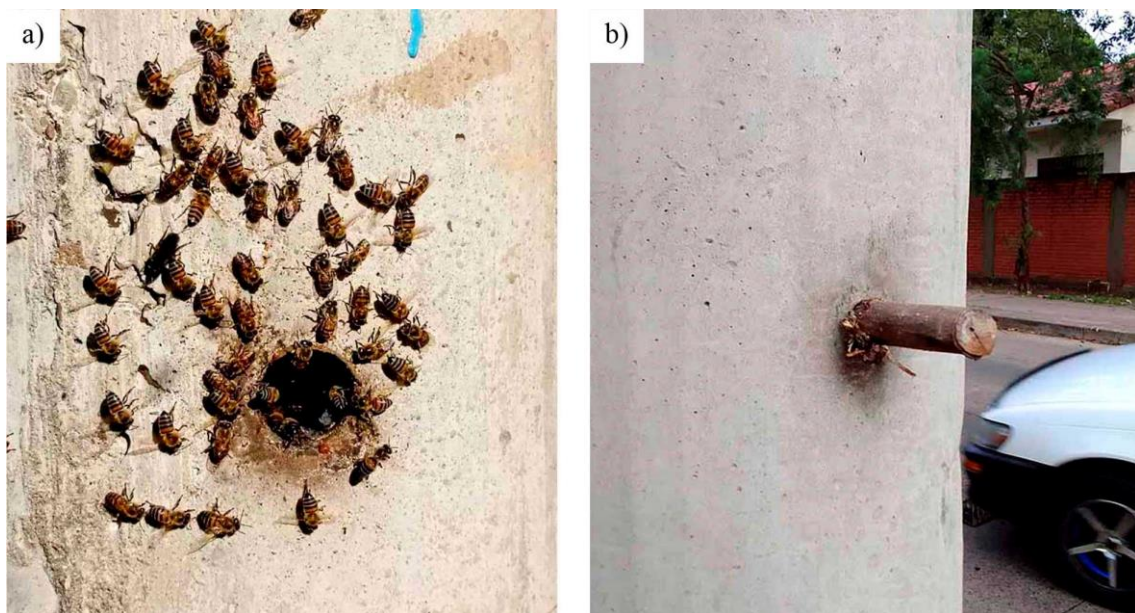


Figure 6. a) Nest of *Apis mellifera* in a concrete electric pole. b) Entrance manually sealed with a wooden piece at 1,5 m height to prevent colony reactivation and protect passers-by.

Overall, these findings indicate that habitat quality, nesting opportunities, and, to some extent, human management jointly shape urban nesting patterns. These environmental differences also contribute to the contrasting nesting strategies observed between stingless bees and *Apis mellifera*.

Contrasting nesting strategies of stingless bees and *Apis mellifera*

The inclusion of *Apis mellifera* in the community analyses revealed that this species occupies a distinct ecological position within the urban bee assemblage. Unlike most stingless bee species, which were associated primarily with trees and termite nests, *A. mellifera* was strongly associated with artificial structures, particularly concrete electric poles, and tended to nest at greater heights. Similar use of human-made structures by feral honey bees has been documented in urban environments worldwide, reflecting the abundance of enclosed cavities created by urban infrastructure (Baum *et al.* 2008, Dubaić *et al.* 2021, Visick & Ratnieks 2024).

The contrasting habitat associations observed in this study suggest that urban environments provide multiple types of nesting opportunities that are exploited differently by native and introduced bees. Rather than indicating direct competition for nesting sites, the CCA suggests a degree of ecological segregation in nest-site use, with most stingless bees remaining associated with natural substrates despite the widespread availability of artificial structures. This pattern may facilitate the coexistence of stingless bees and feral honey bees within highly urbanized landscapes. However, competition for floral resources cannot be excluded, as previous studies have documented the potential for resource overlap between stingless bees and honey bees (Iwasaki & Hogendoorn 2022, Casanelles-Abella *et al.* 2025), although this aspect was not evaluated in the present study.

Given the high abundance of feral *Apis mellifera* colonies documented here, their ecological role in the urban bee assemblage warrants explicit consideration for conservation planning. The spatiotemporal overlap between flowering resources and foraging activity, rather than simple co-occurrence, has recently been shown to be a stronger predictor of realized plant–pollinator interactions in cities than either partner's abundance (Silva *et al.* 2026), indicating that resource-based competition between *A. mellifera* and stingless bees in Santa Cruz de la Sierra cannot be ruled out without direct foraging data. From a management perspective, the informal sealing of low-height *A. mellifera* nest entrances observed during this study (Figure 6) indicates that some degree of colony control is already occurring in an unregulated, ad hoc manner, motivated primarily by public-safety concerns rather than ecological criteria. Formalizing this practice (for example, through municipal protocols for monitoring, humane relocation, or selective removal of accessible feral colonies in high pedestrian-traffic areas, combined with periodic surveys of colony density) could help reduce potential resource competition with native stingless bees while addressing the safety concerns that currently drive informal intervention.

Taken together, the findings demonstrate that urban areas can support diverse assemblages of stingless bees alongside abundant feral *Apis mellifera* populations when suitable nesting substrates, vegetated habitats, and appropriate colony management are maintained. The marked differences in nesting strategies among species indicate that conserving heterogeneous urban landscapes, including mature trees, naturally occurring termite nests, and well-connected green spaces, is likely more important than increasing the availability of any single nesting substrate. Long-term studies integrating nesting ecology, floral resource use, and population dynamics will be essential to determine how ongoing urban expansion influences the persistence of stingless bee communities in tropical urban landscapes.

CONCLUSION

This study provides the first comprehensive assessment of stingless bee nesting ecology within the urban core of Santa Cruz de la Sierra, documenting a remarkably diverse assemblage of twelve stingless bee species coexisting with the introduced honey bee, *Apis mellifera*. Stingless bees occupied a wide variety of natural and artificial substrates, although nesting patterns differed markedly among species. Nesting patterns were influenced primarily by substrate type, vegetation cover, and nest height, whereas nest entrance orientation and tree size had little effect on nest occurrence. These findings indicate that urban landscapes can support diverse stingless bee communities when suitable nesting resources and green infrastructure are maintained.

From a broader urban planning perspective, maintaining mature trees, termite nests where naturally present, and structurally complex green spaces is likely to enhance the long-term persistence of stingless bee communities. Because different species exhibited distinct nesting strategies and microhabitat associations, urban management should preserve a variety of natural nesting resources capable of supporting this ecological diversity. At the same time, given the high abundance of feral *Apis mellifera* colonies recorded in this study, targeted monitoring of this introduced species is recommended, together with management protocols, such as periodic colony surveys and selective, non-lethal control of accessible urban nests, that address public-safety concerns while minimizing potential competitive pressure on native stingless bee communities. As one of the first detailed studies of urban stingless bee nesting ecology in Bolivia, this work provides a baseline for future monitoring and offers practical information for integrating pollinator conservation into urban planning and green-space management.

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Appendix 1. Tree species used as nesting substrates.

Family	Species	Status	Trees (n)	Nests (n)	Nest freq. (%)	Bee spp./tree
Moraceae	<i>Ficus elastica</i>	Introduced	14	23	9.13	6
Moraceae	<i>Ficus pertusa</i>	Native	14	20	7.94	5
Mimosaceae	<i>Neltuma chilensis</i>	Native	14	17	6.75	4
Fabaceae	<i>Chloroleucon tenuiflorum</i>	Native	11	16	6.35	6
Fabaceae	<i>Cojoba arborea</i>	Native	12	15	5.95	6
Fabaceae	<i>Tipuana tipu</i>	Native	10	14	5.56	7
Lamiaceae	<i>Vitex cymosa</i>	Native	12	13	5.16	6
Cordiaceae	<i>Cordia alliodora</i>	Native	7	8	3.17	5
Fabaceae	<i>Albizia berteriana</i>	Native	7	7	2.78	4
Fabaceae	<i>Enterolobium contortisiliquum</i>	Native	5	7	2.78	4
Moraceae	<i>Ficus benjamina</i>	Introduced	5	6	2.38	4
Moraceae	<i>Ficus eximia</i>	Native	6	6	2.38	4
Bignoniaceae	<i>Handroanthus impetiginosus</i>	Native	6	6	2.38	2
Fabaceae	<i>Anadenanthera colubrina</i>	Native	4	5	1.98	4
Fabaceae	<i>Erythrina mulungu</i>	Native	5	5	1.98	3
Fabaceae	<i>Swartzia jororii</i>	Native	5	5	1.98	5
Sapindaceae	<i>Cupania cinerea</i>	Native	1	5	1.98	2
Fabaceae	<i>Lonchocarpus pluvialis</i>	Native	3	4	1.59	3
Anacardiaceae	<i>Mangifera indica</i>	Introduced	4	4	1.59	1
Lauraceae	<i>Persea americana</i>	Introduced	3	4	1.59	2
Fabaceae	<i>Platymiscium fragrans</i>	Native	2	4	1.59	2
Meliaceae	<i>Guarea guidonia</i>	Native	3	4	1.59	4
Fabaceae	<i>Pterogyne nitens</i>	Native	2	3	1.19	3
Nyctaginaceae	<i>Bougainvillea modesta</i>	Native	3	3	1.19	3
Malvaceae	<i>Guazuma ulmifolia</i>	Native	3	3	1.19	3
Moraceae	<i>Batocarpus amazonicus</i>	Native	1	2	0.79	2
Euphorbiaceae	<i>Hura crepitans</i>	Native	2	2	0.79	2
Meliaceae	<i>Melia azedarach</i>	Introduced	2	2	0.79	2
Fabaceae	<i>Samanea tubulosa</i>	Native	2	2	0.79	1
Rutaceae	<i>Zanthoxylum caribaeum</i>	Native	1	2	0.79	2
Malvaceae	<i>Ceiba camba</i>	Native	2	2	0.79	2
Annonaceae	<i>Annona montana</i>	Native	1	1	0.40	1
Boraginaceae	<i>Cordia dentata</i>	Native	1	1	0.40	1
Celastraceae	<i>Salacia elliptica</i>	Native	1	1	0.40	1
Combretaceae	<i>Terminalia catappa</i>	Introduced	1	1	0.40	1
Fabaceae	<i>Bauhinia forficata</i>	Native	1	1	0.40	1
Fabaceae	<i>Delonix regia</i>	Introduced	1	1	0.40	1
Fabaceae	<i>Erythrina poeppigiana</i>	Native	1	1	0.40	1
Fabaceae	<i>Hymenaea stigonocarpa</i>	Native	1	1	0.40	1
Fabaceae	<i>Ormosia sp.</i>	Native	1	1	0.40	1
Fabaceae	<i>Peltophorum dubium</i>	Native	1	1	0.40	1
Fabaceae	<i>Platymiscium pinnatum</i>	Native	1	1	0.40	1
Lauraceae	<i>Ocotea puberula</i>	Native	1	1	0.40	1

Family	Species	Status	Trees (n)	Nests (n)	Nest freq. (%)	Bee spp./tree
Myrtaceae	<i>Campomanesia xanthocarpa</i>	Native	1	1	0.40	1
Myrtaceae	<i>Syzygium cumini</i>	Introduced	1	1	0.40	1
Rhamnaceae	<i>Rhamnidium elaeocarpum</i>	Native	1	1	0.40	1
Rutaceae	<i>Citrus reticulata</i>	Introduced	1	1	0.40	1
Sapindacea	<i>Melicoccus lepidopetalus</i>	Native	1	1	0.40	1
Ulmaceae	<i>Phyllostylon rhamnoides</i>	Native	1	1	0.40	1
	Unidentified sp. 1	Native	1	1	0.40	1
	Unidentified sp. 2	Native	1	1	0.40	1
	Unidentified sp. 3	Native	1	1	0.40	1
	Unidentified sp. 4	Native	1	1	0.40	1
	Unidentified sp. 5	Native	1	1	0.40	1
	Unidentified sp. 6	Native	1	1	0.40	1
	Dead tree		9	9	3.57	4

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