Variations of structural niche, floristic sources and density of *Tetragonisca angustula* Latreille 1811 (Apinae, Meliponini) in the dry forest of Huallaga, peruvian Amazon †

[Variaciones del nicho estructural, fuentes florísticas y densidad de *Tetragonisca angustula* Latreille 1811 (Apinae, Meliponini) en el bosque seco del Huallaga, Amazonía peruana]

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SUMMARY

Background: *Tetragonisca angustula* is a highly adaptable stingless bee in anthropic landscapes, but there are few studies on its trophic relationships and ethology in the Amazon. **Hypothesis and objective**: Unlike other stingless bees, whose nesting density is regulated by territoriality and the availability of food resources, it is inferred that the nest density of *T. angustula* is limited by the availability of nesting spaces. To demonstrate it, the trophic-structural niche variations of *T. angustula* colonies were compared in the Seasonal Dry Forest of the Central Huallaga region, Peruvian Amazon. **Methodology:** Between 2019 and 2023, nests of this species were studied in an agroforestry landscape dominated by remnant secondary forest (N) and an urban community (U). The ecological niche amplitude B_i was estimated from data of nesting frequency by substrate B_1 (rock crevices, trees, concrete, dry mud, plastic, pottery, wooden boxes, ground) and nest distance above or below ground level B_2. Structural niche overlapping O_{ij} was calculated, as well as nest density and foraging range. Flowering patterns of plants visited by the species and changes in the vegetation landscape were assessed. **Results:** Of 23 nests, 30% were found in the field and the remaining 70% in the urban area. Structural nest niche by substrate type and height above ground level showed a greater amplitude in urban (B_{U1}=0.62 and B_{U2}=0.59, respectively) compared to natural landscapes (B_{N1}=0.17 and B_{N2}=0.33) with overlaps OU_{N1}= 0.00 and OU_{N2}=0.83. A higher density and clustering of nests was found in the urban area. Of the 59 morphospecies of bee flora, 48% were trees and 52% shrubs, climbers and herbs; 80% native and 20% exotic, and 80% wild and 20% cultivated, ensuring a floristic supply throughout the year. **Implications**: A new ecological basis for the recovery of landscapes and productive strategies for *T. angustula* are provided. **Conclusion**: Limiting nesting space is the main factor determining *T. angustula* density.

Key words: agroforestry; bee flora; nesting ethology; stingless bees; urban pollinators.

RESUMEN

Antecedentes. *Tetragonisca* angustula es una abeja sin aguijón altamente adaptable a los paisajes antrópicos, pero existen pocos estudios sobre sus relaciones tróficas y etología en la Amazonía. **Hipótesis y objetivo**. A diferencia de otras abejas sin aguijón cuya densidad de anidación está regulada por la territorialidad y la disponibilidad de recursos alimentarios, se infiere que la densidad de nidos de *T. angustula* está limitada por la disponibilidad de espacios de anidación. Para demostrarlo, se compararon las variaciones trófico-estructurales del nicho de las colonias de *T. angustula* en el bosque seco estacional de la región del Huallaga Central, Amazonía peruana. **Metodología**. Entre 2020 y 2023, se estudiaron nidos de esta especie en un paisaje agroforestal dominado por un bosque secundario remanente

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(N) y una comunidad urbana (U). Se estimó la amplitud del nicho ecológico B_i a partir de datos de frecuencia de anidación por sustrato B_1 (grietas en rocas, árboles, concreto, lodo seco, plástico, cerámica, cajas de madera, suelo) y la distancia del nido sobre o debajo el nivel del suelo B_2. Se calculó el solapamiento del nicho estructural O_{ij}, así como la densidad de nidos y el rango de pecoreo. Se evaluaron los patrones de floración de las plantas visitadas y los cambios florísticos en el paisaje. **Resultados**. De 23 nidos, 30% se encontraron en el campo y el 70% restante en el área urbana. El nicho estructural del nido por tipo de sustrato y altura sobre el nivel del suelo mostró una mayor amplitud en los paisajes urbanos (B_{U1}=0,62 y B_{U2}=0,59, respectivamente) en comparación con los naturales (B_{N1}=0,17 y B_{N2}=0,33), con solapamientos O_{UN1}= 0,00 y O_{UN2}=0,83. Una mayor densidad y agrupación de nidos en el área urbana fue observada. De 59 morfoespecies de flora apícola, 48% fueron árboles y 52% arbustos, trepadoras y hierbas, 80% nativas y 20% exóticas, 80% silvestres y 20% cultivadas; lo cual garantizó el abastecimiento florístico todo el año. **Implicaciones**. Se aportan nuevas bases ecológicas para la recuperación de paisajes y estrategias productivas para *T. angustula*. **Conclusión**. La limitación del espacio de anidación es el principal factor que determina la densidad de *T. angustula*.

Palabras clave: agroforestería; flora apícola; etología de nidificación; abejas sin aguijón; polinizadores urbanos.

INTRODUCTION

Tetragonisca angustula (Latreille 1811) is a widely distributed species between southern Mexico and northern Argentina, where it is known by various names, of which "angelita" and "ramichi" are the most popular (Nates-Parra *et al*., 2021, Rasmussen and Castillo, 2003).

The abundance of *T. angustula* is related to its high adaptability to diverse ecosystems, many of which are landscapes affected by human activities (de Matos *et al*., 2022, Vélez-Ruiz *et al*., 2013). Few studies (Arboleda and González, 2024, Centeno *et al*., 2021) have been carried out on the trophic and behavioral relationships of this species with the local flora under the diverse conditions of the Amazon, while large-scale processes such as deforestation threaten the integrity of these ecosystems and perhaps, in the medium term, the conservation of stingless bee diversity.

The foraging behavior of *T. angustula* has been studied (Biesmeijer and Slaa, 2004, 2006, Villa and Weiss, 1990), but competition for nests and spacing patterns has received little attention (Fierro *et al*., 2012, Copa-Alvarado, 2004). Hubbell and Johnson (1977) found no evidence that 'nest availability limits colony density or determines dispersal' in *Trigona* species in a dry forest in Costa Rica. However, they proposed three essential elements of the colony spacing mechanism: 'pheromone marking of potential nest sites, recruitment of workers, and aggression between workers from rival nests'. Hubbell and Johnson (1977) suggested that access to food resources (floristic), conditioned by a linear relationship between colony mass and foraging area, appeared to be the main constraint.

This study aimed to evaluate variations in the nesting densities of *T. angustula* colonies in two communities: an urban area and a fragmented forest. The study took place in a seasonal dry forest ecosystem in the upper Amazon basin in central Peru.

MATERIALS AND METHODS

The study was conducted in the seasonally dry Huallaga Forest (Linares-Palomino et al. 2022), in the municipality of Utcurarca, Department of San Martin, Peru (reference: -6.6630° S, -76.2870° W) (Figure 1). From January 2019 to January 2023, *T. angustula* nests were surveyed and monitored in a fragmented landscape dominated by remnant secondary forest (N) and an urban community (U). In the agroforestry scenario, six bands of 10 m width and variable length (656 ± 158 m, total: 39,310 m^2) were traversed, while in the urban village a set of five contiguous quadrats (9,227 ± 5,056 m, total: 46,100 m^2) were surveyed (Figure 2).

Ecological niche breadth index $B_i=S.\Sigma p_i^2$, based on Levin (1968) (Vecco-Giove *et al*., 2015) was estimated for each N and U community from data on frequency by nesting substrate B_1 (e.g. rock crevices, trees, etc.) and nest height above or below ground B_2 (50 cm classes in the range <-50:300] cm), and structural niche overlap $O_{ij}=\Sigma[p_i.p_j].[\Sigma p_i^2.\Sigma p_j^2]^{-½}$ (Pianka, 1974). The indicators of density (d) and foraging range were determined. The latter was expressed as the ratio of area (1/d) and as the radius $r = [1/d)/\pi]^{1/2}$.

Flowering patterns of plants visited by *T. angustula* were evaluated throughout the study period. The taxonomic positions of the forest and non-forest morphospecies were determined by ethnobotanical criteria and bibliographic support. Changes in the vegetation landscape (proportion of forest and recovering areas, crops and grasslands) were modelled in ArcGis v.10.8 based on GoogleEarth 2019 images and 2023 digital photos taken with a DJI - MAVIC 3 drone at 500 m. For this purpose, two circles of 1.21 km^2 - whose radius of 621 m is the minimum foraging range for *T. angustula* according to Araujo *et al*. (2004) - were applied by analyzing the urban and agroforestry zones.

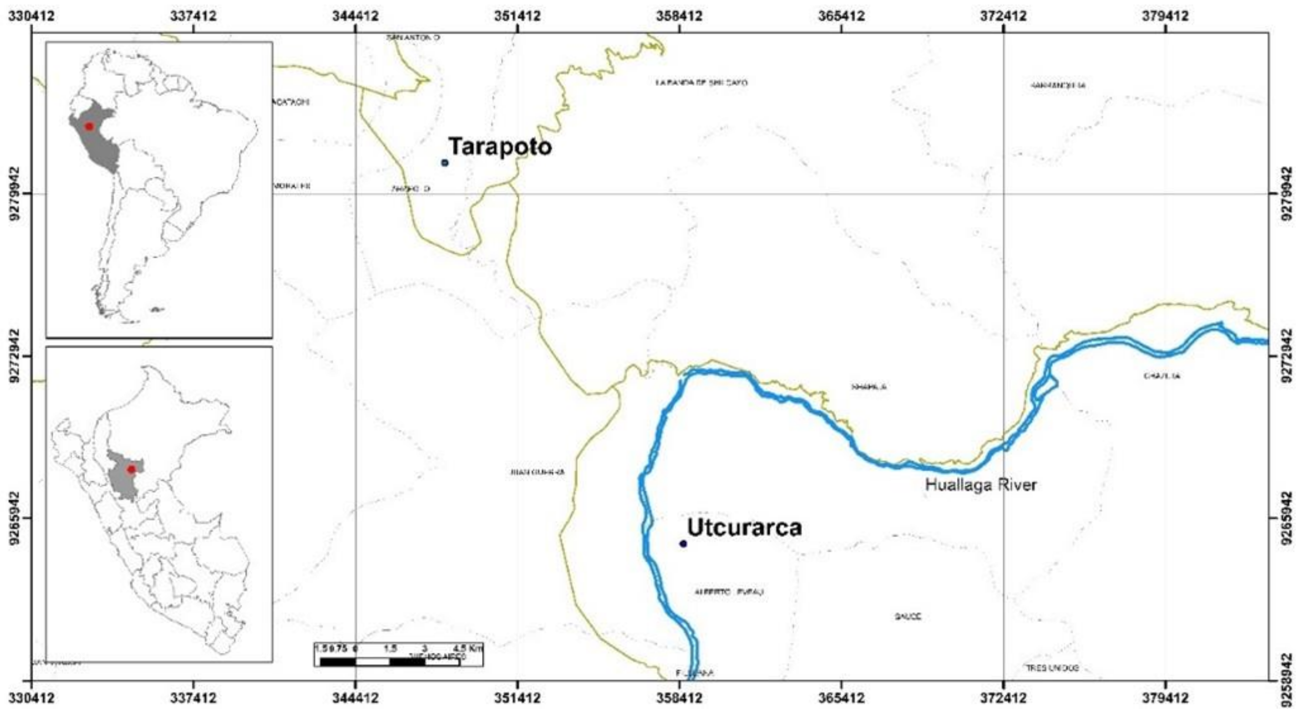

Figure 1. Location of the village of Utcurarca in relation to the nearest major city in the region (Tarapoto, Peru).

RESULTS

A total of 23 *T. angustula* nests were identified at the beginning of the assessment: seven (30%) in agroforestry conditions and 16 (70%) in the urban area (see Table 1). By the end of the assessment period, the number of nests in the study area had decreased slightly in both the urban (6.25%, or one fewer nest) and the agroforestry (14.71%, or one fewer nest) zones.

Ecological niches in U and N appeared to be mutually exclusive for eight dimensions of nesting substrate: rock crevices and tree cavities (N), cavities or cracks in concrete, dry wall mud, plastic pipes, pottery artefacts, wooden boxes and dry soil associated with wooden poles (U) (Figure 3), with a greater amplitude in urban landscapes (B_{1U} = 0.62) than in natural conditions (B_{1N} = 0.17).

Structural niche by height respecting ground level in the urban landscape (B_{2U} = 0.59, >-50:300]) was also superior to agroforestry conditions (B_{2N} = 0.33, >-50:100]), both showing an overlap of 0.83 where B_{2N} was included in B_{2U}. This was confirmed by the results of higher density and clustering of nests in the urban area (Table 2, Figure 2-centre).

Of the 59 morphospecies of bee flora, 48% were trees and 52% shrubs, climbers and herbs; 80% native and 20% exotic, and 80% wild and 20% cultivated (Table 3, Figure 4), determining floristic abundance throughout the year (Figure 5).

The wooded area increased by 35% in the agroforestry zone between 2019 and 2023, while that change was much lower in the urban area (4.2%). At the end of this period, the landscape in the agroforestry zone showed 66% original forest, 24% recovering forest and 9% grassland. No dead trees were found in the sampling strips. The urban area was 23% smaller than the agroforestry zone due to the Huallaga River area, and was mainly characterized by grassland (43%), riparian forest (34%), crops (11%) and buildings (8%) (Figure 6).

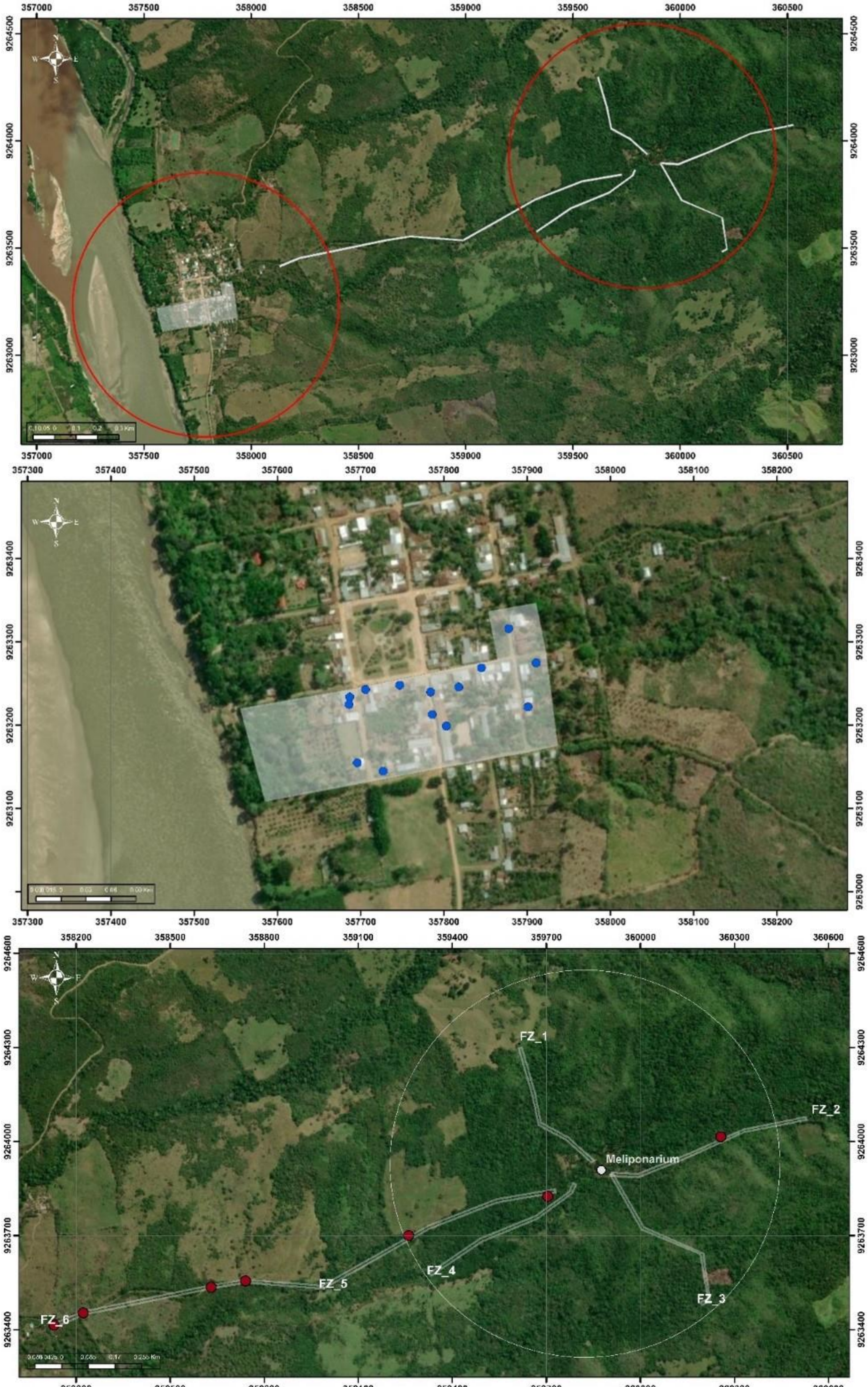

Figure 2. Study area and assessment units. Top: general view of the urban area (U) on the left and the agroforestry zone (N) on the right. Centre: Area assessed in U. Bottom: details of the assessment strips in the N area. T. angustula nests are indicated with blue and red dots in the U and N areas, respectively. Source: prepared by the authors using Google Earth images (2019).

Table 1. Location and characteristics of the nesting of Tetragonisca angustula in the agroforestry and urban areas of Utcurarca, Central Huallaga, Peru.

Zone	Order	Code	East x (m)	South y (m)	Elevation (m)	Origin of resource	Structural resource	More details about nesting resource	Height (cm)	Min. distance of neighbor (m)
Agroforestry	1	ZF-T6-1	358 130	9 263 414	241	Natural	Rock	Crevice	0	101
Agroforestry	2	ZF-T6-2	358 223	9 263 453	258	Natural	Tree	Cavity in Bolakiro (*Schinopsis peruviana*)	50	416
Agroforestry	3	ZF-T6-3	358 631	9 263 535	309	Natural	Tree	Cavity in Bolakiro (*Schinopsis peruviana*)	50	112
Agroforestry	4	ZF-T6-4	358 741	9 263 555	317	Natural	Tree	Cavity in Bolakiro (*Schinopsis peruviana*)	100	540
Agroforestry	5	ZF-T5-5	359 261	9 263 700	387	Natural	Tree	Cavity in Yawarkaspi (*Pterocarpus* sp.)	10	461
Agroforestry	6	ZF-T5-6	359 705	9 263 825	447	Natural	Tree	Cavity in Pashaka (*Parkia* sp.)	80	584
Agroforestry	7	ZF-T2-1	360 257	9 264 015	547	Natural	Tree	Cavity in undetermined species.	30	
Urban	1	Q-2-1	357 727	9 263 145	206	Artificial	Wood	Box	180	32
Urban	2	Q-1-1	357 696	9 263 155	206	Artificial	Concrete	Cement block wall	200	70
Urban	3	Q-1-2	357 687	9 263 234	208	Artificial	Dry mud	Mud wall	25	9
Urban	4	Q-1-3	357 686	9 263 225	208	Artificial	Wood	Box	220	0
Urban	5	Q-1-4	357 686	9 263 225	208	Artificial	Pottery	Jar	220	21
Urban	6	Q-2-2	357 706	9 263 243	208	Artificial	Plastic	Tube (2" D)	50	41
Urban	7	Q-2-3	357 747	9 263 248	209	Artificial	Plastic	Tube (2" D)	35	37
Urban	8	Q-3-1	357 784	9 263 240	210	Artificial	Dry mud	Mud wall	250	27
Urban	9	Q-2-3	357 786	9 263 213	210	Artificial	Concrete	Crevice in wall	30	22
Urban	10	Q-3-2	357 803	9 263 199	210	Artificial	Concrete	Crevice in wall	35	49
Urban	12	Q-3-3	357 845	9 263 269	213	Artificial	Dry mud	Mud wall	15	35
Urban	11	Q-3-4	357 818	9 263 246	211	Artificial	Wood/ground	Wooden post, hollow under the floor, under roof	-35	57
Urban	13	Q-5-1	357 878	9 263 316	214	Artificial	Wood/ground	Under cover	-35	52
Urban	14	Q-4-1	357 901	9 263 222	217	Artificial	Wood/ground	Wooden post, hollow under the floor, under roof	-15	53
Urban	15	Q-4-2	357 901	9 263 222	217	Artificial	Wood/ground	Wooden post, hollow under the floor, under roof	-15	0
Urban	16	Q-4-3	357 911	9 263 275	208	Artificial	Dry mud	Mud wall	60	

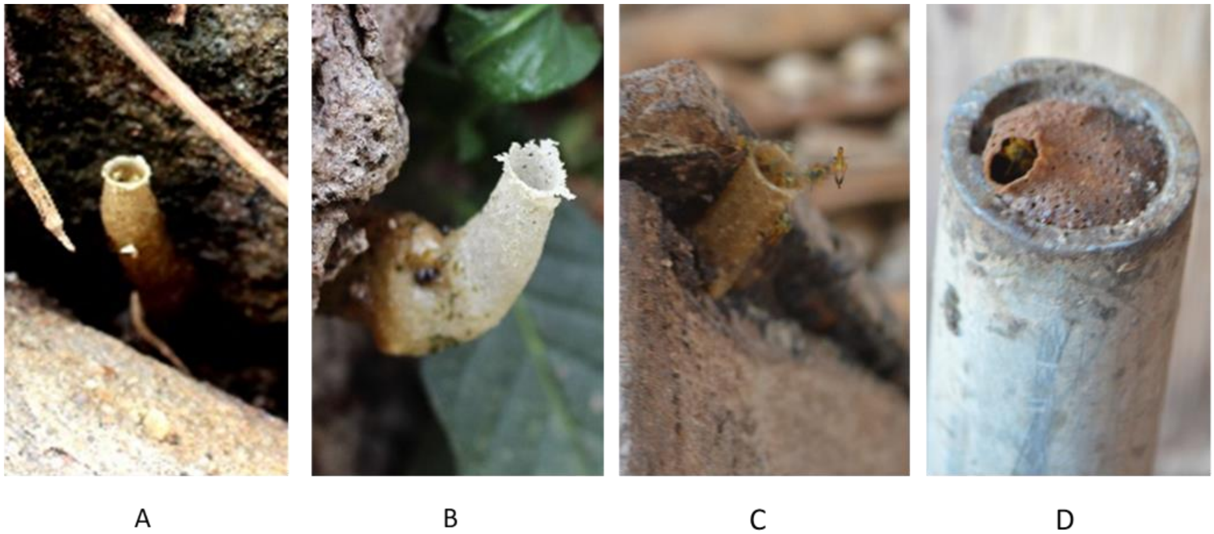

Figure 3. ***Tetragonisca angustula*** **nesting in different substrates. In the agroforestry zone: A) a rock crevice, B) a tree hollow; in an urban area: C) a wooden box, D) a plastic pipe.**

Table 2. Main density and spacing traits of ***Tetragonisca angustula*** **nests in urban and agroforestry zones.**

Communities	Average distance (m) between nests (± sd)	Density of colonies (per km^2)	Foraging range	
			Surface (km^2/ colony)	Radius (m)
Agroforestry	369.0 ± 211.7	178.07	0.006	422.79
Urban	33.7 ± 20.9	347.07	0.003	302.84

Table 3. List of plants visited by ***Tetragonisca angustula*** **in the seasonal dry of Huallaga Forest.**

N	Common names	Taxonomy	Origin	Habit
1	Algarrobo	*Prosopis* sp. (Fabaceae)[1]	Native	Arboreal
2	Añallo caspi	*Cordia* sp. (Boraginaceae)	Native	Arboreal
3	Atadijo	*Trema micrantha* (Ulmaceae)	Native	Arboreal
4	Bolakiro	*Schinopsis peruviana* (Anacardiaceae)	Endemic	Arboreal
5	Bolayna blanca	*Guazuma crinita* (Malvaceae)	Native	Arboreal
6	Bugambilia	*Bougainvillea* spp. (Nictaginaceae)	Exotic	Woody fickle
7	Caimito	*Pouteria caimito* (Sapotaceae)	Native	Arboreal
8	Calambre sacha	*Croton* sp. (Euphorbiaceae)	Native	Herbaceous
9	Camaroncito	Acanthaceae	Native	Herbaceous
10	Capirona	*Calycophyllum spruceanum* (Rubiaceae)	Native	Arboreal
11	Cherry, acerola	*Malpighia emarginata* (Malpighiaceae)	Exotic	Shrubby
12	Chicharra caspi	*Lippia* cf. *virgata (Verbenaceae)*	Native	Shrubby
13	Chirimoya	*Annona squamosa* (Annonaceae)	Exotic	Shrubby
14	Chukchumbo	*Myrcia* (Myrtaceae)	Native	Arboreal
15	Copa de novia	*Ixora finlaysoniana* (Rubiaceae)	Exotic	Shrubby
16	Cucarda	*Hibiscus rosa-sinensis* (Malvaceae)	Exotic	Shrubby
17	Estribo caspi	*Guazuma* sp. (Malvaceae)	Native	Shrubby
18	Fapina	*Cupania cinérea* (Sapindaceae)	Native	Arboreal
19	Girasol	*Helianthus annuus* (Asteraceae)	Exotic	Herbaceous
20	Guava	*Psidium guajava* (Myrtaceae)	Native	Shrubby
21	Huaba	*Inga* cf. *edulis* (Fabaceae)	Native	Arboreal
22	Huito, jagua	*Genipa americana* (Rubiaceae)	Native	Arboreal
23	Insira	*Maclura tinctoria* (Moraceae)	Native	Arboreal
24	Ishanga	Urticaceae	Native	Shrubby
25	Isma moena	*Ocotea sp.* (Lauraceae)	Native	Arboreal
26	Jasmine	*Murraya* cf. *paniculata* (Rutaceae)	Exotic	Shrubby

N	Common names	Taxonomy	Origin	Habit
27	Kinilla	*Manilkara bidentata* (Sapotaceae)	Native	Arboreal
28	Subtle lemon	*Citrus aurantifolia* (Rutaceae)	Exotic	Shrubby
29	Llambo pashaca	*Acacia* sp. (Fabaceae)	Native	Arboreal
30	Machete vaina	*Bauhinia* sp. (Fabaceae)	Native	Arboreal
31	Mango	*Mangifera indica* (Anacardiaceae)	Exotic	Arboreal
32	Moringa	*Moringa oleífera* (Moringaceae)	Exotic	Shrubby
33	Black ocuera	*Vernonanthura patens* (Asteraceae)	Native	Shrubby
34	Paliperro	*Vitex* sp. (Lamiaceae)	Native	Arboreal
35	Papaíllla	*Momordica charantia* (Cucurbitaceae)	Feral	Fickle herb
36	Pashaca	*Cassia spinescens* (Fabaceae)	Native	Arboreal
37	Pashaquilla	*Acacia* sp. (Fabaceae: Mimosoidea)	Native	Woody fickle
38	Pasto braquiaria	*Urochloa brizantha* (Poaceae)	Exotic	Herbaceous
39	Patko-sacha	*Vernonia* sp. (Asteraceae)	Native	Woody fickle
40	Pichana	Verbenaceae	Native	Herbaceous
41	Red pinion	*Jatropha gossypiifolia* (Euphorbiaceae)	Native	Shrubby
42	Pucunguy sacha	*Corchorus* sp. (Malvaceae)	Native	Herbaceous
43	Retama	*Senna* cf. *reticulata* (Fabaceae)	Native	Shrubby
44	Sacha inchik	*Plukenetia volubilis* (Euphorbiaceae)	Native	Flickly
45	Sapote	*Matisia cordata* (Malvaceae)	Native	Arboreal
46	Shawinto	*Psidium* sp. (Myrtaceae)	Native	Arboreal
47	Shillka	*Baccharis* sp. (Asteracea)	Native	Shrubby
48	Shimbillo asnak	*Inga* sp. (Fabaceae)	Native	Arboreal
49	Shimbillo	*Inga* sp. (Fabaceae)	Native	Arboreal
50	No local name	cf. *Albizia* sp.	Native	Shrubby
51	No local name	*Serjania* sp. (Sapindaceae)[2]	Native	Woody fickle
52	Tobacco	*Nicotiana tabacum* (Solanaceae)	Native	Herbaceous
53	Yellow tahuarí	*Tabebuia* cf. aurea (Bignoniaceae)[3]	Native	Shrubby
54	Red tangarana	*Triplaris americana* (Polygonaceae)	Native	Arboreal
55	Tingana	*Sapindus saponaria* (Sapindaceae)	Native	Arboreal
56	Uchumullaka	*Trichilia* cf. *ulei* (Meliaceae)[4]	Native	Arboreal
57	Yawar-kaspi	*Pterocarpus* sp. (Fabaceae)	Native	Arboreal
58	Yumanasa	*Muntingia calabura* (Muntingiaceae)	Native	Arboreal
59	Walaja	*Xanthoxylum* sp. (Rutaceae)	Native	Arboreal

[1] A record of *P. pallida* from Bagua was found in herbarium by Burghardt *et al*. (2010).
[2] Genus reported for the dry forests of Jaén by Marcelo-Peña (2008).
[3] Species distribution reported by Linares-Palomino (2006) for the seasonally dry eastern forests of Tarapoto.
[4] Genus reported for the dry forests of Tarapoto by García-Villacorta (2009). Linares-Palomino (2006) reports *T. ulei* for the seasonally dry eastern forests of Tarapoto. According to deposits of Herbarium of The Field Museum (https://collections-botany.fieldmuseum.org/list?genus=Trichilia&species=ulei), a specimen of this species was collected in Rumisapa (San Martin) by L. Williams and identified by T. D. Pennington in 1979; another specimen comes from Juan Guerra (1902).

Figure 4. Some plants visited by *Tetragonisca angustula in the seasonal dry of Huallaga Forest*. A) *Acacia* sp. B) *Prosopis* sp. C) *Inga* sp. D) *Murraya* cf. *paniculata*. E) *Serjania* sp. F) *Tabebuia* sp. G) *Calycophyllum spruceanum*. H) *Nectandra* sp.

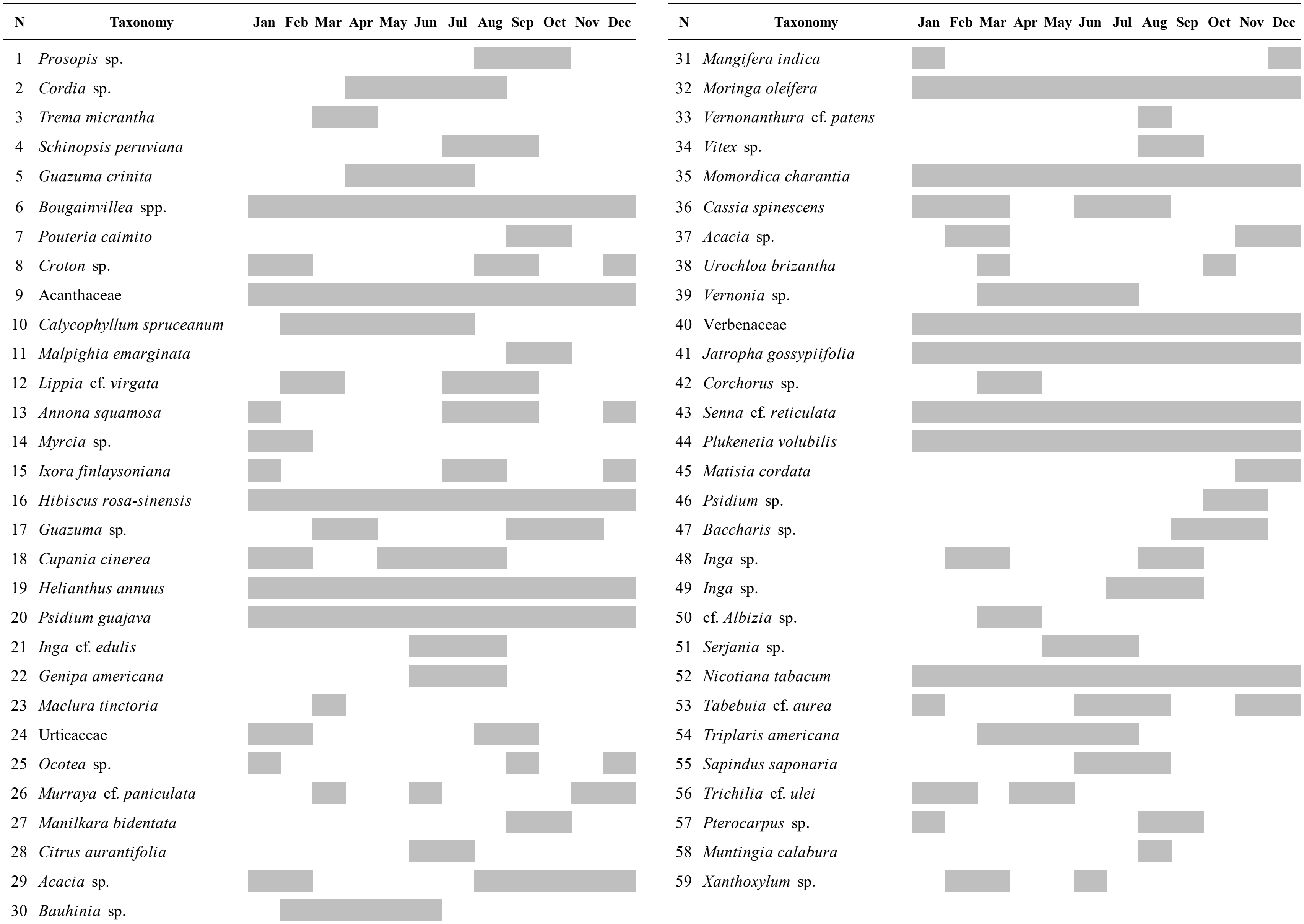

Figure 5. Floral phenology of plant species visited by *Tetragonisca angustula* in the agroforestry and urban zones of dry forest of Huallaga, Peru.

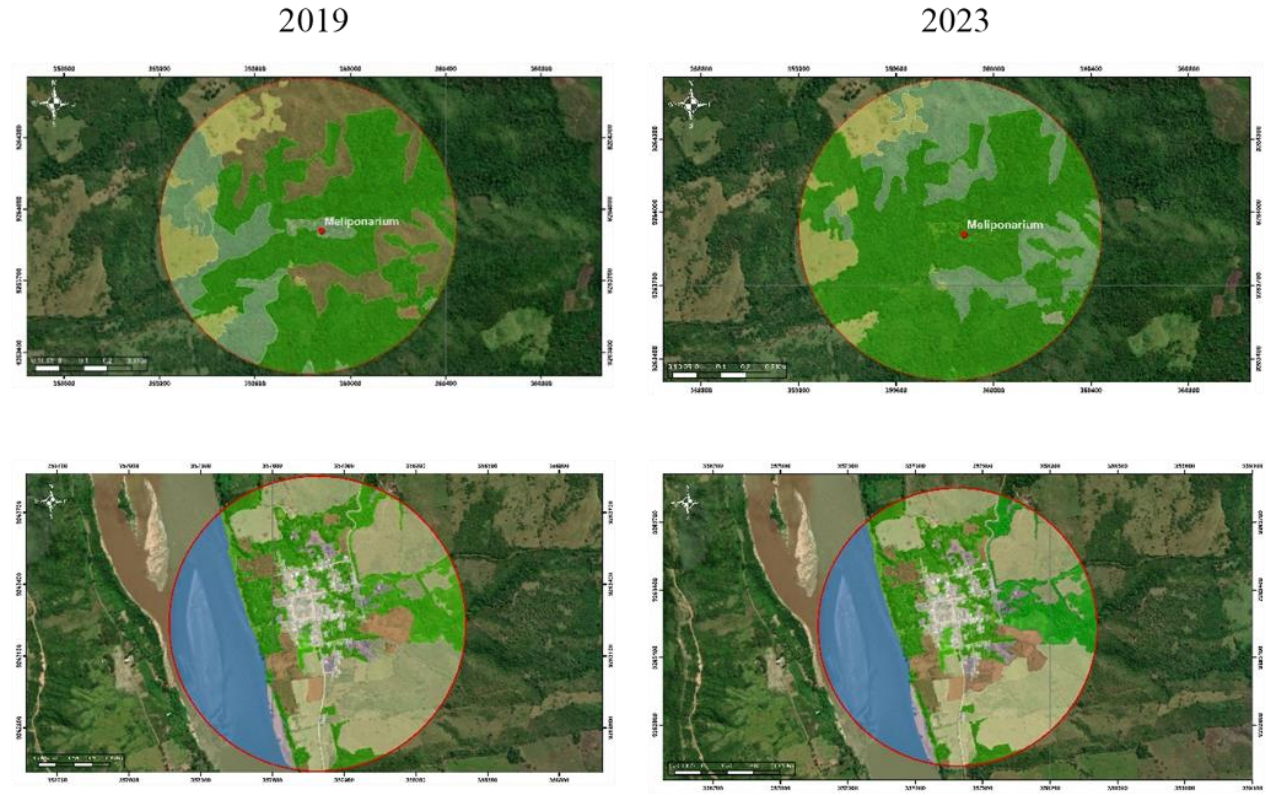

Figure 6. Representation of the landscape in the agroforestry (top) and urban (bottom) zones, between 2019 (left) and 2023 (right).

DISCUSSION

Despite an increase in forest, primarily in the agroforestry zone (N), the number of *T. angustula* colonies decreased slightly in both study areas. This suggests that changes in food availability did not influence the results observed. The nest density in urban (3.47 per hectare) and agroforestry (1.78 per hectare) zones were the highest compared to those reported by Fierro *et al*. (2012) in southern Mexico (0.54-1.00 per hectare). In contrast to what was observed by Copa-Alvaro (2004) in northern La Paz, Bolivia, occupation of dead logs in the field was not recorded due to the scarcity of this resource, possibly due to anthropic pressure on the landscape (fires, wood and shrub vegetation dominance). The severe modification of the original forest landscape in the agroforestry zone may have influenced the low availability of nesting sites, due to the predominance of secondary vegetation or reduced tree diameters. However, the success of *T. angustula* in urban and other disturbed ecosystems in the region has been reported in numerous studies (e.g. Vélez-Ruiz *et al*., 2013; Fierro *et al*., 2012; Copa-Álvaro, 2004). This seems to be due to the greater availability of cavities under urban conditions, which compensates for the absence of trees and exceeds the number of existing nesting niches in the field.

The greater availability of nest sites in the urban area, which correlates with increasing nest density (X^2= 4.565e^{-31}, df= 1, p-value ≈ 1), suggests that nest site selection in *T. angustula* is determined by the availability of cavities in the home range over and above environmental constraints of space and floral sources. This nesting behavior has also been observed in other stingless bee species, such as *Nannotrigona mellaria* (Martinez-Lopez et al., 2017), which share traits with *T. angustula*, including a smaller body size (less than 4.5 mm) and smaller colony sizes, as well as lower levels of aggressiveness at the floral source (Villa and Weiss, 1990; Hubbell and Johnson, 1977).

Despite the wide trophic niche of *T. angustula* (Vélez-Ruiz *et al*., 2013, Biesmeijer and Slaa, 2006) and its rapid adaptation to the exotic flora, it is likely that the species compensates for the trophic limitations of the urban environment with a smaller population per colony and the alternative use of food sources other than the local flora (e.g. sugar inputs and domestic waste). In addition, the protective properties of materials such as concrete, walls or wooden poles in urban infrastructure should be considered, as well as the protection provided by village location from deliberate fires in pastures that extend into forest areas. Nevertheless, nests in villages are more vulnerable to human predation and exposure to chemicals (Toledo-Hernández *et al*., 2022).

CONCLUSION

The variations in the nest density of *Tetragonisca angustula* in urban and agroforestry environments suggest that limited nesting space is the main factor affecting the density of this species. Unlike other stingless bee species that exhibit territorial and aggressive behavior, the availability of floral resources does not restrict the formation or persistence of *T. angustula* colonies.

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