JEE ISSN: 2288-1220
https://doi.org/10.5141/jee.25.021
Journal of Ecology and Environment (2025) 49:13
RESEARCH

Spatial distribution, tree host associations, and deforestation threats on two stingless bee species in the Peruvian Amazon

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ARTICLE INFO
Received March 26, 2025
Revised May 19, 2025
Accepted May 23, 2025
Published on July 2, 2025

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Background: Stingless bees (Apidae: Meliponini) are critical pollinators in the Peruvian Amazon, sustaining biodiversity, crop productivity, and indigenous livelihoods. Despite their ecological and economic importance, the effects of deforestation and illegal logging on their populations remain poorly understood. Nesting tree loss, habitat fragmentation, and changes in elevation influence stingless bee distribution, yet conservation efforts remain insufficient due to a lack of spatial data on their vulnerability.

Results: This study examines the spatial distribution, elevation trends, and deforestation threats affecting *Melipona eburnea* and *Tetragonisca angustula*, with a focus on tree nesting preferences in the Biosphere Reserve Avireri-Vraem. Using literature reviews, field observations, and GPS surveys, we assessed species distribution patterns, deforestation risks, and nesting tree associations. Our findings reveal that over 50% of their habitats overlap with high deforestation risk zones, largely driven by illegal logging of key nesting trees. Elevation analysis indicates species-specific adaptations, with *M. eburnea* predominantly in lowland regions, while *T. angustula* is more frequent at higher altitudes. GPS fieldwork identified strong associations with specific host trees, notably *Guarea guidonia* and *Ficus insipida*, with larger trees (> 60 cm DBH) serving as critical nesting sites. Several of these, including *Aniba gigantiflora* and *Cedrelinga cateniformis*, are among the most ilegally harvested species, intensifying threats to bee populations.

Conclusions: Deforestation-driven habitat loss and fragmentation pose an immediate threat to stingless bee populations by reducing nesting availability, limiting pollination networks, and disrupting genetic exchange. Our findings emphasize the urgent need for targeted conservation strategies, including the preservation of key nesting trees, the establishment of biological corridors, and the promotion of sustainable forestry practices. Given the role of stingless bees as keystone pollinators, their protection is crucial for maintaining biodiversity and ecosystem stability. Recognizing stingless bee habitats under a Rights of Nature framework would provide a legal mechanism to safeguard their nesting sites from further exploitation. Furthermore, strengthening community-led conservation efforts in high-risk areas can enhance long-term resilience. This study provides a baseline for future conservation policies, bridging scientific data and indigenous knowledge to protect Amazonian stingless bees and their ecosystems.

Keywords: Amazon rainforest, biodiversity, deforestation, nesting preferences, stingless bees

Introduction

Bees represent a fundamental life form of our planet's ecosystems, playing a vital role in pollination processes that maintain biodiversity stability and contribute significantly to global food security (Biscassi et al. 2024; Cevallos Erazo et al. 2023; Katumo et al. 2022). Stingless bees (Apidae: Meliponini) form a diverse group of eusocial bees, distributed pantropically, with over 500 species ranging from South and Central America to Africa, India, Australia, and Asia (Bueno et al. 2023; Roubik 2023; Vit et al. 2013).

Considered the most ecologically, economically and culturally important group of tropical pollinators (Meléndez Ramírez et al. 2018; Roubik 2023; Vit et al. 2013), stingless bees are crucial for the Amazon rainforest. They contribute to plant propagation (Masaquiza-Moposita et al. 2023) ensuring ecosystem stability in one of the world's most critical carbon dioxide-absorbing biomes (Ocaña-Cabrera 2023). Their high functional diversity maintains crop pollination services, even in the face of Amazon deforestation (Campbell et al. 2022), significantly contributing to the region's ecology (Garcia Bulle Bueno et al. 2023). These bees are emerging as essential pollinators, supporting 75% of agricultural crops by increasing fruit and seed productivity, particularly in tropical zones (Gonzalez et al. 2021).

Beyond pollination, stingless bees hold substantial economic and cultural importance in the Amazon rainforest (Delgado et al. 2020, 2023; de Sousa Silva et al. 2023; Quezada-Euán et al. 2018). Meliponiculture, the traditional practice of keeping stingless bees, is an ancestral tradition, particularly among indigenous communities, where honey, pollen, and propolis are valued for their nutritional and medicinal properties (Baena-Díaz et al. 2023). Products from these bees are highly valued for their nutritional and medicinal properties, partly due to the bees' collection of resin and other substances from medicinal trees (Delgado and Espinoza 2023; Sanguinetti et al. 2024).

Peru, a biodiversity hotspot due to its tropical geography (Móstiga et al. 2023), hosts 175 known stingless bee species, with many more species awaiting discovery (Rasmussen and Delgado Vásquez 2019). Two key species, *Melipona eburnea* and *Tetragonisca angustula,* hold particular ecological and cultural significance, playing key roles in pollination, food security, nutrition and traditional medicine (Carrillo et al. 2016; Delgado and Espinoza 2023; Delgado et al. 2020, 2023; Demetrio et al. 2025; Rasmussen and Delgado 2019). However, their populations are increasingly threatened by deforestation, habitat fragmentation, and climate change, which alter their nesting dynamics and geographic distribution (Brooks et al. 2002; Marconi et al. 2022; Rasmussen and Sánchez 2024).

Despite the richness of stingless bee species in Peru, significant gaps remain in understanding their spatial distribution in the Peruvian Amazon and how deforestation and climate change affect them (Baillie et al. 2004; Marconi et al. 2022; Rasmussen and Sánchez 2024). According to Parenti and Ebach (2009), "*distribution maps are among the most fundamental and historically informative data of any biogeographic study.*" Understanding stingless bee distribution and their environmental vulnerabilities is critical for developing conservation strategies that preserve these pollinators, protect forest ecosystems, and support indigenous communities that rely on them (Katumo et al. 2022; McShea 2014; Zumaeta et al. 2023).

While prior studies have assessed forest cover loss and its impact on pollinators in Brazil and Costa Rica (Brosi 2009; Brown and Albrecht 2001), few studies have examined how altitude, microclimatic variation, and deforestation interact to shape stingless bee distribution in Peru's montane and lowland forests. Given that stingless bees typically nest in tree cavities (Delgado et al. 2022; Vossler 2012), understanding tree species associations, nesting availability, and the long-term effects of climate change is critical for conservation planning. Rising temperatures, shifting precipitation patterns, and changing forest compositions could impact bee foraging efficiency, reproductive success, and species migration patterns, making these threats as pressing as deforestation itself (Imbach et al. 2017).

Globally, bee populations are declining, with one in three key food products relying on pollinators (Klein et al. 2007). Tropical deforestation has a particularly severe impact on stingless bees, altering their distribution, abundance, and ecological functions (Brown and de Oliveira 2014). This decline jeopardizes indigenous bee-based economies, traditional cultural practices, and entire ecosystems that rely on pollination services (Cangussu et al. 2022; Potts et al. 2010).

Studies in Brazil and Costa Rica suggest that richness and abundance of stingless bees are strongly linked to forest cover and proximity, sometimes more so than the availability of floral resources (Brosi 2009; Brown and Albrecht 2001). Given that stingless bees frequently inhabit cavities of large trees (Delgado et al. 2022; Vossler 2012), forest loss and tree harvesting can be fatal to their colonies. This highlights the critical need to integrate nesting preferences into forest management and conservation policies (Eltz et al. 2003).

Beyond deforestation, climate change and the frequency of fires present additional threats, affecting bee foraging efficiency, colony longevity, and geographic distribution (Imbach et al. 2017). Rising temperatures and altered precipitation patterns could force population shifts, potentially reducing their availability as pollinators in certain regions. Predictive models suggest that wild bee pollination may increase by 4.5%, whereas honeybee pollination is expected to decline by 14.5% in the coming decades, indicating that native stingless bees may be better adapted to future climate conditions than their domesticated counterparts (Rader et al. 2013).

The central Peruvian Amazon, a region of immense biodiversity, is increasingly threatened by deforestation, climate change, and pesticide use (Bax et al. 2019; Sebastiani and Falcinelli 2018; Zevallos and Lavado-Casimiro 2022). The UNESCO-recognized Avireri-Vraem Biosphere Reserve, spanning altitudes from 280 to 6,271 meters, is home to numerous endemic and endangered species and a large population of local and indigenous communities (Lehr et al. 2023). As one of the largest nature reserves in Central and South America (Latin American and Caribbean Geographic 2024), it harbors 12 unique ecosystems, including the Amazon rainforest, the montane and cloud forests of the Yungas, and the Andean highlands (UNESCO 2023). Within this Biosphere Reserve lies the Reserva Comunal Ashaninka and the National Park Otishi, a natural protected area where the Ashaninka people practice traditional polyculture farming and ancestral meliponiculture, both of which are deeply tied to forest conservation (Demetrio et al. 2025).

Deforestation and climate change not only drive biodiversity loss but also heighten the vulnerability of Indigenous populations in the Peruvian Amazon (Hofmeijer et al. 2013; Rojas et al. 2021). However, significant knowledge gaps remain regarding stingless bee populations, particularly their tree host associations, spatial distribution, and resilience to environmental changes on a regional scale.

Given their role as keystone pollinators and their increasing vulnerability to deforestation and habitat fragmentation, conservation strategies must go beyond traditional protected areas. A Rights of Nature framework provides a legal mechanism to recognize stingless bee habitats as essential ecological entities requiring protection. Similar legal precedents, such as Ecuador's constitutional recognition of nature's rights and Bolivia's Law of Mother Earth, demonstrate how legal personhood for ecosystems can strengthen conservation enforcement (Calzadilla and Kotzé 2018; Tanasescu 2013).

In this study, we map the distribution of both managed and wild beehives of *M. eburnea* and *T. angustula* across Peru using scientific literature databases and opportunistic observations. We analyze spatial distribution patterns and tree nest associations of wild stingless bee hives in Junín, Central Peruvian Amazon, while also assessing deforestation risks and habitat fragmentation to evaluate their impact on bee populations and tree nest availability. Furthermore, we propose biological corridors as a conservation strategy to maintain connectivity between fragmented bee habitats and safeguard pollination networks. Recognizing these corridors and nesting sites under a Rights of Nature framework could ensure their long-term legal protection, reinforcing conservation policies and preventing further habitat loss. By establishing a baseline for future climate change impact assessments, this study seeks to guide conservation strategies, inform policy-making, and promote sustainable forest management for the long-term protection of stingless bee biodiversity in the Amazon.

Materials and Methods

Data collection

This study integrates three datasets to assess the distribution, nesting preferences, and deforestation vulnerability of stingless bees (*M. eburnea* and *T. angustula*) across the Peruvian Amazon. (1) A literature review compiles published records on species distribution across Peru. (2) Opportunistic observations document field sightings of stingless bees from various locations in Peru. (3) GPS-based fieldwork was conducted in the Biosphere Reserve of Avireri-Vraem exclusively and focuses on nesting tree preferences and microhabitat characteristics. We conducted a broad-scale deforestation risk analysis using all three datasets, while a finer-scale investigation of nesting tree vulnerability and localized habitat fragmentation was conducted with the GPS dataset.

Systematic literature review

We conducted a systematic literature search using Scopus, Web of Science and Google Scholar databases, along with other general literature databases, to compile presence-only records of stingless bee species, specifically *M. eburnea* and *T. angustula*, in the Peruvian Amazon. The search, conducted between October 2023 and August 2024, used the following search terms: "bee," "stingless bee," "meliponine," "Peru," "Amazon rainforest," and "native bee," along with their equivalents in Spanish and Portuguese. The search period spanned 1995 to 2024, and results were filtered to include only published articles, thesis dissertations, and book chapters.

Studies were included based on the following criteria: (1) the study had to be original; (2) it provided either a list of species or their abundance; (3) it specified whether the hives were wild or managed; and (4) it contained accurate geographic information (coordinates or detailed location descriptions sufficient for mapping). From each study, we extracted the year of publication, species name, journal (or university/publisher), coordinates (latitude and longitude), political location (region), and hive type (wild or managed). All the extracted data, along with the complete reference list, are provided in Supplemental Information.

Opportunistic observations

During opportunistic travels across the Peruvian Amazon (August 2023–June 2024), we recorded the presence of stingless bee hives based on direct field observations. For each sighting, we documented the GPS coordinates, species identification, hive quantity, and hive type (wild or managed).

GPS-based data collection Biosphere Reserve Avireri-Vraem

Recognizing the significance of stingless beekeeping and bee biodiversity within the Biosphere Reserve of Avireri-Vraem (Demetrio et al. 2025), we conducted a geospatial survey in four communities located in the buffer zones of the Ashaninka Communal Reserve (Junín region).

The Ashaninka Communal Reserve is located in a mountainous and hilly region covered by tropical vegetation, featuring various altitudinal zones that host a rich biodiversity. Politically, it is situated in the Río Tambo district of Satipo province in the Junín department. It is also adjacent to the district of Pichari and Unión Ashaninka, province of La Convención in the Cuzco department, within the broader Avireri-Vraem Biosphere Reserve. Precipitation varies across the area: in the lower zone, it averages approximately 2,000 mm annually, while in the higher zone, it reaches around 3,000 mm annually. Temperatures up to 1,000 masl average around 25°C. Between 1,000 and 2,000 masl, temperatures decrease to about 22°C, and above 2,000 masl, they drop below 20°C.

Consent was obtained from Eco Ashaninka and from each community, in collaboration with local indigenous Ashaninka leaders and park rangers. The areas surveyed comprised primary and secondary rainforest, with the following dominant tree species: *Pseudolmedia laevigata* (Chimicua), *Nectandra* sp. (Moena), *Inga ruiziana* (Shimbillo), *Pouteria* sp. (Quinilla), *Guarea* sp. (Requia), *Quararibea bicolor* (Zapotillo), *Virola peruviana* (Cumala), *Guatteria* sp. (Carahuasca), *Clarisia racemosa* (Mashonaste), *Pouteria* sp. (Caimitillo), *Spondias mombin* (Ubos), *Macrolobium* sp. (Pashaco), *Trichilia* sp. (Uchumullaca), *Ficus* sp. (Renaco), *Zanthoxylum risianum* (Hualaja), *Osandra* sp. (Espintana), *Brosimum alicastrum* (Manchinga), and *Aspidosperma macrocarpon* (Pumaquiro).

The study took place between August and December 2023 in the tropical climate of the Junín region, focusing on four communities located in the buffer zones of the Reserva Comunal Ashaninka: Caperucia (11°18′12.44″S – 74°9′45.13″W; 814 meters above sea level, masl) Pichiquia (11°26′0.25″S – 74°6′39.16″ W; 350 masl), Chimiato (12°10′15.45″S – 73°52′9.35″W; 931 masl) and Cheni (11°17′50.77″S – 73°43′12.92″W; 277 masl). This dataset provides precise geolocation records to support a detailed analysis of stingless bee distribution and habitat use in the region.

Nest location

We conducted the survey by walking through the rainforest to locate wild bee colonies. The areas selected for data sampling were based on direct observations or reports from community members (“comuneros”) about the presence of stingless bees. For each colony, we recorded the species identity, geographic coordinates using a GPS eTrex 10 (accuracy: +/- 5 m), elevation (m), temperature (°C), relative humidity (RH, %), and tree host used for nesting. For each tree host, we documented the tree’s genus, species, and diameter at breast height (DBH, cm) (Figs. S1-S3).

Stingless bees and tree host identification

Bees were identified based on morphological characteristics, using taxonomic keys and the distinctive hive entrances unique to each species (Rasmussen and Delgado 2019). Tree species were identified using morphological features.

Density of nests

The location of the identified nests was mapped in ARCGIS-PRO. Nest density was calculated by dividing the number of nests identified by the total area surveyed (ha). To estimate the surveyed area, we measured the total distance walked along the transects and multiplied it by the estimated transect width. A flight distance of 300 m was assumed as an average for both species (Araújo et al. 2004; Kuhn-Neto et al. 2009), and the transect area was calculated using the ‘Buffer’ tool in the Analysis Toolsbox of ArcGIS-PRO. Given the significant height of Amazonian trees, it is likely that some bee nests located high in the canopy were missed during surveys. Therefore, nest density calculations should be interpreted as a relative index for site comparisons (Eltz et al. 2002).

Data analysis

Dispersion maps of native bees were created from published literature, observational data, and fieldwork data from the Junín region using ArcGIS Pro. Bar charts were also generated, analyzing native bee species, hive types, and locations. We used the *ggplot2* package version 3.3.3 (Wickham 2016) in RStudio version 04.2 (R Core Team 2024) for visualizations.

The relationship between stingless bees and tree flora (family and species) was analyzed using polar diagrams created with the *ggplot2* package in RStudio. Additionally, chord diagrams were created to depict the relationships between native bee species and tree flora using the *circlize* package version 0.4.1 (Gu et al. 2014).

The association between native bees, flora, DBH, and climate variables (humidity and temperature) was assessed using multiple factor analysis (MFA). MFA is a multivariate analysis method that examines datasets containing both qualitative and quantitative variables (Kassambara 2017). The multivariate analysis was conducted using the *Factoextra* package version 1.0.7 (Kassambara and Mundt 2020).

Deforestation vulnerability analysis

The vulnerability of stingless bees to deforestation was evaluated by assessing the risk of forest loss in the Peruvian Amazon. The classification of the risk of deforestation at the district level in the Amazon for the year 2022 was analyzed, following the methodology established by Casas et al. (2023), the categories used were low, medium, high, very high and extremely high risk. We employed a Kohonen neural network, using variables such as Forest Cover Loss, Forest Cover, Topography, Climate, Hydrographic Networks, and Logging Concessions. The *aweSOM* package version 1.3 (Boelaert et al. 2022) was used with the Online algorithm. Statistical goodness was evaluated through quantization error (QE), explained variance percentage (EV%), topographic error (TE), and Kaski-Lagus error (KL).

In addition, reports of Administrative Sanctioning Processes (PAS) from the National Forest and Wildlife Service (SERFOR) for 2023 were analyzed (Table 1). We evaluated the forest species exploited without authorization and determined whether these species were recorded as hive supports during field inspections.

Results

Geographic distribution of stingless bees in the Peruvian Amazon: literature and opportunistic observations

A total of 11 published studies met the inclusion criteria for stingless bee records in the Peruvian Amazon, specifically for *M. eburnea* and *T. angustula*, across six regions (Table S1). Loreto and San Martín accounted for the highest number of studies, with eight and four publications, respectively (Fig. 1A).

The geographic distribution of hives in the Peruvian Amazon revealed that *M. eburnea* was the predominant species, comprising 66.3% (57/86) of all reported hives. Notably, most of these hives were managed (66.6%, 38/57) (Fig. 2A). Conversely, in the Junín region (Provinces of Chanchamayo and Satipo), managed hives of *T. angustula* were more prevalent (62.7%, 27/43) compared to *M. eburnea* (9.3%, 4/43) (Nestares Rojas 2023).

In terms of opportunistic observations recorded during travel, stingless bee hives were documented across six Amazonian regions (Fig. 1B). The majority of these records consisted of managed hives, with *M. eburnea* and *T. angustula* representing 36.4% (28/77) and 29.9% (23/77) of the total observations, respectively (Fig. 2C). Notably, Junín had the highest number of observed hives, accounting for 66.2% (51/77) of all records (Fig. 2D).

When combining insights from both published literature and opportunistic observations, *M. eburnea* and *T. angustula* were found to be widely distributed across ten Peruvian Amazon regions: Loreto, Amazonas, Cajamarca, San Martín, Huánuco, Pasco, Ucayali, Junín, Cuzco, and Madre de Dios. These regions span diverse ecosystems, from lowland floodplains to the Amazon-Andes transition zone, each characterized by distinct environmental conditions, including variations in elevation, temperature, and humidity.

GPS-based hive mapping and stingless bee distribution in the Biosphere Reserve Avireri-Vraem

In the Biosphere Reserve Avireri-Vraem (Junín region), GPS-collected data recorded 51 stingless bee hives, with notable spatial overlap between *M. eburnea* and *T. angustula* (Fig. 1C). The vast majority were wild hives (50/51), with *M. eburnea* and *T. angustula* representing 51.0% (26/51) and 45.1% (23/51) of the total, respectively (Fig. 2E). The Community of Caperucia accounted for 80.4% (41/51) of all recorded hives, making it the most hive-dense locality (Fig. 2F).

A preliminary analysis of the spatial distribution reveals variation in nest placement. While some hives formed localized clusters, others appeared as isolated outliers scattered farther away. To assess clustering patterns, we excluded the more distant outliers and focused on 34 hives out of the total 51, estimating an approximate nest density of 0.06 nests per hectare.

This study provides the first formal documentation of

Table 1 Variables analyzed to assess the vulnerability of stingless bees to deforestation in the Peruvian Amazon

Data	Type	Source	Link
Forest cover loss (Ha)	.xls	Geobosques	https://geobosques.minam.gob.pe/geobosque/view/index.php#
Forest cover (Ha)	.xls	Geobosques	https://geobosques.minam.gob.pe/geobosque/view/index.php#
Corrected precipitation (mm/day)	Raster	NASA	https://power.larc.nasa.gov/data-access-viewer/
Maximum temperature (°C)	Raster	NASA	https://power.larc.nasa.gov/data-access-viewer/
Minimum temperature (°C)	Raster	NASA	https://power.larc.nasa.gov/data-access-viewer/
Topographic data (elevation)	Raster	Instituto Geográfico Nacional - IGN	https://www.geoidep.gob.pe/instituto-geografico-nacional
Hydrographic networks	Vector	Instituto Geográfico Nacional - IGN	https://www.geoidep.gob.pe/instituto-geografico-nacional
Forest concessions	Vector	Servicio Nacional Forestal y de Fauna Silvestre - SERFOR	https://geo.serfor.gob.pe/visor/
15 departamentss and 400 districts	Vector	Ministerio del Ambiente - MINAM	https://geoservidor.minam.gob.pe/
PAS Registry -2023	.xls	Servicio Nacional Forestal y de Fauna Silvestre – SERFOR	https://repositorio.serfor.gob.pe/handle/SERFOR/948

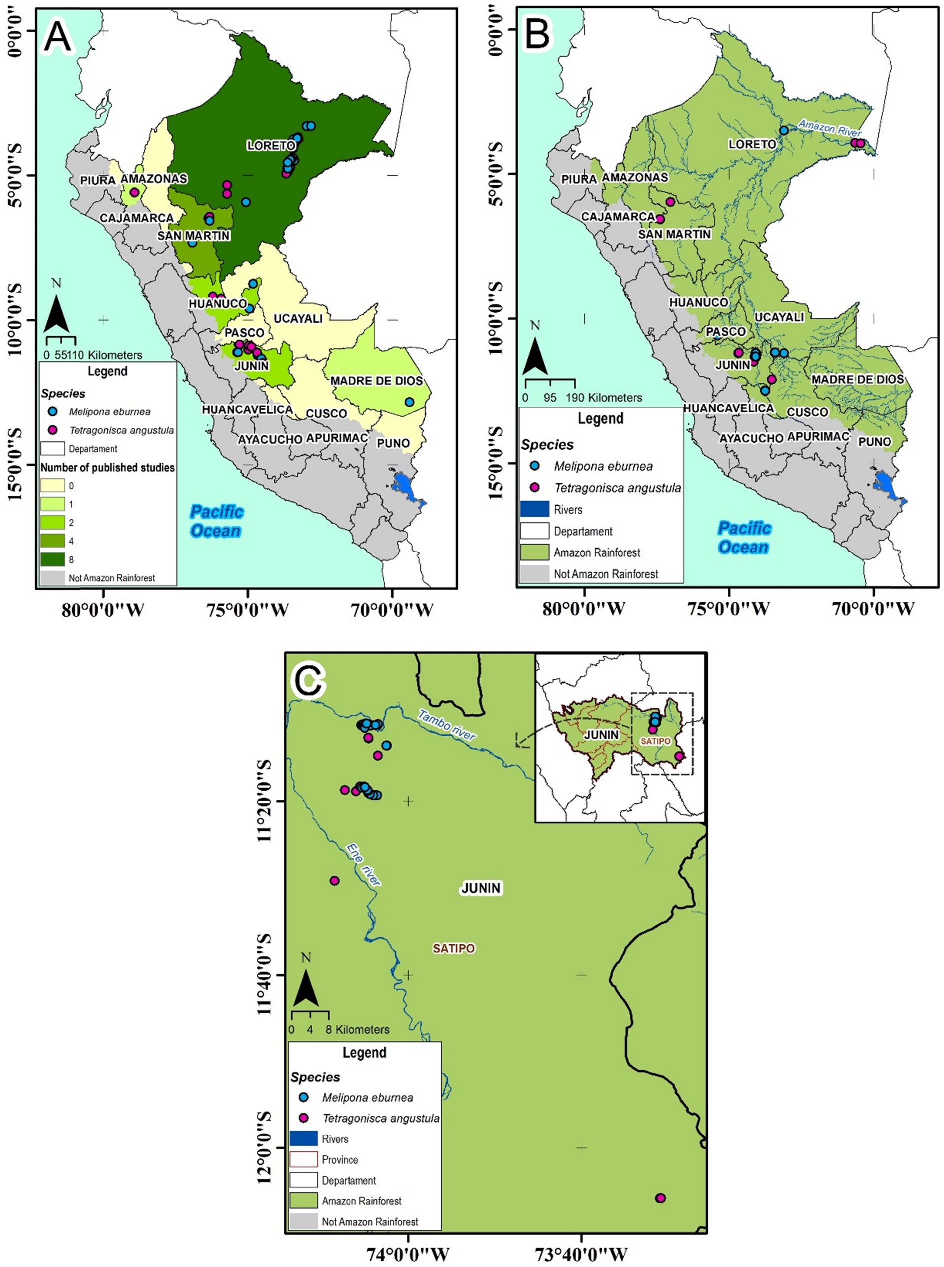

Fig. 1 Geographic distribution of stingless bees in Peru. (A) Records from published literature. (B) Opportunistic observations. (C) GPS-based field data from the Junín Region.

wild stingless bee hive distribution and species richness in the Junín area of the Peruvian Amazon, serving as an important baseline for future monitoring.

Stingless bee distribution across elevation gradients in the Amazon

From the combined datasets, we analyzed data points with available elevation information. Some elevation records from literature sources exhibited discrepancies when cross-referenced with Google Earth DEM, potentially due to unit conversion issues or GPS errors arising from limited satellite coverage in the rainforest. Recognizing these potential errors, we conducted a preliminary analysis to identify patterns in the distribution of bee nests across elevations, spanning three Peruvian bioregions: Low Jungle (Omagua: 50–400 masl), High Jungle (Rupa-rupa: 400–1,000 masl), and Cloud Forest (Yungas: 1,000+ masl).

In the Low Jungle (Omagua), 73 data points (45%) were recorded, with 81% representing *M. eburnea* and 19% *T. angustula*. In the High Jungle (Rupa-rupa), 48 data points (29%) were observed, where 37.5% corresponded to *M. eburnea* and 62.5% to *T. angustula*. The Cloud Forest (Yungas) yielded 42 data points (26%), with 45% *M. eburnea* and 55% *T. angustula*.

A noticeable trend emerged, the number of data points decreased with increasing elevation (45% → 29% → 26%), and species distribution patterns shifted. *Melipona eburnea* was dominant at lower elevations, declined in the High Jungle, and showed a slight resurgence in the Cloud Forest. Conversely, *T. angustula* followed an opposite trend, peaking in the High Jungle before decreasing in the Cloud Forest.

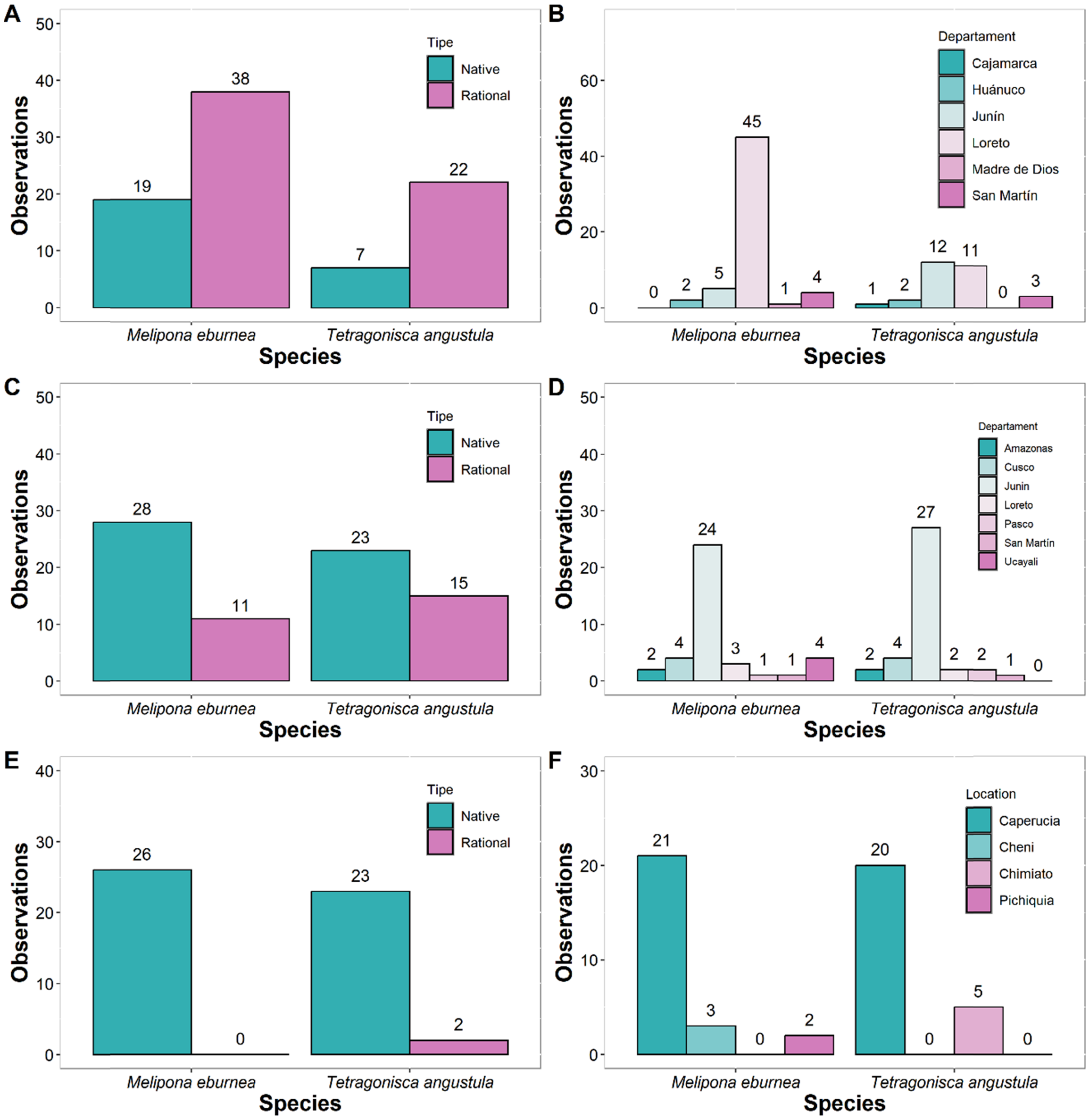

Fig. 2 Reports of stingless bees in the Peruvian Amazon. (A) Hive type distribution from literature records. (B) Departmental distribution from literature records. (C) Hive type distribution from opportunistic observations. (D) Departmental distribution from opportunistic observations. (E) Hive type distribution from GPS-based records in Junín. (F) Locality-based distribution from GPS-based records in Junín.

Stingless bee nesting preferences: tree species, climate, and structural factors

In the Biosphere Reserve Avireri-Vraem (Junín region), native hives were observed in ten tree families, with Moraceae, Fabaceae, and Meliaceae having the highest number of records at 30.6%, 20.4%, and 12.2% (15/49, 10/49, and 6/49), respectively (Fig. 3A). At the species level, *M. eburnea* was observed in seven tree families, with the highest incidence in Fabaceae, Moraceae, and Meliaceae at 23.1%, 23.1%, and 19.2% (6/26, 6/26, and 5/26), respectively (Fig. 3B). *Tetragonisca angustula* was recorded in nine tree families, with the highest incidence in Moraceae, Calophyllaceae, and Fabaceae at 39.1%, 17.4%, and 17.4% (9/23, 4/23, and 4/23), respectively.

Regarding tree species, 21 were recorded as hosts for native hives, with *Guarea guidonia*, *Aniba gigantiflora*, *Calophyllum brasiliense*, *Cedrelinga cateniformis*, *Ficus insipida*, and *Pourouma cecropiifolia* being the most frequent at 12.2%, 8.2%, 8.2%, 8.2%, 8.2%, and 8.2% (6/49, 4/49, 4/49, 4/49, 4/49, and 4/49), respectively (Fig. 3C).

Melipona eburnea was identified in 14 tree species, with the highest incidence in *G. guidonia* and *P. cecropiifolia* at 19.2% and 11.5% (5/26 and 3/26), respectively (Fig. 3D). *Tetragonisca angustula* was found in 13 tree species, with the highest incidence in *C. brasiliense*, *C. cateniformis*, and *F. insipida* at 17.4%, 17.4%, and 13.0% (4/23, 4/23, and 3/23), respectively.

Among the trees identified in this study, seven hives were found in large trees (> 60 cm DBH), while 16 hives were in smaller trees, including 11 in trees with a DBH of 16–29 cm and five in trees of 30–59 cm, typical for younger trees (Fierro et al. 2012).

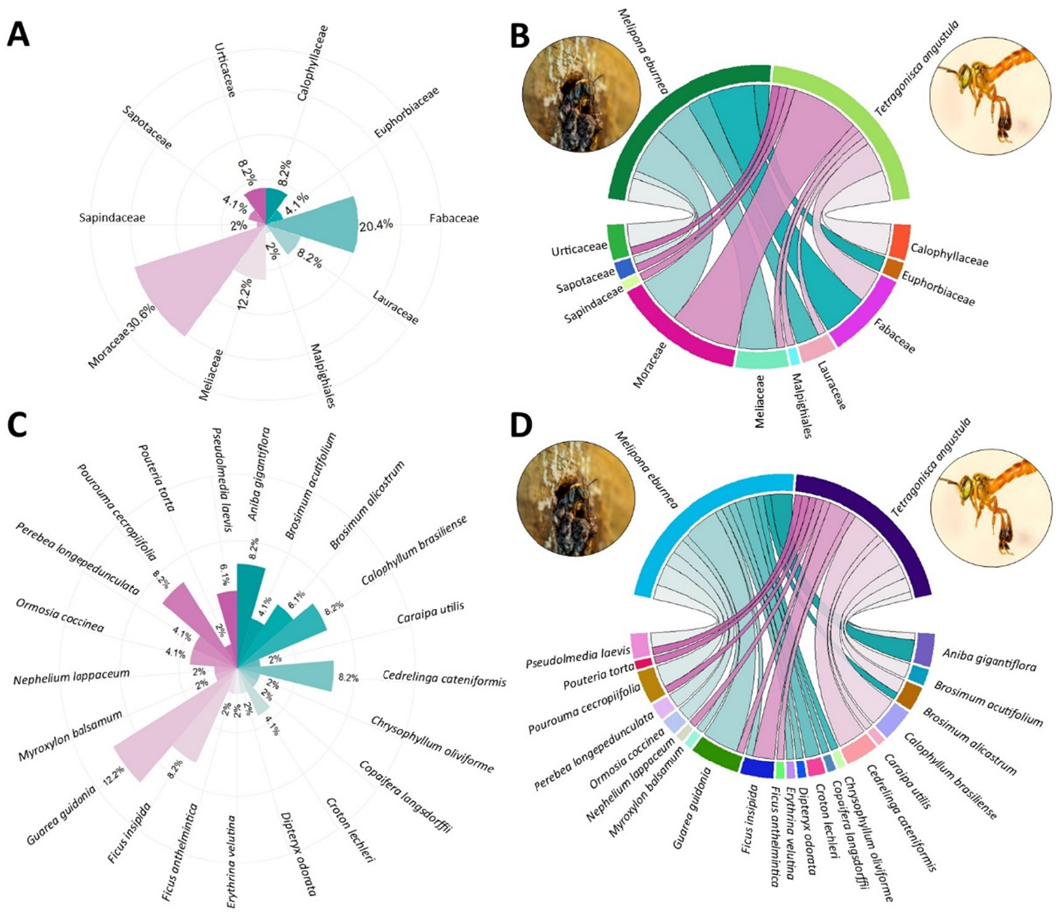

Fig. 3 Association of native bee hives with tree flora. (A) Percentage of incidence by tree family. (B) Bee species network by tree family. (C) Percentage of incidence by tree species. (D) Bee species network by tree species.

The MFA explained 71.1% of the data variability, with 49.3% and 31.0% attributed to dimensions 1 and 2, respectively (Fig. 4). A stronger association between native bees and tree families/species was observed compared to tree structure (DBH) and climate (humidity and temperature) (Fig. 4A, B). Specifically, common taxa such as Fabaceae and Moraceae were associated with both bee species, while *M. eburnea* was linked with Euphorbiaceae, and *T. angustula* with Calophyllaceae, Malpighiales, and Sapindaceae (Fig. 4C).

Deforestation and its impact on stingless bee populations

The Kohonen neural network accurately classified the risk of forest loss in the Amazon rainforest for the year 2022, yielding a QE of 0.4269577, an EV of 94.66%, a TE of 0.2992045, and a KL of 2.220126. The network categorized 7.3%, 2.3%, 46.8%, 38.8%, and 5.0% (29/400, 9/400, 187/400, 155/400, and 20/400) of districts into low, medium, high, very high, and extremely high-risk categories for deforestation, respectively (Fig. 5A). Statistical indicators and classifications to those obtained by Casas et al. (2023) for the period 2001–2021 in the same study area.

In relation to native bee observations, more than 50% of the districts were classified as being at high to very high risk (Fig. 5B). Regions such as Junín and San Martín, which experience the highest deforestation rates, present the greatest threats to stingless bee populations due to the rapid expansion of agro-industrial frontiers (Bax 2018; Lucich et al. 2015). Similarly, in Madre de Dios, increasing mining activity poses a significant risk to both forest ecosystems and native bee populations (Diringer et al. 2020).

Melipona eburnea accounted for 19.0% and 20.9% (31/163 and 34/163) of hives, while *T. angustula* represented 21.1% and 14.7% (36/163 and 24/163) of hives in the high and very high-risk categories, respectively. These results underscore the vulnerability of stingless bee populations to deforestation, as a significant proportion of their habitats overlap with areas at high risk of forest loss.

In 2022, the National Forest and Wildlife Service (SERFOR), through its PAS, reported the unauthorized extraction of 21 forest species. Among these, 33.3% (7/21) were identified as host species for native bee hives (Fig. 5C). The tree species included in the PAS list were *A. gigantiflora*, *B. alicastrum*, *C. cateniformis*, *Dipteryx odorata*, *Myroxylon balsamum*, *Ormosia coccinea*, and *Pouteria torta*. Of these, *B. alicastrum*, *C. cateniformis*, and *A. gigantiflora* were recurrent host species for both *M. eburnea* and *T. angustula* hives, with *A. gigantiflora* showing a particularly strong correlation with *T. angustula*.

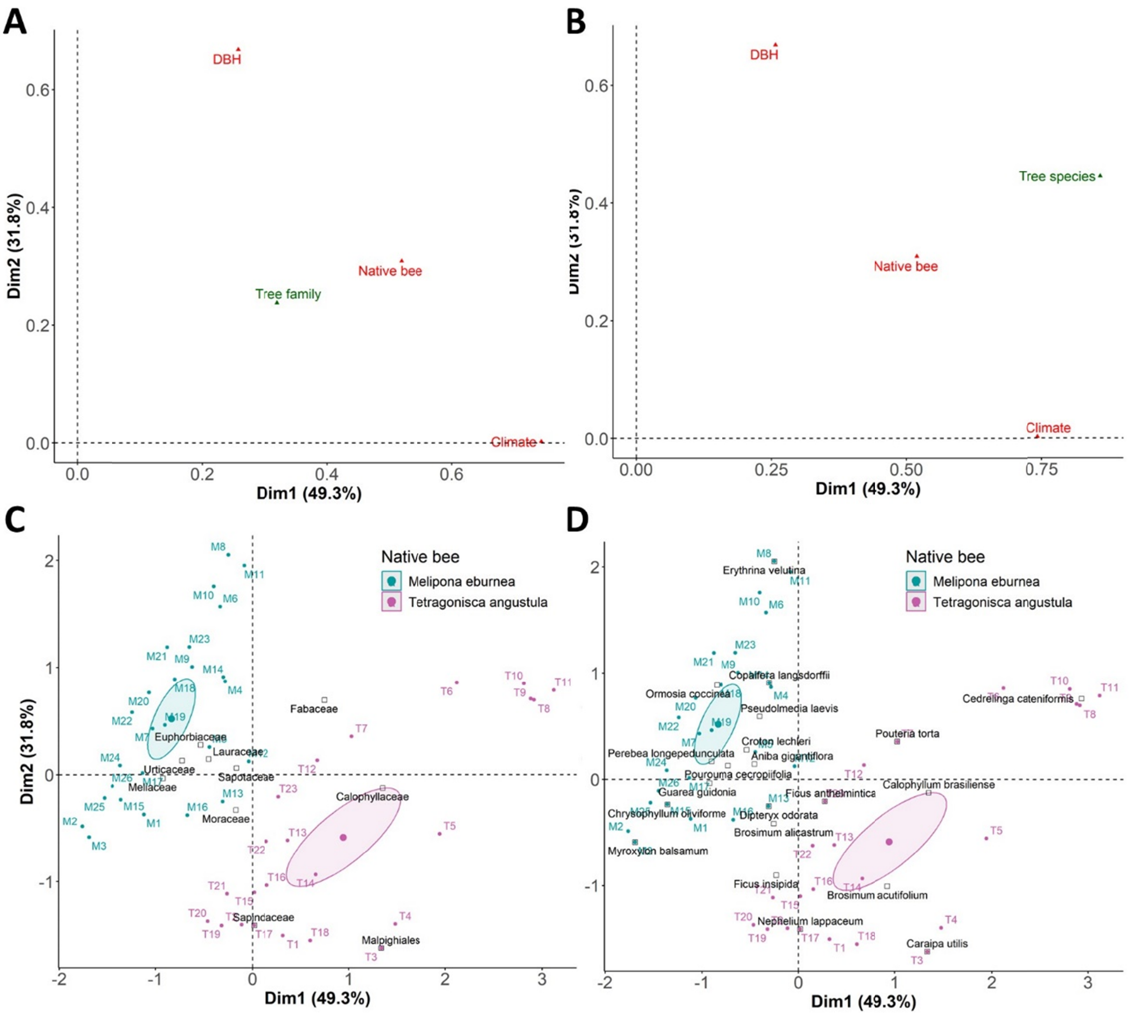

Fig. 4 Multiple factor analysis for native bee hives with tree flora, structure (DBH), and climate (humidity and temperature). (A) Variable group analysis for tree family. (B) Bee species individual plot with tree family. (C) Variable group analysis for tree species. (D) Bee species individual plot with tree species. DBH: diameter at breast height.

Discussion

Species distribution and adaptation to environmental changes

The prevalence of *M. eburnea* in managed hives aligns with previous research, which highlights its broad Amazonian distribution, spanning Peru, Ecuador, Colombia, Bolivia, and Brazil (Domínguez et al. 2023; Rodriguez Bustamante et al. 2022). Conversely, *T. angustula* exhibits a wider geographic range, extending from Mexico to Argentina (Castanheira and Contel 2005). Its high ecological plasticity allows it to thrive in diverse habitats, including primary and secondary forests and even urban settings (Vélez-Ruiz et al. 2013). This adaptability may explain why managed hives of *T. angustula* were more prevalent in Junín, where it thrives in secondary forests expanding due to land-use changes (Batista et al. 2023; Braga et al. 2012).

The species' ability to nest in varied environments, facilitated by its smaller body size and gentle nature (Mayes et al. 2019), likely contributes to its widespread distribution in managed hives. Furthermore, the high medicinal and economic value of *T. angustula* honey may increase its cultivation (Delgado and Espinoza 2023).

The dominance of Loreto and San Martín in documented stingless bee hives (65.11% of all records) is consistent with prior assessments of stingless bee biodiversity, which have historically focused on the northern Amazon regions of Peru (Delgado et al. 2023; Rasmussen and Delgado Vásquez 2019). The broad distribution of both *M. eburnea* and *T. angustula* across ten regions suggests that both species exhibit significant ecological adaptability, allowing them to persist across diverse habitats and climatic conditions. This resilience may indicate a level of resistance to environmental changes, including climate change-driven alterations in Amazonian ecosystems.

Spatial clustering and environmental influences

The observed clustering of hives may reflect localized host tree abundance or food resource concentration, while the presence of outliers may indicate micro-climatic variability or other environmental factors not yet assessed. Habitat structure, particularly tree species composition

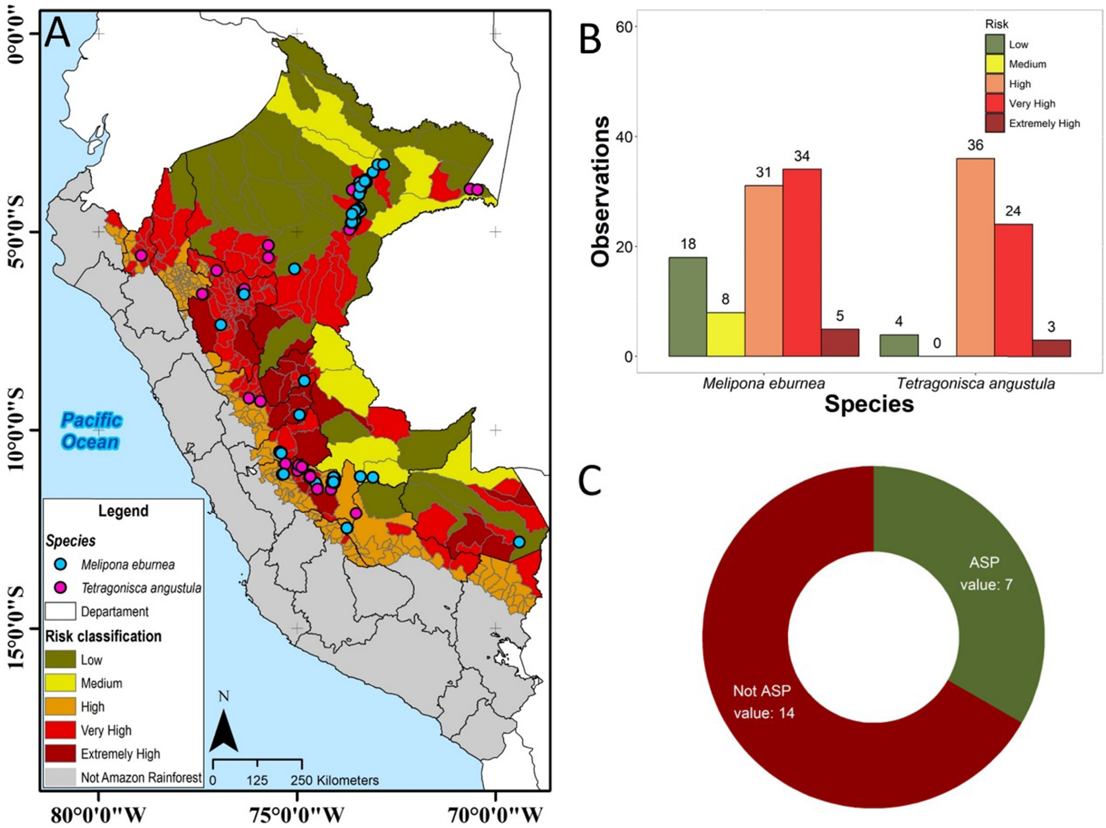

Fig. 5 Report on stingless bees and deforestation. (A) Forest loss risk map in the Amazon rainforest and distribution of native bees. (B) Forest loss risk by native bee species. (C) Report on PAS for melliferous trees. PAS: Administrative Sanctioning Processes.

and density, may also play a role in hive placement, though its specific influence remains unclear. Comparative data from neighboring Amazonian countries remain scarce, making cross-regional comparisons difficult (Gonzalez et al. 2021). In Ecuador, both species have been documented, but *M. eburnea* appears more frequently in managed hives - potentially a reflection of limited study coverage of meliponiculture sanctuaries rather than actual distribution patterns. In Bolivia, most data focus on *T. angustula* in both wild and managed settings, while information on *M. eburnea* remains limited. In Brazil, *T. angustula* is widely regarded as the most commonly kept stingless bee species (Simões-Vieira et al. 2024), which may contribute to literature bias favoring this species over others in distribution studies.

Although the slight differences in abundance between *M. eburnea* and *T. angustula* are not statistically conclusive at this stage, our findings highlight the need for further research into ecological factors shaping hive distribution. Future studies should investigate host tree preferences, resource availability, and micro-climatic influences to improve our understanding of the ecological drivers of stingless bee populations. It is equally important to explore anthropogenic factors that may influence species distribution and abundance, including pollution-related stressors such as pesticide residues and microplastic contamination, which can be transported via air and water systems (Brahney et al. 2020; Silva et al. 2019). This knowledge is essential for informing conservation strategies and ensuring the protection of these key pollinators.

Elevation gradients and their influence on stingless bee distribution

Our findings align with a study in the Amazonas Region, which reported a similar trend - *M. eburnea* predominated at lower elevations, while *T. angustula* became more frequent at higher elevations (up to 1,400 masl) (Delgado et al. unpublished data). However, the increase in *T. angustula* occurred gradually, rather than at a specific elevation threshold, with no distinct breakpoint where one species abruptly replaced the other.

Human influence must also be considered. In the Colombian Andes, relocating *T. angustula* nests across elevations often led to colony loss or poor establishment (Gonzalez et al. 2021). Such regional contrasts may reflect subspecies variations, epigenetic adaptations, or microclimatic factors (temperature, humidity, flora) that shape local adaptations.

For instance, in Colombia, *M. eburnea* has been recorded at 498 masl (Rupa-rupa) and its subspecies at 1,413 masl (Yungas) (Nates-Parra and Rodríguez-C 2011; Obregon and Nates-Parra 2014). Meanwhile, *T. angustula*, the most commonly cultivated species in meliponiculture, is primarily abundant in low-elevation areas. Similarly, in Costa Rica, stingless bee biodiversity declines at higher elevations, and *T. angustula* is found exclusively between 200 to 1,000 masl (Ortiz-Mora et al. 1995). These patterns suggest that elevation-based distribution may be influenced by plant associations and region-specific ecological conditions.

Further research is needed to explore how elevation influences plant preferences and foraging behavior in stingless bees. Elevation correlates with temperature, precipitation, and other microclimatic variables, all of which impact nesting success and survival. Investigating these patterns will provide insights into species' thermal tolerances, which is crucial for predicting their adaptability to rising global temperatures and changing environmental conditions.

According to the IPCC (2013), climate change is expected to disrupt plant-pollinator interactions, causing latitudinal and elevational shifts with major implications for food security. Our findings emphasize the urgency of conserving bioregional ecosystems that support stingless bee populations, particularly as they face the dual threats of habitat loss and climate change.

Tree nesting preferences: implications for conservation

The strong association between stingless bees and specific tree species highlights their ecological role in nesting site selection. *Melipona eburnea* exhibited a preference for *G. guidonia* and *P. cecropiifolia*, while *T. angustula* was most frequently recorded in *C. brasiliense*, *C. cateniformis*, and *F. insipida*. This aligns with previous studies in Mexico, where *T. angustula* preferred *Ficus* sp., nesting in 11 tree species (Martins et al. 2004).

In Peru, *M. eburnea* has been documented nesting in more than 16 tree species, with *Callicophyllum spruceanum* identified as the most frequently used species (Delgado et al. 2022). While this suggests that *M. eburnea* has flexibility in tree selection, certain species likely play a disproportionate role in their nesting ecology. The frequent presence of *M. eburnea* in *G. guidonia* and *T. angustula* in *F. insipida* indicates that these trees provide suitable cavities or other ecological benefits that make them preferred nesting sites.

Similar findings have been reported across South America. In Brazil, stingless bees were observed using 12 tree species for nesting, favoring *Caesalpinia pyramidalis* and *Commiphora leptophloes* (Martins et al. 2004), while in Minas Gerais, *T. angustula* nested widely, including in *Ficus* species (Siqueira et al. 2012). In Bolivia, nearly half of *T. angustula* hives were found in *Astronium urundeuva*, indicating strong regional dependence on certain tree species.

Tree species preferences are difficult to define, likely depending on availability, cavity formation, and local diversity (Nates-Parra et al. 2008). Still, findings suggest frequent associations with specific trees, reinforcing the role of tree diversity in shaping distribution.

Tree size also influenced nesting site selection. *Melipona eburnea* was frequently recorded in large trees (> 60 cm DBH), consistent with studies in Malaysia and Uganda, where larger trees provided more suitable nesting cavities (Eltz et al. 2002; Kajobe 2007). However, *T. angustula* displayed flexibility, nesting in both young trees (37–39 cm DBH) and larger trees (57–78 cm DBH) in Mexico (Fierro et al. 2012). This suggests that cavity formation and tree structure, rather than just age, may influence nest site selection.

The MFA results indicate tree species were more influential than temperature or humidity in nesting patterns. However, given the regional microclimatic uniformity, further research is needed to assess how broader climatic gradients affect distribution.

Notably, *Guarea* sp. ("requia") and *Ficus* sp. ("renaco"), both abundant in the region, were frequently used as nesting trees. This strong association underscores the need to protect these species, as their loss could significantly impact wild bee populations. The findings support conservation policies that preserve key trees and ensure nesting resources across wild and managed landscapes.

As deforestation threatens key nesting trees, conservation strategies should focus on safeguarding these species, particularly in areas of high meliponine diversity. Protecting forests with diverse tree assemblages is vital to maintaining stingless bee populations, ensuring their role as keystone pollinators remains intact.

Deforestation, habitat fragmentation, and conservation strategies

High-risk deforestation zones overlap with stingless bee habitats, underscoring the threats of land-use changes. These pressures fragment habitats, reducing nesting trees and floral resources, while disrupting colony stability, foraging, and reproduction.

In Loreto, *M. eburnea* nests in a diverse range of tree species (Delgado et al. 2022), suggesting that land-use changes near cultivation may affect tree availability and bee distribution. Similar studies in other regions could clarify how agriculture influences nesting and species interactions.

For instance, *M. eburnea*, which exhibits flexibility in nesting site selection, may temporarily adapt to disturbed environments. However, long-term agricultural encroachment could diminish suitable nesting substrates, leading to population declines and disrupted ecological networks.

While our study focused on correlations within the Biosphere Reserve Avireri-Vraem (Junín region), we observed that certain tree species—such as *G. guidonia*, *C. brasiliense*, and *C. cateniformis*—are preferred nesting substrates. These findings suggest that deforestation, particularly of these tree species, could disproportionately impact stingless bee populations.

The widespread loss of these key nesting trees is not only an ecological concern but also raises questions about how to legally safeguard critical pollinator habitats. The urgency of this issue is compounded by the devastating fires that have burned hundreds of hectares of the Peruvian Amazon in 2024 (GeoBosques 2024; NASA Firms 2024). Current conservation policies focus on reforestation and protected areas, yet they do not recognize the intrinsic role of trees as essential components of stingless bee survival.

A Rights of Nature framework could fill this gap by granting legal recognition to these interconnected ecosystems, ensuring protection beyond isolated conservation measures. Precedents such as the Te Awa Tupua Act (New Zealand) and Ecuador's constitutional recognition of nature's rights demonstrate how such legal frameworks can be applied to prevent ecosystem degradation (Constitution of the Republic of Ecuador 2008; Parliament of New Zealand 2017).

Fragmented landscapes may limit bees' ability to find adequate pollen and nectar sources, leading to decreased population resilience and reduced pollination services in forest ecosystems. Without intervention, this isolation could further threaten the long-term survival of stingless bees in deforested regions.

To counteract these effects, strategies that restore habitat connectivity are urgently needed, particularly through biological corridors (Zumaeta et al. 2023). These corridors serve as landscape elements that connect fragmented habitats, enabling species movement and genetic exchange. They have been widely promoted as a conservation strategy to mitigate habitat isolation (Beier and Noss 1998; Hilty et al. 2012; Rudnick et al. 2012).

In Colombia, Gutiérrez-Chacón et al. (2020) found that stingless bee colonies successfully established along biological corridors, both in natural and restored sections. Their study highlights the effectiveness of corridors in mitigating population isolation and enhancing landscape connectivity for fragmented bee populations.

As central place foragers with limited flight ranges, stingless bees are particularly vulnerable to habitat fragmentation (Araújo et al. 2004; Michener 2007). Disconnected resources may decrease genetic flux (Araújo et al. 2004) and limit colony establishment, making corridor networks an essential conservation tool. Ensuring habitat continuity is imperative to maintaining pollination functions for both wild and crop plants (Greenleaf et al. 2007).

In Peru and across the Amazon basin, integrating bee-friendly corridors into conservation planning is not just beneficial but essential. Future initiatives should prioritize their establishment alongside other habitat restoration efforts to secure the long-term viability of stingless bee populations and their ecological functions.

The establishment of such corridors should not only be an ecological priority but also a legal one. While biological corridors provide critical habitat connectivity, their long-term effectiveness depends on strong conservation policies that protect both the landscape and its keystone species.

Recognizing stingless bee habitats within a Rights of Nature framework would create legal accountability for habitat destruction, ensuring that conservation corridors are not merely policy recommendations but legally enforceable protections.

Conclusions

This study provides critical insights into the spatial distribution, tree nesting preferences, and deforestation vulnerability of two key stingless bee species, *M. eburnea* and *T. angustula*, in the Peruvian Amazon. While previous research has primarily focused on Loreto and San Martín, our findings contribute new data from the Biosphere Reserve Avireri-Vraem (Junín region), offering a deeper understanding of these species' nesting and distribution patterns in underrepresented areas. *Melipona eburnea* was predominantly found in lowland areas, whereas *T. angustula* was more frequent at higher elevations, suggesting potential ecological adaptations influenced by microclimate and resource availability, key factors that should inform conservation planning.

GPS-based fieldwork confirmed strong nesting associations with specific tree species, particularly *G. guidonia* and *F. insipida*. *Melipona eburnea* demonstrated a preference for *G. guidonia* and *P. cecropiifolia*, while *T. angustula* frequently nested in *C. brasiliense*, *C. cateniformis*, and *F. insipida*. Many of these trees, including *A. gigantiflora* and *C. cateniformis*, are among the most trafficked, intensifying deforestation risks. Alarmingly, over 50% of the bees' habitats overlap with high-risk deforestation zones, exacerbated by illegal logging, agricultural expansion, and habitat fragmentation. Given that stingless bees rely on large, contiguous forest patches for survival and have limited flight ranges, these threats jeopardize not only their populations but also the broader pollination networks they sustain.

Future research should expand to other Amazonian regions to assess how microclimate, vegetation structure, and floristic composition influence stingless bee populations. Species distribution modeling can help predict habitat suitability under current and future climate scenarios. Finer-scale analyses of nest density and habitat heterogeneity would also improve our understanding of how anthropogenic changes affect population dynamics. Additional ecological variables such as predator presence, nest-site competition, and parasite or pathogen load, may also influence nest site selection and colony success. Although pollution effects were not observed directly in this study, it would be important to consider how residues from pesticides and plastics may travel from remote areas posing an indirect threat to the species and ecosystems.

As bioindicators of ecosystem health, stingless bees are vital for monitoring forest conservation outcomes. Protecting their populations requires urgent action, including preserving nesting trees, establishing biological corridors, and promoting sustainable forestry and agroecological practices. Recognizing stingless bees and their habitats under a Rights of Nature framework would provide stronger legal protections. Implementing these policies demands collaboration between conservation agencies and Indigenous communities to ensure legal frameworks reflect local ecological knowledge.

Declines in stingless bee populations threaten pollination networks and ecosystem stability. This study provides a critical baseline for research and policy, emphasizing the need for conservation strategies that unite ecological protections with legal recognition to ensure the long-term survival of these keystone pollinators.

Supplementary Information

Supplementary information accompanies this paper at https://doi.org/10.5141/jee.25.021.

Table S1. Overview of stingless bee data from original fieldwork and literature sources included in this study. **Fig. S1.** Researchers documenting the size and species of a tree where a native stingless beehive was recorded. **Fig. S2.** SERNANP rangers inspecting rational hives kept by Indigenous communities. **Fig. S3.** Instruments used to record elevation, GPS location, and humidity data at the entrance of a native stingless bee hive.

Abbreviations

DBH: Diameter at breast height
EV: Explained variance
KL: Kaski-Lagus error
MFA: Multiple factor analysis
PAS: Administrative Sanctioning Processes
QE: Quantization error
TE: Topographic error

Acknowledgements

We thank the Apus (leaders and spirits) of the communities of Caperucia, Chimiato, Cheni and Pichiquia, as well as Eco Ashaninka, for facilitating access to collect data. We are also grateful to the local stingless beekeepers for their support in hive identification and to the park rangers of the Reserva Comunal Ashaninka for their leadership in introducing technology-driven methods for biodiversity monitoring. This research was supported by the National Geographic Society's STEM Field Assistant program. We thank National Geographic Society for facilitating access to ArcGIS Pro. We thank Ana Elisa Sotelo for the bee images.

Authors' contributions

RVE, CD, and RD conceived the ideas. RD and OMS conducted the field data collection. OMS, JF, and MI conducted the literature data collection. OMS, JRBV, AR, RD, CD, and RVE conducted the data analysis. RVE, RD, OMS, JF, and JRBV wrote the manuscript. RVE, DC, and CD reviewed the manuscript.

Funding

The study was financed with funds from Amazon Research Internacional and For Nature.

Availability of data and materials

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

Consent was obtained from each community, in collaboration with local indigenous Ashaninka leaders and park rangers. The Reserva Comunal Ashaninka and Eco Ashaninka groups and committees approved the study.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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