



Diversity, floral visitation pattern, and conservation of stingless bees (Apidae: Meliponini) in the Brazilian Legal Amazon

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ABSTRACT

The Amazon Rainforest is one of the most biodiverse regions worldwide and faces significant challenges in conserving its fauna and flora. Stingless bees (Meliponini) play a crucial role as pollinators in both natural and agricultural ecosystems. We aimed to estimate the distribution and diversity of meliponines in the Legal Amazon, assess the number of meliponines species recorded as floral visitors and the number of plants they visited, evaluate the representativeness of meliponines within protected areas, and investigate the influence of the remaining habitat on species richness. We used species distribution modeling to estimate species distribution and derive species richness map. We performed a literature review to compile information of floral visitors. Of the 132 species studied, 77 were floral visitors to 756 plant species, many of which are economically important. *Tetragonisca angustula*, *Trigona spinipes*, *Tetragona clavipes*, and *Scaptotrigona bipunctata* had the highest number of interactions with plants. *Euterpe oleracea*, *Syzygium malaccense*, and *Bertholletia excelsa* were the most frequently visited plants. Representativeness within protected areas for all meliponines and floral visitors were 37 % and 39 %, respectively. The areas with the highest species richness were along the major rivers of the Amazon basin, mostly outside the protected areas. Regions with the least remaining habitat were found in areas of lower species richness located in the “Arc of Deforestation”. Although the richest areas are outside protected areas, they are far from regions with high habitat loss. Therefore, it is crucial to expand protected areas, especially in the most vulnerable regions.

1. Introduction

The Amazon region is a large area that spans across nine South American countries region, with Brazil hosting the largest portion (60 %), followed by Peru (Myster, 2016; Vergara et al., 2022). This region is predominantly covered by rainforest, characterized by high canopy cover and exceptional species diversity (Antonelli et al., 2018; Gatti et al., 2022; Myster, 2016). Legal Amazon is a Brazilian administrative region that covers ~60 % of the country and encompasses the entire Amazon biome plus parts of the Cerrado and Pantanal (IBGE, 2014). The Legal Amazon is crucial for maintaining climate patterns, ecosystem services, hydrological cycles, and carbon storage (Lovejoy & Nobre, 2018; Poorter et al., 2015; Strand et al., 2018).

Meliponini tribe (Apidae), commonly known as stingless bees or

meliponines, is characterized by the absence of a functional stinger, although vestigial parts are present, and by their high eusociality (Michener, 2007). Being restricted to tropical and subtropical areas, meliponines perform critical ecosystem services. These bees contribute significantly to the pollination of a wide range of plants, pollinating ~73 % of cultivated and native edible plants (Grüter, 2020a; Michener, 2007; Nicholls & Altieri, 2013; Quezada-Euán, 2019; Santos et al., 2014). Local communities have long recognized the value of meliponines, using their products for diverse purposes, including food, crafts, and medicine (Gonzalez et al., 2018), contributing to the subsistence and economy of local populations (Carvalho et al., 2023; de Oliveria et al., 2013; da Souza et al., 2004).

The Amazon region is home to a diverse range of meliponines with high morphological, physiological, and behavioral adaptability, capable

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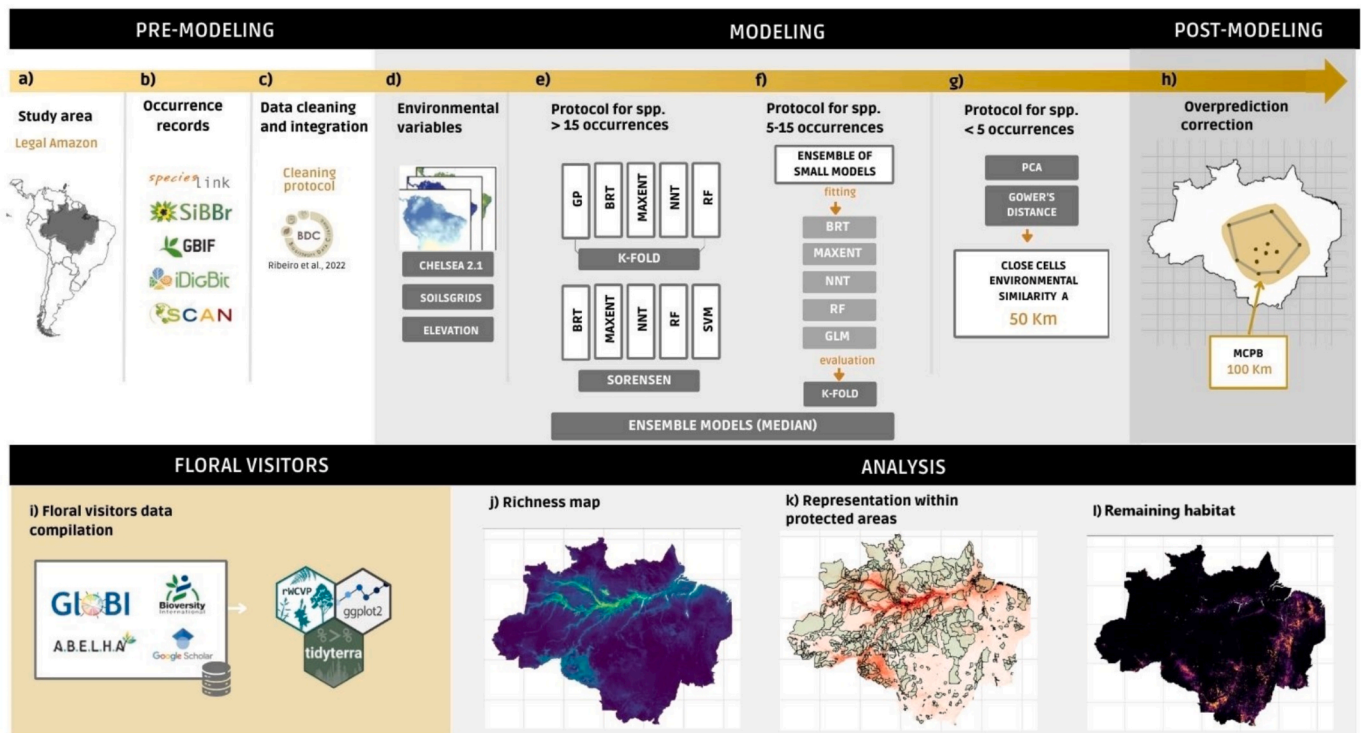


Fig. 1. General method workflow structured into **Pre-modeling**: (a) selection of the study area, (b) search and compilation of species occurrences in different databases, and (c) data filtering and cleaning; **Modeling**: (d) compilation and selection of environmental variables, (e) modeling protocol for species with > 15 occurrences, (f) between 5-15 occurrences, (g) estimation of environmental similarity for species with < 5 occurrences, and (h) correction of model overprediction. **Floral visitors database** (i): It was necessary to perform a literature review for each species to detect which plant species were visited by the different meliponines species. **Analyses**: (j) Create species richness maps, (k) calculate the representativeness within the PAs of species distribution and species richness classes, and (l) explore the relationship between remaining habitat and species range and richness.

of exploiting resources other than flowers (Dos Santos et al., 2015; Maia-Silva et al., 2013). These insects exhibit diversified foraging behaviors, seeking micronutrients from non-floral resources (Dorian & Bonoan, 2021). Meliponines in the Amazon region are crucial for the pollination of economically important plant species, such as *Euterpe oleracea* (açai), *Myrciaria dubia* (camu-camu), *Averrhoa carambola* (carambola), *Cocos nucifera* (coconut), *Theobroma grandiflorum* (cupuaçu), *Spondias mombin* (taperebá), and *Bixa orellana* (Urucum) (Nogueira et al., 2023; Paz et al., 2021; Venturieri & Leon, 2012). While the Mayans and other indigenous peoples have managed meliponines for millennia (Ayala et al., 2013; Quezada-Euán, 2019), and techniques to promote meliponiculture have been developed, wild meliponines remain essential for most crop pollination activities (Cortopassi-Laurino et al., 2006). Recent studies have highlighted the diversity of meliponines management practices among Amazonian communities, emphasizing their cultural and economic significance (Campbell et al., 2023; Delgado et al., 2023). Beyond their role as pollinators, meliponines have a high rate, frequency, and constancy of floral visitation, i.e., they interact with flowers for various purposes, mainly feeding (nectar and pollen), which could result in pollination (Rios-Carrasco et al., 2022). In this sense, studying plant-bee interactions is crucial for conservation biology, offering insights into bees ecological requirements, ecosystem services provision and resilience, plants reproductive success, and potential coevolutionary relationships (Assunção et al., 2022; Mathiasson & Rehan, 2020; Vaudo et al., 2024).

Changes in land use affect bee biodiversity and ecosystem services, particularly in natural habitats that have been converted into areas for livestock, mining, logging, and agricultural activities (Duarte et al., 2020; Foley et al., 2005; Rossoni and de Moraes, 2020). Forest loss affects meliponines differently, e.g., reducing food availability and nesting sites, threatening long-term species survival due to slow biological

swarming, promoting genetic losses and inbreeding (Giannini et al., 2020; Grüter, 2020b). In 2022, the deforestation rate in the Legal Amazon reached 12.2 km²/year, violating environmental agreements and laws related to combating climate change, illegal land appropriation, and mining on Indigenous lands (Mataveli et al., 2022; Villén-Pérez et al., 2018, Villén-Pérez et al., 2020). Conversion to pasture is the main cause of deforestation in the Brazilian Amazon (MapBiomas, 2025), and deforestation rates are expected to continue to increase, especially in parts of the states of Acre, Amazonas, Pará, Rondônia, and Mato Grosso, known as the Arc of Deforestation (Carvalho & Domingues, 2016; Tollefson, 2018). Preliminary studies in the Carajás National Forest, located in the Legal Amazon, have estimated a decline of 95 % in meliponines species in the coming years (Giannini et al., 2020).

Area-based conservation approaches, including protected areas and other effective area-based conservation measures, serve as pivotal tools in global efforts to conserve biodiversity worldwide (Bhola et al., 2021; Gray et al., 2016). An essential role of protected areas is to capture the largest variety of biodiversity, which can be measured by calculating the degree of representativeness of biodiversity (e.g., species range or other attributes of biodiversity) within protected areas (Margules & Pressey, 2000; Rodrigues et al., 2004; Velazco et al., 2021). In the Legal Amazon, protected areas include conservation units, indigenous lands, and quilombola areas (Chape et al., 2005a). In this region, a diversified protected area system was created to maintain inclusiveness, sustainable development, and conserve biodiversity and ecosystem services (Chape et al., 2005b; Nogueira et al., 2018). Protected areas have been increasing over the years in the Legal Amazon, with an important reduction in deforestation (den Braber et al., 2024; Qin et al., 2023). However, protected areas do not always coincide with regions with the highest species richness, and species range can be underrepresented within protected areas (e.g., Fagundes et al., 2016; Sousa et al., 2024).

Considering the ecological, economic, and social roles of meliponines, understanding their diversity in specific regions like the Amazon is crucial for conservation efforts. Although some studies exist in the region (Barros et al., 2022; Brosi, 2009; Brown and Albrecht, 2001; Campbell et al., 2022; Ferreira et al., 2022), they have often focused on small-scale assessments or on specific species. To address this knowledge gap we aimed to (1) estimate the distribution and diversity of meliponines in the Legal Amazon region, (2) assess the number of meliponines species that have been recorded as floral visitors and the number of plants they visit, (3) assess the degree of representativeness of species range and richness within protected areas, and (4) estimate the influence of the remaining habitat on species distribution and species richness.

2. Methods

2.1. General method workflow

Our methodology included compiling a species list for the Legal Amazon region, collecting species occurrence data, and modeling species distributions. Based on a literature review, we compiled information about plant species visited by meliponines. For all meliponines and floral visitors, we explored patterns of species richness, the representativeness degree of species distribution and species richness (i.e., the proportion of species range or richness classes within protected areas), and the relationship between species distribution or richness with the meliponines remaining habitat (Fig. 1).

2.2. Study area

This study was conducted in the Legal Amazon in Brazil, a region geopolitically defined and established by Law 5,173 of 1966. Approximately 28 % of this territory is covered by different protected area designations (PAs; Supplementary Material, Fig. S1), including protected areas, sustainable use areas, and indigenous lands (BRASIL, 1966; Delahaye et al., 2015).

The Legal Amazon is covered by forests, including dense, open, and seasonal areas, which occupy ~63 % of the territory. Non-forest formations, such as savannas, pastures, and grasslands, account for ~22 % of the area, whereas the remaining 15 % are deforested areas (Souza and Shimbo, 2020). The climate is equatorial, hot, and humid, with seasonal variations in rainfall (Madigosky & Vátnick, 2000). The dry season occurs between June–November and the rainy season occurs between December–May, with ~75 % of annual rainfall (Almeida et al., 2017; de Ribeiro and Adis, 1984).

2.3. List of species

Initially, we listed 167 species of meliponines from the Legal Amazon compiled from the database of the Taxonomic Catalog of Brazilian Fauna (<http://fauna.jbrj.gov.br/>; Oliveira et al., 2024). Scientific names were updated according to the nomenclature in the Moure Catalog in 2023 (Camargo & Pedro, 2003; Nogueira, 2023). Some meliponines genera have high taxonomic uncertainty and many species have recently been divided into new species. Therefore, we revised our species list and excluded 39 species with taxonomic uncertainty from our analyses (i.e., we used 132 species; Table S1).

2.4. Compiling data on floral visitors

The definition and classification of floral visitors as pollinators is complex, as it involves assessing the pollination effectiveness of these visitors and requires the analysis of factors such as visitation frequency, contact with reproductive structures, and specialized morphophysiological structures (Leal et al., 2020). Specialized and generalist differ in the quality of services they provide to the ecosystem (Araujo et al., 2018). Therefore, we chose to use the nomenclature of floral visitors for

the species in this analysis, considering the greater data availability.

We created a floral visitor database for listed meliponines. Initially, we used the Globi database (<https://www.globalbioticinteractions.org/>), ABELHA Interaction Database (http://abelhaseplantas.cria.org.br/busca_abelha), and the species list of Gazzoni (2021). We also performed individual species searches in scientific articles using the Web of Science (<https://www.webofscience.com/wos/woscc/basic-search>), Scopus (<https://www.scopus.com/>), and Google Scholar (<https://scholar.google.com/>) platforms, using the keywords Meliponini, floral visitors, pollinators, stingless bees, bee-plant interaction, and Amazon. Additionally, other references, such as books, were included to complement the bibliographic resources. After compiling all bibliography, we used R and Python codes to automatically search for species names within each file. Finally, floral visitors' data were obtained from 75 bibliographic and database sources (Appendix S1). Plant scientific names were corrected and updated using Plants of the World Online (<https://powo.science.kew.org>) as a taxonomic authority using the R package *rWCVP* (Brown et al., 2023). All analyses relating to species richness patterns, representativeness within protected areas, and remaining habitat were performed for all the meliponines species and those recorded as floral visitors separately (see below).

2.5. Species occurrences

We searched and compiled occurrence records for the meliponines species list from the following databases: speciesLink (<https://specieslink.net/>), Global Biodiversity Information System (GBIF; <https://www.gbif.org/>, doi: 10.15468/dl.udkhjp), Integrated Digitized Biocollections (iDigBio, <https://www.idigbio.org/>), Symbiota Collections of the Arthropod Network (SCAN-Bugs, <https://scan-bugs.org/portal/>), and the Brazilian Biodiversity Information System (SibBr, <https://www.sibbr.gov.br/>). Occurrence data from different sources were integrated into a single database, selecting only occurrences recorded between 1950–2023. We used the *bdc* package for the occurrence cleaning protocol (Ribeiro et al., 2022), which consists of pre-filtering, taxonomic correction, spatial correction, and temporal correction.

In the pre-filtering step, occurrences with invalid taxonomic terms (occurrences identified at the genus level) and spatial terms (invalid coordinates or records without coordinates) were removed (Table S2). The taxonomic correction consisted of homogenizing and updating the scientific names, using as taxonomic authority Camargo et al. (2023) from the “Moure Catalog”. Spatial correction consisted of removing occurrences with duplicate geographical coordinates, with < 3 decimal places, georeferenced in the sea, centroids of countries or states/provinces, and cities. Additionally, in QGIS v3.36.1 (<https://www.qgis.org>), we checked and eliminated occurrences outside species distribution limits (Tables S2 and S3). To do so, we used the Moure Catalog as a source of species distribution. The temporal correction consisted of correcting and eliminating occurrences with invalid dates and retaining occurrences collected after 1950. Generally, species occurrences tend to be biased toward the most accessible areas and near human infrastructure (Boakes et al., 2010; R. L. Carvalho et al., 2023). Such bias can be transferred to the environmental space where models are created, which consequently affects model prediction (Beck et al., 2014; Moudry et al., 2024). To address this problem, we filtered occurrences in the environmental space by defining a multidimensional environmental grid and then randomly selected a single occurrence within each grid (Varela et al., 2014). Because this approach is sensitive to the number of bins, we tested four, six, eight, and 10 bins for each species. The best bin was the one that reduced the spatial autocorrelation but at the same time retain the maximum number records (Velazco et al., 2021). Only species with ≥ 5 clean occurrences were modeled (van Proosdij et al., 2016). Data processing and analyses were performed in R v.4.4.0 (R Core Team, 2024) using different packages (Table S4).

2.6. Environmental variables

Changes in temperature and rainfall patterns can affect the availability and quality of bee food resources, such as nectar and pollen, altering the synchronization between bee activity and plant flowering, affecting the ability of bees to collect food, and consequently, their nutrition and health (Cortopassi-Laurino & Nogueira-Neto, 2007). For this reason, we considered a set of 10 climate variables from Chelsa v.2.1 platform, with 1 km resolution (<https://chelsa-climate.org>, Karger et al., 2017). In addition, we used the SRTM altitude (<https://srtm.csi.cgiar.org>) with 1 km resolution and SoilGrid 2.1 (<https://soilgrids.org>) as a source of edaphic variables with 250 m resolution (Table S5). We chose to add edaphic variables because soil type and conditions can affect the availability and quality of cavities used by meliponines for nesting (Barbosa et al., 2013; Camargo & Pedro, 2003). All variables were upscaled to a 5 km spatial resolution, covering the Neotropical region. To reduce multicollinearity between the environmental variables, we calculated a correlation matrix based on the Pearson correlation. We selected a set of uncorrelated variables (i.e., correlation < |0.7|) with the highest biological significance (Table S5, Fig. S2).

2.7. Species distribution models

We used species distribution models (SDMs) to estimate species distribution and derive species richness patterns throughout the Legal Amazon. SDMs are tools with great potential for biodiversity conservation, especially in regions with limited data (Franklin, 2023; Guisan et al., 2013), such as the Amazon.

Training areas used to construct species distribution models (SDM) were delimited by selecting polygons of terrestrial ecoregions containing species occurrences (Dinerstein et al., 2017, <https://ecoregions.appspot.com>). Because no algorithm can deal with all modeling conditions (Norberg et al., 2019; Qiao et al., 2015), we used the following algorithms: Artificial Neural Network (NET), Boosted Regression Trees (BRT), Gaussian Process (GAU), Generalized Additive Model (GAM), Generalized Linear Model (GLM), Maximum Entropy (MAX), Random Forest (RAF), and Support Vector Machine (SVM). For the algorithms that have hyperparameters, such as SVM, NET, MAX, BRT, and RAF, we used a hyperparameter optimization technique that selects the combination of hyperparameter values that provide the best performance, as measured by the Sorensen metric (Table S6). We used the same hyperparameter values used by Rose et al. (2023).

Since absence data for the modeled species were not available in the study area, we generated pseudo-absences for model building. For the GAU, BRT, MAX, NET, RAF, and SVM algorithms, we determined the number of pseudo-absences by sampling twice the number of presence points for each species. For the GLM and GAM algorithms, we sampled 10,000 pseudo-absences avoiding cells with presences (Liu et al., 2018). Pseudo-absences were randomly sampled 50 km from species occurrences. For the MAX algorithm, 10,000 background points were randomly sampled throughout the training area.

For species with 5-15 occurrences, we used the Ensemble of Small Models approach (ESM; Breiner et al., 2015). This approach consists of fitting bivariate models with all combinations of variables, and building a consensus model weighted by Somer's D metric (Breiner et al., 2018, 2015). The ESMs were fitted using BRT, MAX, NET, RAF, GAM, and GLM algorithms (Table S7).

Standard models were validated using the k-fold cross-validation technique with five partitions, and repeated k-fold cross-validation with five partitions and repetitions was used to validate the ESM. We used Boyce (threshold-independent metric), Fpb (Proxy of F measure based on presence-pseudo-absences data), and Sorensen as model performance metrics because they are less affected by species prevalence than other more popular metrics such as TSS (True Skill Statistic) and AUC (Area Under the Curve) (Leroy et al., 2018). The final model for each species consisted of an ensemble model calculated by averaging

model suitability of the best models, i.e. only models with Sorensen ≥ 0.7 were used. We used a threshold that maximizes the Sorensen metric to binarise the models.

Species with < 5 occurrences were not modeled, and their distributions were estimated based on environmental similarity measured with Gower distances (Andrella et al., 2023; Carpenter et al., 1993). To do this, we calculated the environmental similarity between cells with occurrences and those up to 50 km around the occurrences. We performed a Principal Components Analysis (PCA) to reduce the number of environmental variables by selecting the first three principal components.

When distribution models are predicted for broad areas, they tend to predict distributions far from the species' real distributions (Mendes et al., 2020). This overprediction can result in errors in estimating diversity patterns, managing species conservation, and calculating metrics related to distributions (e.g., representativeness within PAs or loss of distribution due to land use, Velazco et al., 2022). Therefore, we constrained models to predict habitat suitability closer to each species' real distribution. To do this, we used the MCPB approach (Buffered Minimum Convex Polygon), which restricts the environmental suitability values within the region delimited by a minimum convex polygon based on occurrences in addition to a buffer of 100 km around this polygon (Mendes et al., 2020). SDM modeling protocol were created using *flexsdm* R package (Velazco et al., 2022).

2.8. Evaluation of the degree of representativeness of species within protected areas

We used the Conservation Units and Indigenous areas of the Legal Amazon available from TerraBrasilis to delineate PA polygons (Assis et al., 2019). The PAs were rasterized to the same resolution as the SDMs (i.e., 5 km) by calculating the proportion in which each pixel area covered by PAs. Based on this raster, we calculated the representativeness degree of each species within the PAs as the ratio between the area of the species' range within the PAs and the total range area of each species.

2.9. Proportion of remaining habitat

To calculate the proportion of remaining habitat, we used land use data from MapBiomas (<https://mapbiomas.org/>) for the year 2022 at 30 m resolution. We reclassified the different land cover classes into habitat and non-habitat (Table S8). We calculated the proportion of remaining habitat across the study area for the 5 km resolution cells (i.e., the same resolution as the SDMs) to produce a map of remaining habitat. To do this, we used the formula $Rh = H/(H+N)$ where Rh is the proportion of habitat remaining within a 5 km resolution cell, H is the number of cells (of 30 m) classified as habitat, and N is the number of cells (of 30 m) classified as non-habitat. Thus, values closer to one represent cells with a higher proportion of remaining habitat (Velazco et al., 2023).

The remaining habitat map was used to calculate the remaining species range by calculating the ratio between the remaining distribution area of a species (i.e., excluding proportions of remaining habitat from its distribution) and the total distribution, assuming unaltered landscapes.

2.10. Species richness map

Species richness map consisted of the sum of the semi-binary models to reduce the overprediction of richness when compared to the use of binary models (Guillera-Aroita et al., 2015). Semi-binary models are derived by keeping suitability values continuous above threshold, while setting zero values lower than threshold (Domisch et al., 2019). Richness maps were generated for all meliponines and those recorded as floral visitors separately. To analyze spatial patterns of richness in relation to PA coverage, we categorized the map cells into nine richness class intervals and counted the proportion of cells that were or were not in the

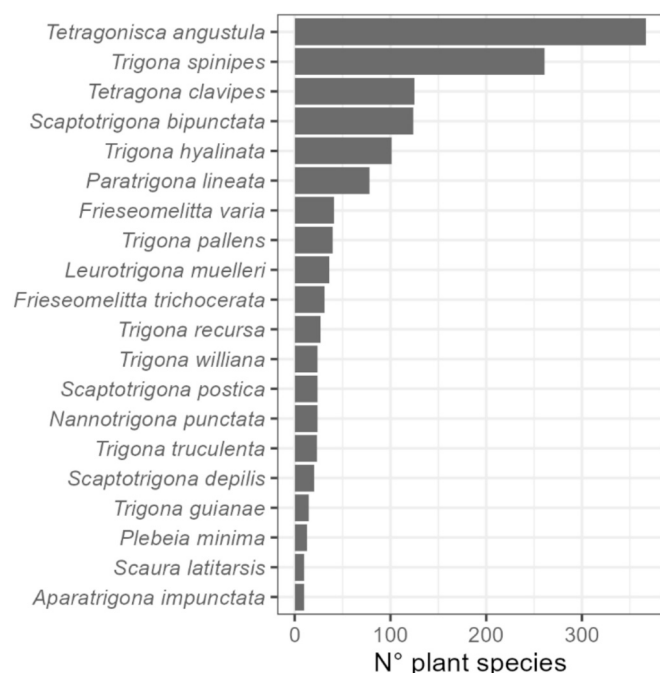


Fig. 2. Number of plant species visited by meliponines native to the Legal Amazon. Data is presented for meliponines species that visit ≥ 10 plant species.

PAs. In the same way, we explored the relationship between species richness and remaining habitat, where the remaining habitat was categorized into five class intervals, thus calculating the proportion of cells within different richness class intervals and remaining habitat class intervals. These relationships between species richness, PA coverage, and remaining habitat were expressed in relative and absolute terms.

3. Results

We identified 169 meliponines species native to the Legal Amazon. However, because of taxonomical uncertainty, 132 species were analyzed, from which we could estimate the distributions of 100 species (i.e., species with high model performance, Table S1). All the algorithms showed high performance according to Boyce index. For the Sorensen metric, most achieved a satisfactory performance, except for the GLM and GAM models. Similarly, FPB indicated that most of the algorithms performed well. The consensus model (mean) performed well for all metrics (Fig. S3).

We found 1,776 unique records of plant-meliponines interactions, which comprised 77 meliponine species. *Tetragonisca angustula* ($n=367$), *Trigona spinipes* (261), *Tetragona clavipes* (125), and *Scaptotrigona bipunctata* (124) where species with the highest number of plant species visited (Fig. 2, see full data in Table S9).

We found 756 plant species that are visited by meliponines (Table S10). Many species with the highest number of visits by meliponines are of economic importance, both native and cultivated. The species with the highest number of visits were *Euterpe oleracea* ($n=35$), *Paullinia cupana* (15), and *Bixa orellana* (13). Other economically important plants visited by > 5 meliponines species were *Anacardium occidentale*, *Cocos nucifera*, *Coffea arabica*, *Myrciaria dubia*, *Hianthus annuus*, *Psidium guajava*, *Passiflora edulis* and (Fig. 3, Table S10).

The areas with the highest richness are mainly concentrated along the rivers, from the Amazon River to the Negro River, and other areas along the Amazon basin (Fig. 4a). As species richness increases, the proportion of unprotected cells also increases, indicating that many of the areas with the greatest biodiversity are not within PAs (Fig. 4a-b). Thus, regions with >30 species had $\sim 26\%$ of their cells protected (Fig. 4a-b; Fig. S4a). In absolute terms, regions with the highest species richness are the least representative of the study area (Fig. S5a). The richness map of floral visitors showed a geographical pattern similar to

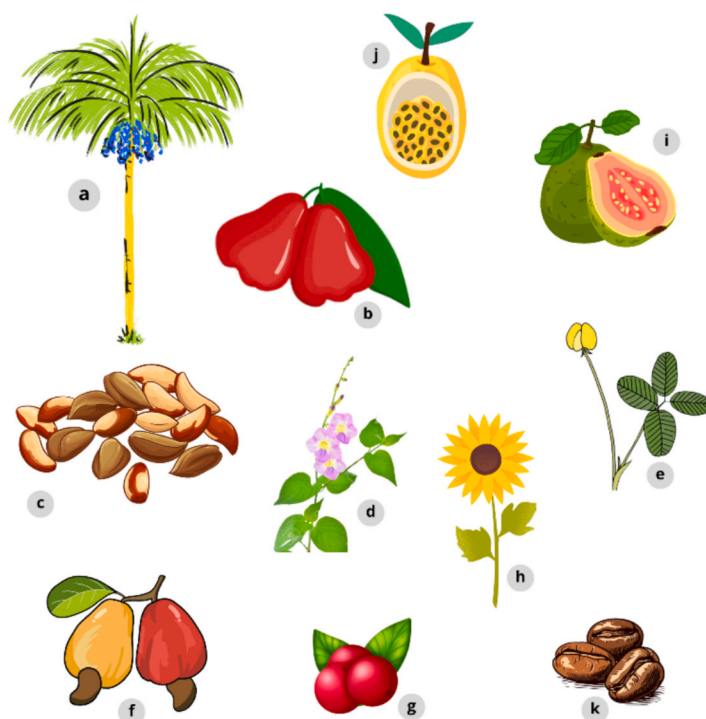
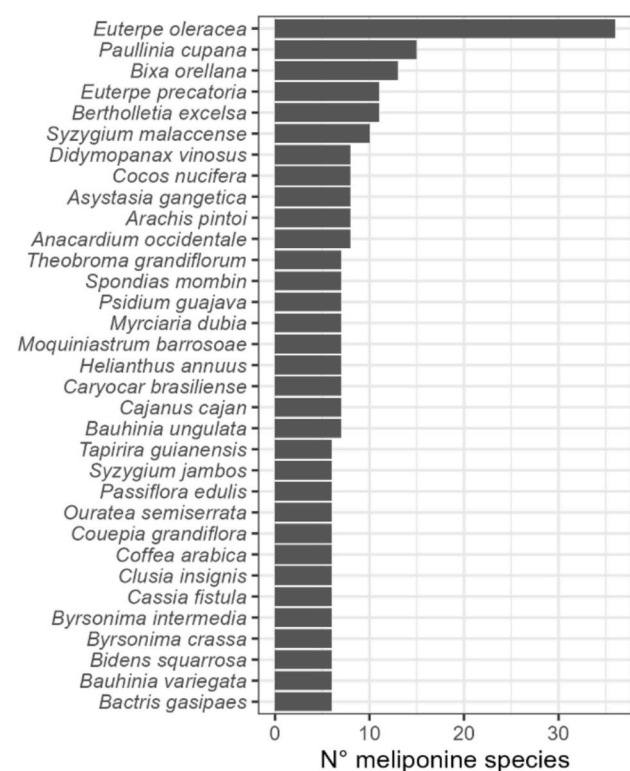


Fig. 3. Number of meliponines in the Legal Amazon visiting plant species. Data is presented for plant species visited by ≥ 5 meliponines species. *Euterpe oleracea* (a*), *Syzygium malaccense* (b*), *Bertholletia excelsa* (c*), *Asystasia gangetica* (d), *Arachis pintoi* (e*), *Anacardium occidentale* (f*), *Myrciaria dubia* (g), *Helianthus annuus* (h), *Psidium guajava* (i), *Passiflora edulis* (j) *Coffea arabica* (k). *species native to the Legal Amazon.

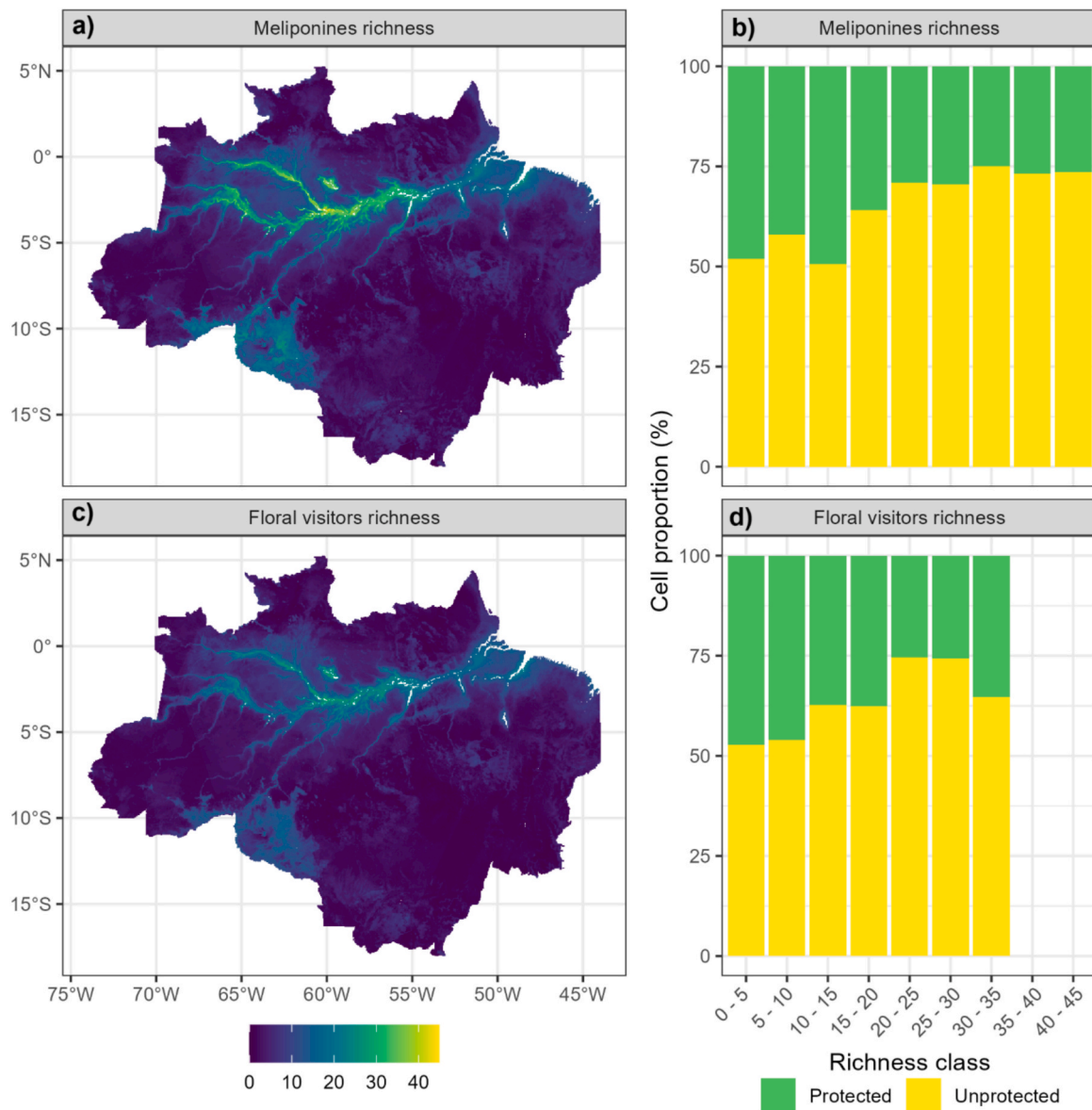


Fig. 4. Species richness for all meliponines (a) and floral visitors (c), proportion of protected and unprotected cells for different richness classes for all meliponines (b), and floral visitors (d) in the Legal Amazon.

all meliponines, with a high richness concentration along the rivers (Fig. 4c). Regarding the relationship between species richness and PA coverage, the floral visitors showed a similar pattern to the total species richness, with the regions with the highest richness (i.e., species richness classes 20-25 and 25-30) represented in relative terms between 25-35 % within the PAs (Fig. 4d; Fig. S4a, Fig. S5b).

Analysis of the representativeness of species within PAs reveals that, on average, species representativeness is $\sim 37\%$ (± 18.77), and 19 species have $>50\%$ of their ranges within PAs. For floral visitors, the representativeness values are similar, with $\sim 39\%$ (± 15.70), and 12 species have $>50\%$ of their ranges within PAs (Fig. S6).

Regarding remaining habitat after accounting for land use patterns, we found that the regions with the least remaining habitat are in the eastern south of the study area, a region known as the Arc of Deforestation (Fig. 5a). When we explored the relationship between species richness classes and the remaining habitat, we found that the most altered regions (i.e., the least remaining habitat) are generally in the regions with the lowest diversity, both for all meliponines (Fig. 4b-d) and floral visitors (Fig. 5c-e). Relationship between remaining habitat and species ranges shows that, in general, species present low species

range loss and have remaining ranges of 94% (± 4.97) and 95% (± 3.99) for all meliponines, and floral visitors respectively (Fig. S7).

4. Discussion

Of the 132 species studied, 52 were floral visitors to 756 plant species. The representativeness within PAs for all species and floral visitors was 37 and 39 %, respectively. The areas with the highest species richness were along the rivers of the Amazon basin, mostly outside the PAs. Regarding the remaining habitat, we found that the regions with the least remaining habitat coincided with the regions with the lowest species richness, and the range of species apparently suffered few losses because of land-use.

Meliponines are generalists, collecting pollen and nectar from various plant species (Aleixo et al., 2013; Gruchowski-Woitowicz et al., 2024). In this study, *Tetragonisca angustula*, *Trigona spinipes*, *Tetragona clavipes*, and *Scaptotrigona bipunctata* were examples of species that visit a wide diversity of plants, which is consistent with previous research (Gazzoni, 2021; Giannini et al., 2020; Krug et al., 2010; Posey and de Camargo, 1985). Notably, many of the plant species most frequently

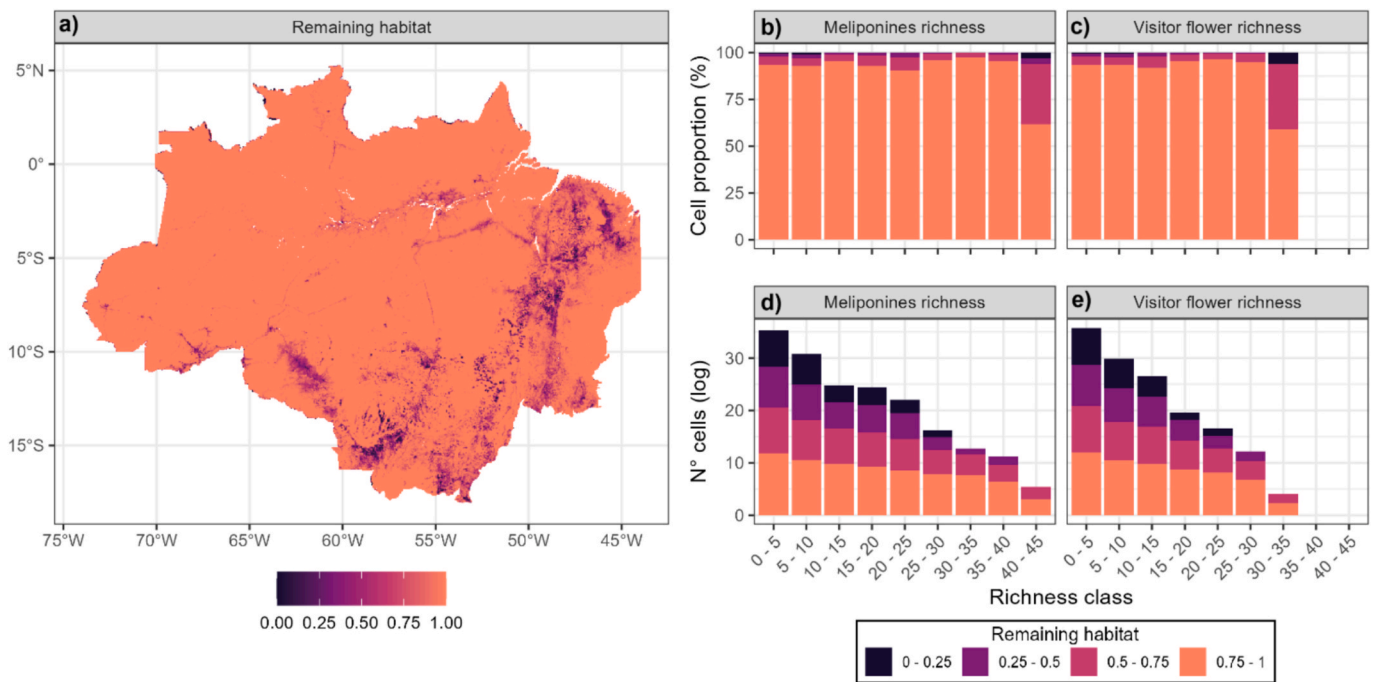


Fig. 5. (a) Map of the remaining habitat (b) and relative (b-c) and absolute (d-e) proportions of different remaining habitat classes by different richness classes for total richness and floral visitor richness.

visited by meliponines, such as *Euterpe oleracea* (açai), *Syzygium malaccense* (jambo), and *Bertholletia excelsa* (brazil nut), are of great economic importance. Nonetheless, the latter is pollinated by large bees such as representatives of Euglossini and Centridini and not by meliponines (Cavalcante et al., 2012). These plants sustain local biodiversity and are fundamental to the economy and livelihood of riverside communities (i.e., humans settled near water bodies, such as rivers, streams, and lakes, and whose socioeconomic and cultural activities are influenced by these aquatic ecosystems). In addition to native plants, non-native species of commercial importance, such as *Coffea arabica* (coffee) and *Helianthus annuus* (sunflower), are also frequently visited by meliponines, demonstrating the importance of these bees in agriculture and other economic activities. The quality of honey produced by meliponines is directly related to their interaction with native plants, suggesting that proper management of the plants they visit can improve honey production and quality. The conservation of areas close to rivers protects biodiversity and sustains the livelihoods of local communities that depend on bees for meliponiculture (Campbell et al., 2022; Delgado et al., 2023). Sustainable practices and natural area preservation are crucial for conserving meliponines, the plants they pollinate, and the economic and social well-being of riverside communities.

The highest richness of meliponines species was found close to large rivers, such as the Amazon and Negro rivers. One potential explanation for the observed patterns could be related to floodplain forests, i.e., flooded forests located close to rivers. These forests are characterized by their high productivity and plant diversity, which are influenced by seasonal flooding (ter Steege et al., 2023; Wittmann et al., 2006). Plant diversity in floodplain forests can offer favorable environments for bee diversity, providing a variety of resources such as nectar, pollen, sap, and fungal spores that are essential for the meliponines survival (Misiewicz et al., 2014; Steege et al., 2000; Terborgh & Andresen, 1998). In addition, this type of vegetation is resilient to environmental stress factors such as megadroughts (Capon & Reid, 2016). Floodplain plants not only depend on bees for pollination, but also offer varied niches that support different insect species, exemplified by the mutualistic relationship evident with açai palm tree (Aguilar et al., 2013; Fründ et al., 2013). Nonetheless, it is important to highlight that expeditions for

specimen collection in the Amazon are logistically difficult because of the inaccessibility of many areas and large unexplored regions still remain (R. L. Carvalho et al., 2023). Therefore, it is expected that most of the records were collected along the main Amazon rivers (de Camargo, 1994; Camargo & Pedro, 2003, 2004). Although we corrected record sampling bias, it may have affected the observed pattern. The distribution and richness of meliponines in the Amazon are likely the result of a more complex combination of these and other factors, which deserves further study.

Protected areas have increased markedly in the Brazilian Amazon since 1990, and have been efficient in reducing deforestation and likely benefiting species within them (Qin et al., 2023). We found that the highest species richness of meliponines was found outside the PAs, and that species representation within the PAs was low. These results are consistent with previous studies in the Legal Amazon, which also found that many species of turtles, fish, and dragonflies are underrepresented within PAs (Brasil et al., 2021; Fagundes et al., 2016; Frederico et al., 2018; Sousa et al., 2024). Despite this finding, remaining habitat for meliponines was high in unprotected areas along the main Amazon rivers (Fig. 4a, 6, and S4). This, combined with the generally lower exploitation of meliponines compared to other regional organisms (e.g., chelonians or fishes), results in a relatively positive scenario. Therefore, higher conservation efforts must be concentrated in the most vulnerable regions, such as the Arc of Deforestation. Next research could seek to identify priority areas for conserving meliponines, and other organisms underrepresented in the Amazonian PAs.

The remaining habitats with the greatest environmental pressure were in the Arc of Deforestation, covering states such as Pará, Mato Grosso, Rondônia, and Maranhão. This region is marked by the intense conversion of forests into agricultural areas and pastures, resulting in significant habitat fragmentation and degradation (Brown & de Oliveira, 2014; Mayes et al., 2019). Rapid loss of forest cover puts extreme pressure on biodiversity, including meliponines species (Farfan et al., 2023). It is also worth noting that the most altered regions were in the areas with the lowest species richness. This pattern is contrary to that observed in other groups and ecoregions in Brazil, such as the Cerrado flora, where the most altered regions have the highest species richness

(Velazco et al., 2019, 2023). We believe that the creation of new PAs in regions with rapidly advancing loss of natural cover, even though these regions are of lower diversity, may be due to the presence of species that are rarer or complementary to the current network of PAs (Leathwick et al., 2010). The fact that the regions with the highest species richness are outside PAs also reveals the importance and opportunity of creating PAs along major rivers. Therefore, conservation of meliponines and their associated biodiversity requires an approach that considers both areas of high richness and vulnerable regions under greater environmental pressure. Further studies could carry out spatial prioritization analyses to identify the most interesting areas for conservation.

To our knowledge, studies like ours are uncommon for Amazon bees, highlighting the unique contribution of our research. However, some limitations constrained our analysis. Lack of records and taxonomic uncertainty, particularly for *Melipona* and *Cephalotrigona* genera, has prevented their inclusion despite their ecological significance as pollinators. The lack of records and taxonomic uncertainty highlights the need for further research to cover more Amazonian meliponines species. Additionally, the absence of detailed pollinator-plant interaction data limits a more comprehensive understanding of the role of meliponines in the pollination of Amazon plants.

5. Conclusion

Meliponines species in the Legal Amazon visit 756 plants species, many of which are economically important, highlighting the economic and ecological importance of this group. The areas with the highest species richness were mainly concentrated along the great rivers of the Amazon basin. However, the representativeness of the species in the PAs was low, and many areas with high richness were outside these PAs. However, the richest unprotected areas are well-conserved and far from regions with high habitat loss, such as the Arc of Deforestation. Therefore, it is important to expand and re-evaluate protected areas, also considering the regions most vulnerable to habitat alteration, to ensure the efficient conservation of meliponines and the continuity of the ecosystem services they provide.

CRediT authorship contribution statement

Iracy Maiany Nunes Soares: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Admir Cesar De Oliveira Junior:** Writing – review & editing, Software, Methodology, Formal analysis, Data curation. **Anderson Igomar Antonio:** Writing – review & editing, Data curation. **David Silva Nogueira:** Writing – review & editing, Data curation. **Santiago José Elías Velazco:** Writing – review & editing, Writing – original draft, Software, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jnc.2025.127120>.

Data availability

Data will be made available on request.

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