Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Ecologia

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Mecanismos que determinam a estruturação das redes de interação abelha-planta no Cerrado

Krissya Norrana da Silva Santos

Orientador: Prof. Dr. Pedro Henrique Brum Togni

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade de Brasília, como requisito parcial para obtenção do título de Mestre em Ecologia Brasília, DF

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BANCA EXAMINADORA:

Prof. Dr. Pedro Henrique Brum Togni

Presidente - Universidade de Brasília

Prof. Dr. Pietro Kiyoshi Maruyama Mendonça

Membro externo – Universidade Federal de Minas Gerais

Dr. Nicholas Ferreira de Camargo

Membro interno – Universidade de Brasília

Profa. Dra. Ludmilla Moura de Souza Aguiar

Suplente - Universidade de Brasília

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Summary

Resumo Geral

As interações entre plantas e polinizadores formam redes complexas e dinâmicas cuja estrutura emerge da interação entre as características das espécies, a disponibilidade de recursos e a variação ambiental. Em ecossistemas altamente sazonais, como o Cerrado, espera-se que as mudanças temporais na fenologia das plantas modulem os mecanismos que regem essas interações. Nesta dissertação, investigamos como as características funcionais das abelhas e das plantas moldam a estrutura e a dinâmica das redes de interação entre plantas e abelhas em períodos climáticos contrastantes. No Capítulo 1, analisamos redes de interação em toda a comunidade para avaliar como as características funcionais influenciam a estrutura da rede ao longo do tempo. Mostramos que as redes de interação, tanto anual quanto dos períodos climáticos, são modulares e especializadas. Quando se considera a rede anual, o *trait-matching* surge como uma propriedade emergente na estruturação da rede. No entanto, quando as redes são analisadas separadamente por período climático, a estrutura de interação é governada principalmente pela substituição de espécies. Também encontramos associações específicas de características, com abelhas maiores sendo associadas positivamente a flores zigomorfas (simetria bilateral), características normalmente ligadas a interações mais especializadas, e negativamente associadas com flores actinomorfas (simetria radial), que são mais associadas a interações generalistas. No Capítulo 2, focamos em três espécies de abelhas-sem-ferrão para explorar com mais detalhes os padrões de interação entre abelhas comumente consideradas generalistas. Apesar da dieta ampla, as abelhas-sem-ferrão concentraram seus esforços de forrageamento em um subconjunto de espécies de plantas, sugerindo uma preferência por flores com perfil generalista e alta disponibilidade de recursos. Em conjunto, nossas descobertas enfatizam os papéis complementares da correspondência de características e da substituição de espécies na manutenção das redes de interação entre plantas e abelhas em ecossistemas sazonais e heterogêneos, como o Cerrado.

Palavras-chave: redes de interação, traços funcionais, correspondência de características, sazonalidade, substituição de espécies.

Abstract

Interactions between plants and pollinators form complex and dynamic networks whose structure emerges from the interaction between species traits, resource availability, and environmental variation. In highly seasonal ecosystems, such as the Cerrado, temporal changes in plant phenology are expected to modulate the mechanisms governing these interactions. In this dissertation, we investigate how the functional traits of bees and plants shape the structure and dynamics of plant-bee interaction networks during contrasting climatic periods. In Chapter 1, we analyze community-wide interaction networks to assess how functional traits influence network structure over time. We show that interaction networks, both annual and across climatic periods, are modular and specialized. When considering the annual network, trait-matching emerges as an important property in network structuring. However, when networks are analyzed separately by climatic period, the interaction structure is governed primarily by species replacement. We also found specific trait associations, with larger bees being positively associated with zygomorphic flowers (bilateral symmetry), traits typically linked to more specialized interactions, and negatively associated with actinomorphic flowers (radial symmetry), which are more associated with generalist interactions. In Chapter 2, we focus on three species of stingless bees to explore in greater detail the interaction patterns among these bees, which are commonly considered generalists. Despite their broad diet, stingless bees concentrated their foraging efforts on a subset of plant species, suggesting a preference for flowers with a generalist profile and high resource availability. Together, our findings highlight the complementary roles of trait matching and species substitution in maintaining plant-bee interaction networks in seasonal and heterogeneous ecosystems, such as the Cerrado.

Key-words: interaction networks, functional traits, trait matching, seasonality, species turnover.

General Introduction

Ecological communities are commonly represented as interaction networks, whose structure plays a central role in determining the stability and resilience of the community to disturbances (Tylianakis et al., 2010). Interaction networks exhibit properties based on the strength of interaction between species, as well as showing how interactions are dynamic over time and space (Bascompte & Jordano 2007; Olesen et al., 2008). The growing recognition of the importance of interactions between species has led to significant advances in understanding the structure of ecological communities, as well as becoming a fundamental tool for conservation, given that the loss of interactions often precedes species extinction (Harvey et al., 2017).

Mutualistic interactions are fundamental to understanding the organization and functioning of ecological communities (Bascompte & Jordano 2007). In particular, interactions between bees and plants form complex ecological networks that provide valuable information about community assembly processes, species coexistence, and ecosystem resilience and stability (Thompson, 2006; Bascompte & Jordano, 2007; Landi et al., 2018). Bees are recognized as the main pollinators worldwide, particularly in the Americas, where they play a central role in maintaining both natural and agricultural ecosystems (Martins et al., 2025). The high diversity of the group, estimated at around 20,000 described species globally (Michener, 2007), contributes to a wide range of interactions with flowering plants. Bees differ markedly in body size, social organization, foraging strategies, and specialization in the collection of floral resources such as pollen, nectar, resin, oils, and floral essences. These morphological, behavioral, and physiological differences directly influence how bees exploit their environment, interact with plants, and ultimately affect their fitness and foraging patterns (Ostwald et al., 2024).

Given this diversity, functional trait-based approaches are a powerful approach for understanding patterns of visitation and interaction between bees and plants (Stang et al. 2006; Violle et al., 2007). Incorporating functional diversity into network analyses allows for a more mechanistic understanding of the processes that structure communities (Dehling et al., 2016) and much of the research do not consider the functional diversity of the organisms involved. However, this perspective is fundamental, as the morphological, behavioral, and physiological characteristics of species directly influence the probability, frequency, and nature of ecological interactions.

Functional traits are important to understanding the mechanisms that govern the organization and dynamics of ecological interaction networks, as they determine when, where, and how species can meet and interact (McGill et al. 2006; Violle et al. 2007). Characteristics related to habitat use, phenology, abundance, and life history shape the probability of species co-occurrence in space and time, establishing neutral expectations for interactions (Vázquez et al. 2007; Poisot et al. 2012). Beyond these neutral processes, interactions are often constrained by trait matching, defined as the functional correspondence between the characteristics of interacting partners that facilitates or limits the establishment and strength of interactions (Dehling et al. 2014; Bartomeus et al. 2016). Classic examples include the correspondence between floral morphology and pollinator proboscis length (Stang et al. 2006) or between fruit size and disperser mouth size (Galetti et al. 2013). Thus, incorporating functional traits into network studies increases our understanding of the patterns of interaction established between species.

In addition to functional traits, phenology and species abundance also play central roles in determining ecological interactions (Peralta et al., 2020). Phenology is particularly important, since the occurrence of an interaction depends on temporal compatibility between partners, i.e., the overlap of their periods of activity (Olesen et al., 2011). Abundance, in turn, influences the probability of encounters between species, so that more abundant species tend to interact more frequently than rare species (Vázquez et al., 2007). As a consequence, interactions are dynamic in time and space, reflecting variations in community composition and partner availability. This dynamic is especially relevant in highly seasonal and heterogeneous environments, such as the Cerrado, where marked climatic changes throughout the year modulate species activity and the structure of interaction networks.

In the Cerrado, the world’s largest tropical savanna, strong seasonality and high environmental heterogeneity play a central role in shaping plant–pollinator interactions (Gottsberger & Silberbauer-Gottsberger, 2006; Rabeling et al., 2019; Aguiar et al., 2024). This biome harbors over 12,000 plant species, of which more than 7,500 are endemic (Reflora, 2025), and approximately 500 species of bees, which act as key pollinators across different vegetation types (Alves-dos-Santos, 2009; Cardoso et al., 2025). Plant–pollinator networks in the Cerrado often exhibit a modular structure, reflecting interactions among distinct groups of plants and pollinators under pronounced seasonal turnover (Aguiar et al., 2024; Rabeling et al., 2019).

From this perspective, the main objective of this dissertation is to understand how the functional traits of bees and plants influence the structure of plant–bee interaction networks in the Cerrado. In Chapter 1, we adopt a community-wide approach to evaluate how functional traits of both bees and plants shape network structure across contrasting climatic periods, identifying the ecological mechanisms underlying these interactions at discrete time intervals and at the metanetwork scale. Chapter 2 constitutes a specific analytical subset of Chapter 1, in which we use three native species of stingless bees, one of the most abundant and functionally influential groups in the system, as a model to explore interaction patterns in greater detail. Specifically, we investigate which floral traits are associated with the most visited plant species, aiming to assess the degree of generalism of eusocial bees and to identify potential patterns of floral preference.

Our hypothesis is that seasonality, by interfering with plant phenology, affects the underlying structure and mechanisms of the interaction network. During periods of greater flowering, bees are expected to have greater resource availability and, consequently, interact preferentially with plants that have greater functional trait correspondence, increasing resource exploitation efficiency. In contrast, during periods of lower flowering, the structure of the network tends to be more strongly governed by species abundance. In addition, we expect that the body size and degree of sociality of bees will be associated with different patterns of interaction, with small, social bees interacting with more generalist flowers, while larger bees exhibit more specialized patterns.

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Chapter 1

Temporal dynamics of a tropical plant–bee network: roles of trait matching and species turnover

Abstract

Interaction networks form complex and dynamically changing networks over time, reflecting community organization and stability. However, the mechanisms underlying the organization of these networks are still poorly understood. In highly seasonal biomes, such as the Cerrado, interaction networks are influenced by climatic conditions, which are reflected in the seasonal turnover of species composition, leading to changes in network structure and the functional roles of species. This is evident in the interactions between plants and bees, in which some species are present year-round, while others occur in a short period of time. This temporal variation affects network structure and results in functional shifts in species roles within the network. To assess how network structure varies across climatic periods and to identify the mechanisms associated with these temporal changes, we constructed a plant–bee interaction network over the course of one year at a grassland site in the Cerrado and integrated functional traits into the analyses. We analyzed the annual network as well as seasonal networks corresponding to the dry and rainy seasons and transitional periods. Functional traits related to morphology were measured, and bee behavioral traits were compiled from the literature. The resulting network showed a relatively stable structure throughout the year, with consistently high modularity and specialization. Networks across time periods showed high turnover of functionally similar species, while the composition of functional traits remained stable. These results suggest that different mechanisms may operate across temporal scales: at the annual scale, network structure may be influenced by trait matching (for example large bee size versus zygomorphic flowers) whereas at the seasonal scale, patterns of interactions? may be associated with species turnover. Overall, our findings highlight the importance of integrating network structure, temporal dynamics, and functional traits to better understand the mechanisms that structure ecological interaction networks.

keywords: plant–pollinator interactions, functional traits, temporal dynamics, Cerrado

Introduction

Pollination is a key ecosystem function for the stability of natural ecosystems (Ollerton, 2017). It is estimated that 94% of angiosperms species relies on animals to reproduce, with bees being the most relevant group (Klein et al., 2007; Ollerton et al., 2011; Tong, Ze-Yu et al., 2023). The interactions between bees and plants form complex networks that may reveal how local communities assemble, the dynamics of species coexistence and community resilience and stability (Thompson, 2006; Bascompte & Jordano, 2007; Landi et al., 2018). Pollination networks are commonly formed by a cohesive core of generalist species to which rarer species are connected (Bascompte & Scheffer, 2023). However, the nature of the prevalent interactions (Thebault & Fontaine, 2010), species richness and abundance (Olesen et al., 2007; Vázquez et al., 2007), plant phenology, and geographical range (Bascompte & Jordano, 2007) are expected to affect its structural patterns in time and space.

In the spatial dimension, in regions with a greater plant, such as in the tropics, or bees richnes, such as in xeric regions (Minckley and Radke, 2021), networks tend to be modular. This is because, niches are also more restricted, niche overlap decreases and networks become more specialized and less stochastic, with tropical networks typically exhibiting modular architectures (Olesen et al., 2007). In the temporal dimension, the network topology may vary when segregating interactions do not occur simultaneously (Blonder et al., 2012). Over time, changes in the weight of interactions and the identity of species promote reconfigurations in the network structure (Petanidou et al., 2008). However, few studies combined the spatial and temporal dimensions to understand the mechanisms affecting plant-bee networks and community structure in the tropics.

For instance, three main ecological mechanisms can explain the variation in the structure of pollination networks in time and space (Vizentin-Bugoni et al., 2018). The "forbidden links hypothesis" predicts that species traits or temporal incompatibility among partners limit interactions, making the network more specialized and modular (Jordano, 2016). On the other hand, the "trait-matching hypothesis" predicts that an evolutionary adjustment to avoid competition drives pollinators to prefer flowers that are compatible with their morphology, thus reducing competition in highly generalized plant sources (Vizentin-Bugoni et al. 2018; Pedraza & Bascompte, 2021). The neutral hypothesis predicts that species interactions occur randomly guided by abundance of pollinators and floral resources. In this case, more abundant individuals interact more frequently, and the opposite is true for rare species (Vázquez et al., 2009). In fact, these ecological mechanisms represent altogether a continuum of possibilities, whose importance may vary over time, especially in seasonal ecosystems (Olesen et al., 2008; Rabelig et al., 2019). However, if functional diversity increases, niche related mechanisms mayexplain the processes more than neutrality (Vizentin-Bugoni et al., 2018). Therefore, incorporating functional traits into network analysis is a key step to understanding the mechanisms underlying the assemble of species interaction in distinct scenarios (Zakharova et al., 2019; Cappellari et al., 2022; Guilherme et al., 2025).

In the Cerrado biome, the world's largest tropical savanna, vegetation types and marked seasonality influence the dynamics of interaction networks (Aguiar et al., 2024; Rabeling et al., 2019). This biome hosts more than 12,000 plant species, of which approximately 7,578 are endemic (Forzza et al., 2012; Reflora, 2025). The approximately 500 species of bees occurring in the Cerrado are the main pollinators of plants with distinct life-history traits in different vegetation types (Alves-dos-Santos, 2009; Cardoso et al., 2025). Plant-pollinator interactions in the Cerrado present a highly modular structure, where different groups of animals interact with plants (Aguiar et al., 2024) under a highly seasonal species turnover (Rabeling et al., 209). Seasonality plays an important role in plant phenology throughout the year in this biome, since climate is characterised by two well-defined periods, the dry (May to September) and rainy (October to April) seasons (Gottsberger & Silberbauer-Gottsberger, 2006). In turn, plant functional traits affect how plants are influenced by seasonality in the Cerrado. For example, herbaceous and subshrub species bloom predominantly during the rainy season (Munhoz & Felfili, 2005), while woody species tend to bloom at the late dry season (Mantovani & Martins, 1988; Oliveira & Gibbs, 2000). Such temporal variation may directly affect interaction dynamics because plant phenology, morphology, and species abundance changes over time (CaraDonna et al., 2021).

Such characteristics makes the Cerrado a good model for investigating the temporal dynamics of plant-bee interaction networks. Our aim was to evaluate how the functional traits of bees and plants contribute to the structuring of the bee-plant interaction network in the Cerrado in different climatic periods. We expect to understand which ecological mechanism is governing the interaction structure through discrete time intervals and at the metanetwork level. Specifically, we seek to answer: (i) how is the bee community affected by the climatic periods?; (ii) how are bee-plant interaction networks structured throughout the seasons, considering transition periods?; (iii) what is the role of different functional groups of bees in the network throughout the seasons?; and (iv) which ecological mechanisms are most relevant in structuring the network throughout the year?

We hypothesize that during periods of greater flowering, bees from different functional groups exploit plants with greater trait compatibility, forming specialized modules based on trait-matching responses. As flowering declines, the network is expected to become less specialized, with interactions driven more by resource availability than by preference. We also expect that the species in the network are mainly small or medium-sized social bees, and that centrality varies over time as a function of species replacements throughout the year in relation to phenology.

Methods

Study area

The field sampling was carried out from March 2019 to February 2020 at the Ecological Reserve of the IBGE - Brazilian Institute of Geography and Statistics (hereafter RECOR). The RECOR is a fully protected area, classified as Category IV by the IUCN. The area is located in the southern part of the city of Brasília, Distrito Federal (Federal District), Brazil (15° 56' 31" S, 47° 52' 47" W) and composes the Gama and Cabeça de Veado Environmental Protection Area (APA) together with the Brasília Botanical Garden and the University of Brasília Experimental Farm (Fazenda Água Limpa). This APA is one of the largest protected areas in the Distrito Federal and encompasses most vegetation types of the Cerrado biome, with high floristic diversity. The RECOR covers an area of 1,931 ha comprising eight out of the eleven vegetation types of the Cerrado (IBGE, 2011). The sampled plots have been subjected to different burning regimes for approximately 20 years, with burning frequency and timing varying as part of a long-term project that investigates impacts of fire in the Cerrado (see Miranda et al., 2010 for further details). The last burning occurred in 2011, but some differences in plant strata and vegetation structure still remain (herbaceous, arboreal, and shrubby) (Miranda et al., 2010).

The Cerrado is South America’s second largest biome, after the Amazon Rainforest (Ratter et al., 1997). It presents a rich mosaic of vegetation types, ranging from open grasslands to dense forests near the watersheds (Eiten, 1972; Ribeiro & Walter, 2008), and is one of the world’s biodiversity hotspots (Myers et al., 2001). Cerrado comprises eight biogeographical districts varying in plant species composition and endemism rates (Françoso et al., 2021). The Distrito Federal is situated centrally in the Center biogeographical district which in turn is located on the Brazilian Central Plateau, at elevations ranging from 900 to 1600 m above sea level (Françoso et al., 2021).

We conducted the study in areas dominated by *Campo Sujo*, a type of grassland vegetation in the Cerrado. *Campo Sujo* is characterised by >90% grass cover, with a shrub-herb layer interspersed with scattered subshrubs and poorly developed trees (<10% canopy cover) (Ribeiro & Walter, 1998). The grassland vegetation types in Cerrado comprises *Campo Sujo*, *Campo Limpo* and *Campo Rupestre* (Ribeiro & Walter, 2008) and covered approximately 6.4% of the total area of the Cerrado in 2024 (MapBiomas, 2026). In RECOR, grassland vegetation types comprise approximately 30% of its total area, 46.2% of which corresponds to *Campo Sujo* (IBGE, 2011). These formations are highly endangered and experienced higher devegetation rates than forest formations (Da Conceição Bispo et al., 2024).

The region's climate is classified as tropical seasonal (Aw) according to the Köppen classification (Alvares et al, 2014), with two well-defined seasons: a dry, cooler period from May to September when air humidity can fall below 15%, and a hot, rainy season from October to April that concentrates more than 90% of the annual rainfall. Average annual temperatures range from 22°C to 27°C, and annual precipitation varies between 1,200 and 1,400 mm (INMET, 2022), which strongly influences the structure and dynamics of plant communities and phenology (Mantovani & Martins, 1988). Despite the two well-defined seasons, interseasonal changes in precipitation and temperature influence vegetation (Batalha & Martins, 2004; Munhoz & Felfili, 2005) and insect dynamics (Silva et al, 2011). From March to April, rainfall decreases sharply (transition from wet to dry season), and it stabilizes from June to August (dry season). Similarly, from September to November, rainfall is sparse (transition from dry to rainy season), and it stabilizes from December to February (Hofmann et al., 2023). Considering the transition periods in plant-bee interactions enhances our ability to detect short-term community responses and to capture the temporal dynamics of interaction networks, particularly phases when ecological shifts are expected to be most pronounced.

Experimental design and sampling

We sampled bee-plant interactions in four plots, measuring 250 × 200 m each (20 ha in total). Plots were separated by 4 m of bare soil to prevent fires. During sampling, we excluded the first 5m of each plot to minimize border effects and increase the independence of each plot. Bee-plant interactions were sampled on a fortnightly basis throughout the whole year. Nevertheless, for the statistical analysis, we pooled data by month to ensure sample completeness and to better understand changes in bees and plant communities across seasons. Sampling took place from 8 a.m. to noon, with two plots sampled per day, alternating collection times between plots to ensure sampling at different times of the day. This totaled 8 hours of sampling effort per plot each month (i.e., 96 hours in total for each plot).

During each sampling, two collectors moved continuously across the entire plot to find flowering plants of different types (herbaceous, shrub, subshrub, and tree). When a plant in bloom was encountered, the visiting bees were collected using a sweep net and spent approximately 5 minutes on each plant. The collected bees were separated by plant species and strata, then taken to the laboratory for sorting and identification. This procedure made it possible to assign each bee to a specific plant species to model plant–bee interactions. Plant and bee samples were identified at the lowest taxonomical level possible or classified into morphospecies when species or genus level identification was not possible. Voucher species of bees were deposited in the Entomological Collection of the University of Brasília (DZUB), and plants were deposited in the Herbarium of the Botany Department at the University of Brasília (Herbário UB).

Functional traits of bees and plants

To understand the role of functional groups of bees in plant-bee interaction networks, we selected specific functional traits related to bee morphology and behavior. Morphological traits reflect the physical accessibility between bees and plants (Stang et al., 2006), while behavioral traits relate to the foraging strategies employed by these bees (Lichtenberg et al., 2010). As a proxy for body size, we used the intertegular distance (ITD), which can limit flower access (Cane, 1987; Stang, Klinkhamer, Van Der Meijden, 2006), obtained mostly from Brazilian Bee Trait Database (BBTD, Cordeiro et al., 2026). We also performed additional measurements following the same procedure adopted in BBTD on 64 species and morphotypes not included in this database (Cordeiro et al., 2026). When only a single individual of a species was available, the ITD measured on that individual was considered. Males and females were not distinguished in the measurements, as both interacted with plants during our sampling, although most of the sampled individuals were females. Behavioral traits were obtained from the literature and BBTD (Cordeiro et al., 2026) and included sociality, oligolecty, and behavior on flowers (e.g., buzz-pollination). Sociality (eusocial, solitary, or cleptoparasitic) reflects differences in foraging strategies and plant-visitation breadth, with eusocial bees generally more abundant and more generalist, whereas solitary and cleptoparasitic bees tend to be less abundant (Pires et al., 2022). Oligolectic bees are those that specialize in a few plant species or families (Schlindwein, 2004). Floral behavior, such as buzz pollination, indicates the ability of certain bees to extract pollen from poricidal anthers (Valejo-Marín, 2018), which helps determine whether buzz-pollinated species show preferences for flowers with poricidal anthers during specific periods of the year when these flowers are available.

To assess how floral traits influence bee visitation, we selected six plant attributes known to affect pollinator behavior (Garibaldi et al., 2015; Peralta et al., 2020). These attributes are related to visual attractiveness. We obtained these data from species descriptions available in online herbariums, such as SpeciesLink, Flora e Funga do Brasil, and peer-reviewed articles. Traits associated with visual attractiveness included the predominant color of the corolla or inflorescence, as well as the largest floral dimension as a proxy for flower size (diameter for disc-shaped flowers and length for tubular or keeled flowers). These traits allowed us to infer whether flower size may act as a limiting factor for bee size. We also assessed the type of floral symmetry (actinomorphic or zygomorphic), which can be related to the occurrence of more generalist and specialist bee visitors. Measurements were taken using ImageJ software directly on exsiccatae containing scales, with the largest flower size used to standardize across different floral morphologies. We considered individual flowers as the basic measurement units rather than entire inflorescences. However, for color, we used the dominant color of the floral display, whether corresponding to the inflorescence or to individual flowers. Traits related to the presence of poricidal anthers (presence/absence data), which help identify flowers accessible to buzz-pollinating bees. Lastly, the plant habit (herbaceous, subshrub and tree) form was used to assess variation in vegetation strata over time.

Plant-bee interaction networks

To investigate temporal patterns in network structure, we first constructed an annual interaction network of bee-plant interactions to capture the overall interaction architecture and compare possible variations throughout the seasons. Then we created temporal networks considering the months (i.e., summing the data from the two samples each month in each plot) to capture the temporal variation of bee-plant interactions and compare it with the annual pattern. We also constructed networks for each plot in each period, totalizing 4 networks per period; however, for most analyses, the plot data were grouped into a single network. For that, we modelled a weighted interaction matrix to calculate the size based on the number of links (total and binary), nestedness using Nestedness Based on Overlap and Decreasing Fill (NODF) (Almeida-Neto et al., 2008), modularity using the QuanBiMo algorithm (Dormann and Strauss, 2014), connectivity based on Weighted Connectance (WC), Specialization (H_2'), Niche Overlap (NO) and Robustness (R) (Bersier et al., 2002, Blüthgen et al., 2006). The NODF method quantifies the extent to which less common species interactions are subsets of more common interactions with generalist and dominant species (Almeida-Neto et al., 2008), reflecting a hierarchical structure in which specialists interact primarily with species that also interact with generalists. The QuanBiMo algorithm assesses whether the network is organized into interaction modules, in which interactions occur more frequently within modules than between them (Dormann and Strauss, 2014). This approach enabled us to identify the species that compose each module, providing insight into the community's organization and functional structure.

To identify the roles of bee species within the network, we used ZC-score analysis. This approach characterizes the role of each species based on its within-module (z-value) and among-module (c-value) connectivity in the network (Olesen et al., 2007). This analysis classifies species into four quadrants, with “peripherals” ($z \leq 2.5$ and $c \leq 0.6$), “connectors” ($z \leq 2.5$ and $c > 0.6$), “module hubs” ($z > 2.5$ and $c \leq 0.6$), and “network hubs” ($z > 2.5$ and $c > 0.6$) (Guimerà & Amaral, 2005). However, for our analysis, we used z- and c-values adjusted for the network's size and architecture (Olensen et al., 2007). Thus, for each network, a c and z value was adopted using the ‘bipartite’ package czvalues function (Dormann et al, 2009).

To identify the most relevant species in the interaction network over time, we used three centrality metrics: degree (DC), closeness centrality (CC), and betweenness centrality (BC) for both the annual network and the seasonal networks. DC represents the number of interactions for each species, indicating that the higher this value, the more central the species is in the network CC quantifies how close a species is, on average, to the others, while BC measures how much a species acts as an intermediary in connections between other species (González et al., 2010; Vasas and Jordán, 2006). Species with high DC, CC, and BC values play central roles in the network structure and make up its cohesive core. The analysis of seasonal networks, compared with the annual network, allowed us to assess whether centrality patterns remain constant throughout the year or vary between seasons and to identify potential emergent properties in the annual network.

Statistical analyses

All statistical analyses were performed in the R version 4.5.2 (R Core Team, 2025). To compare bee species richness among climatic periods, we used individual-based rarefaction curves with the Chao-1 estimator. Species richness (observed and estimated) and diversity were further quantified using Hill numbers ($q = 0$, 1, and 2) based on abundance data. Analyses were performed with the function *iNEXT4steps* from the 'iNEXT' package in R (Hsieh & Chao et al., 2025). Confidence intervals were set at 95% and obtained through bootstrap resampling with 200 replications.

To assess the influence of climatic periods on species richness and abundance (response variables), we fitted Generalized Linear Models (GLMs). The predictor variable was the climatic periods (rainy–dry, dry, dry–rainy and rainy), with each period consisting of a grouping of three months of sampling in each plot. For both models (richness and abundance), GLMs were modelled using a negative binomial distribution for overdispersed data. The adequacy and goodness-of-fit of the final models were assessed with the 'DHARMa' package. When significant effects were detected, pairwise comparisons were made by model contrast analysis using the Tukey method in the 'emmeans' package (Lenth & Piaskowski, 2025).

To assess whether the network structure reflects ecological processes rather than random assembly, we compared the network metrics (modularity, NODF, H2′, niche overlap and robustness for higher and lower trophic levels, and weighted connectance) of the annual and partial interaction networks for climatic periods with those expected under chance using null models. We performed 1,000 randomizations of our matrix using the "r2dtable" method, which preserves marginal totals, and then calculated metrics for all randomizations using the 'bipartite' package

(Dormann et al., 2011). Statistical significance was assessed using null models and permutation tests, where observed network metrics were compared to a distribution generated from randomized networks.

To evaluate how network metrics varied across seasons, we also fitted multiple GLMs using the same procedures described above. Network metrics (modularity, NODF, H2′, niche overlap and robustness for higher and lower trophic levels, and weighted connectance) were used as response variables, and climatic periods (rainy–dry, dry, dry–rainy, and rainy) were included as predictor variables. Based on the ‘DHARMa’ package (Hartig, 2024) results, the Gaussian error distribution provided the best fit for modularity, H2′, niche overlap at the lower trophic level, and robustness at the lower trophic level, whereas the Gamma distribution was more appropriate for NODF, niche overlap, and robustness at the higher trophic level, and weighted connectance.

To assess whether trait matching is the main driver of bee–plant interaction networks architecture, we performed a Parafit test (Legendre et al., 2002) for the temporal and annual networks. The analysis was based on two trait matrices, one for bees and one for plants, and an interaction matrix. The first two trait matrices were organized with species as rows and functional traits as columns, with cells containing the trait values or categories for each species. These trait matrices were subsequently transformed into trait similarity matrices using Gower’s distance coefficient (Gower, 1971), which is based on pairwise comparisons among species. Similarity matrices were computed using the function *daisy* from the ‘cluster’ package in R (Maechler et al., 2025). In addition to the two trait similarity matrices, a binary interaction matrix was required, corresponding to the same matrix used to construct the interaction networks. The only difference was the exclusion of species for which trait information was unavailable. Consequently, the original interaction matrix, which included 110 bee species and 102 plant species, was reduced to 90 bee species and 97 plant species for the Parafit analysis. Despite this reduction, 91% of the total community abundance was retained. The Parafit test was then applied to correlate the bee and plant trait similarity matrices through the interaction matrix. Overall significance was assessed using 999 permutations and the *cailliez* correction. This test assesses whether species with similar traits interact more frequently with similar partners than expected by chance (Legendre et al., 2002). Rejection of the null hypothesis indicates a significant congruence between bee and plant traits, supporting trait matching as a mechanism structuring the interaction network (Peralta et al., 2020).

To identify which bee and plant characteristics contribute to trait matching, we conducted a combined RLQ and Fourth-corner analysis (Dray et al., 2014). While Parafit assesses whether trait matching occurs at the community level, RLQ identifies which functional traits drive these patterns, providing a more detailed understanding of the mechanisms shaping plant–pollinator networks. We conducted the RLQ analysis in R using the ‘ade4’ package (Thioulouse et al., 2018). RLQ relies on a three-matrix framework, similar to Parafit, comprising a plant-trait matrix (R), an interaction matrix (L), and a bee-trait matrix (Q). Although originally developed to assess relationships between species traits and environmental variables, RLQ can be adapted to examine associations between traits of interacting species (Albrecht et al., 2018; Buitrón-Jurado & Sanz, 2021). Prior to the RLQ analysis, the plant (R) and bee (Q) trait matrices were ordinated using Hill–Smith principal component analysis (dudi.hillsmith), which is appropriate for mixed trait data. The interaction matrix (L) was ordinated using correspondence analysis (dudi.coa). To reduce the influence of differences in interaction abundance, the L matrix was log-transformed. Statistical significance of the RLQ analysis was assessed using a global Monte Carlo Type 6 permutation test, which simultaneously evaluates two models: Model 2, testing whether bee traits are associated with plant traits, and Model 4, testing whether bee traits influence the structure of the interaction network and determine which plants they visit. The Fourth-corner analysis was then used to test pairwise associations between individual bee and plant traits, thereby identifying specific trait combinations exhibiting significant correlations (Dray & Dufour, 2007; Dray et al., 2014).

To evaluate the composition of bee and plant communities across the climatic periods, we used a Non-metric Multidimensional Scaling (NMDS). The matrices were constructed with plots per month as rows and species as columns, with abundant square-root transformed to reduce the influence of highly abundant species. The ordinations were calculated with the *metaMDS* function from ‘vegan’ R package (Oksanen et al., 2025) using Bray-Curtis dissimilarities and 100 randomisations. The differences between periods were tested with PERMANOVA (*adonis2*, ‘vegan’) using 9,999 permutations. The assumption of homogeneous dispersion was verified with PERMDISP (*betadisper*, ‘vegan’). Next, a paired PERMANOVA with a Bonferroni correction was performed to assess differences across all combinations of seasonal periods, providing a detailed view of compositional changes over time. To assess the variation in trait composition across climatic periods, we performed an NMDS using the same configuration described above, but with the matrix constructed from the traits in the columns and their respective abundances in the cells.

Results

Bee-plant community structure

We recorded 1,154 bees classified into 110 species and five families, with Apidae being the most species-rich (74 species), followed by Halictidae (19), Megachilidae (16), and both Colletidae (1) and Andrenidae (1) (Supplementary Table S1). Bees visited 102 plant species from 35 families, with *Oocephalus grazielae* (Lamiaceae), *Croton goyazensis* (Euphorbiaceae) and *Eremanthus glomerulatus* (Asteraceae) together accounting for 28.2% of observed bee visits. Six species accounted for 56% of the total bee abundance: the eusocial *Paratrigona lineata* (Apidae, Meliponini) (20.34 ± 5.91 SE individuals/month), *Apis mellifera* (Apidae, Apini) (18.67 ± 7.22) and *Trigona spinipes* (Apidae, Meliponini) (6.58 ± 1.89), and the solitary *Ceratina (Crewella) gossypii* (Apidae, Ceratitini) (3.17 ± 0.74), *Exomalopsis tomentosa* (Apidae, Exomalopsini) (2.84 ± 1.25) and *Paratetrapedia punctata* (Apidae, Tapinotaspidini) (2.67 ± 1.12).

Bee-plant community showed a high proportion of rare species, with singletons and doubletons comprising 50% of bees and 41% of plant species (Fig S1). Based on the Chao1 estimator, our sampling reached approximately 74% of the estimated number of bee species for the whole year (Fig 1a), 73% in the dry period, 48% in dry–rainy, 78% in the rainy, and 63% in rainy–dry. According to the rarefaction curves, bee species richness was similar across the seasons, although higher in the rainy-dry period than other, lower in the rainy season (Fig 1b). Based on the analysis with Hill numbers, diversity of orders $q = 1$ and $q = 2$ was higher during the rainy season (${}^1D = 24.5$; ${}^2D = 16.7$) and lower in the dry season (${}^1D = 13.7$; ${}^2D = 5.4$), indicating greater evenness and lower dominance in the rainy period (Figure S2). Species abundance did not differ significantly among seasons ($\chi^2 = 4.34$, df = 3, $p = 0.27$) (Fig. S2).

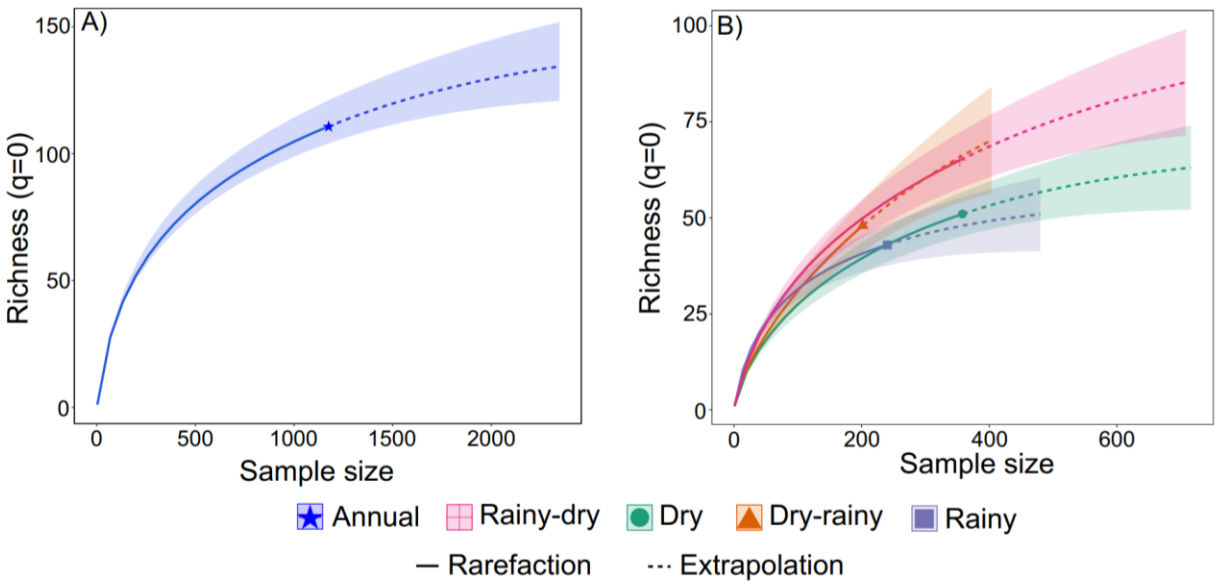


Fig. 1. Individual-based rarefaction curves for the sampled bee community considering (A) the entire year and (B) the four seasons. The solid lines represent the rarefaction curves, while the dashed lines indicate the extrapolation of species richness. The shaded areas correspond to the 95% confidence intervals. The overlap of these intervals indicates no significant difference in estimated richness between periods for the same sampling effort.

Temporal variations in bee-plant interactions

The annual network comprised 1,154 interactions and 456 links distributed across four climatic periods (Fig 2a), with the dry season showing the highest number of interactions (358, 150 binary), followed by the rainy–dry transition (354, 125), rainy season (240, 139), and dry–rainy transition (202, 91) (Fig 2b). All network metrics differed from random expectations in the annual network (Fig 2b, Table S2), revealing a strongly modular ($Q = 0.54$ vs. 0.21 ± 0.006; $t = -1674.8$; $df = 999$; $p < 0.001$) and specialized structure ($H2' = 0.42$ vs. 0.11 ± 0.007; $t = -1416.2$; $df = 999$; $p < 0.001$). These patterns were associated with low connectance (w.conect = 0.39 vs. 0.07 ± 0.002; $t = 603.1$; $df = 999$; $p < 0.001$), low niche overlap among bees (niche.overlap = 0.09vs. 0.11 ± 0.008; $t = 101.8$; $df = 999$; $p < 0.001$), and low nestedness (NODF = 18.01 vs. 0.31 ± 1.730; $t = 248.8$; $df = 999$; $p < 0.001$), indicating a highly compartmentalized and specialized interaction network.

Seasonal networks exhibited a modular and specialized structure, with both modularity and specialization consistently higher than expected by chance, while NODF was low (Table S2). Modularity varied only subtly among seasons, being highest during the rainy–dry transition ($Q = 0.62$ vs. 0.35 ± 0.02; $t = -429.77$; $df = 999$; $p < 0.001$) and lowest in the rainy season ($Q = 0.52$ vs. 0.39 ± 0.02; $t = -203.36$; $df = 999$; $p < 0.001$). In contrast, specialization showed stronger seasonal variation, reaching its highest value in the dry season ($H2' = 0.51$ vs. 0.12 ± 0.01; $t = -786.64$; $df = 999$; $p < 0.001$) and the lowest during the rainy season ($H2' = 0.35$ vs. 0.16 ± 0.01; $t = -786.64$; $df = 999$; $p < 0.001$; Table S3). Despite these tendencies, network metrics did not vary significantly over periods, except for niche overlap ($\chi^2 = 12.67$, $df = 3$, $p = 0.0054$) and robustness among the flowers ($\chi^2 = 11.42$, $df = 3$, $p = 0.0097$). Which indicates that plants share more bee species among themselves, resulting in lower network robustness in the dry-rainy period (Fig. 3F and H).

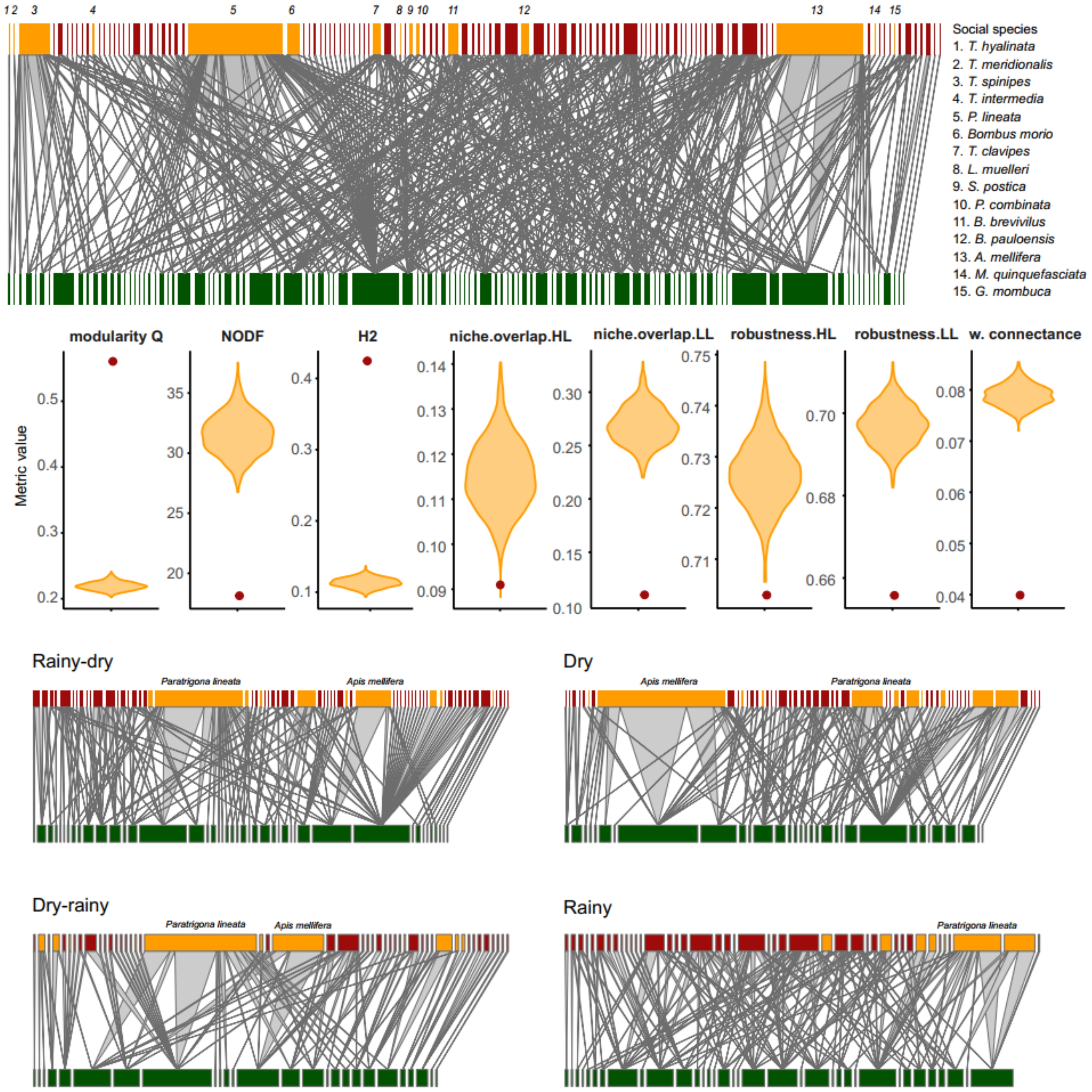
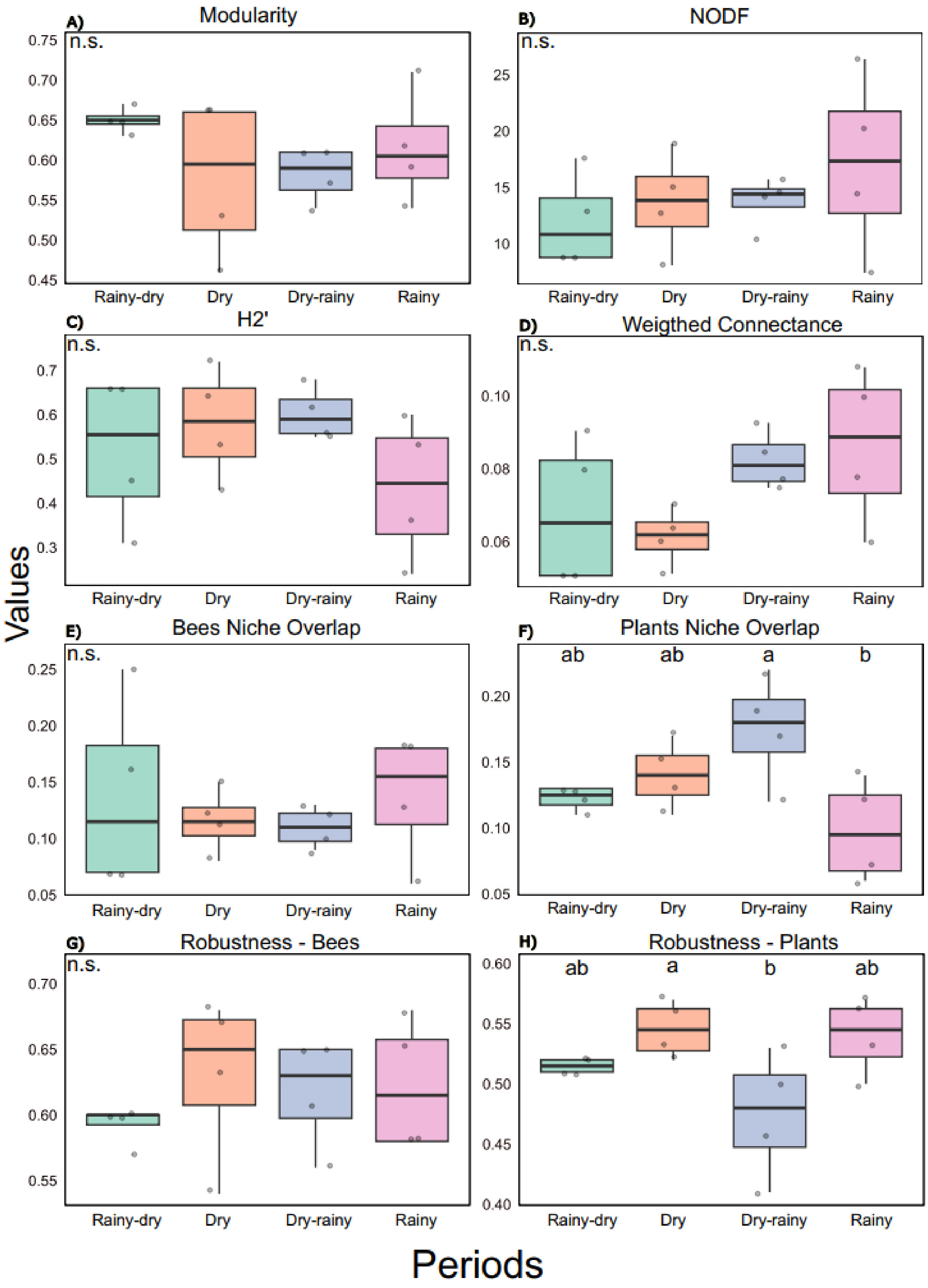


Figure 2. Annual and seasonal bee-plant interaction networks in an area of Cerrado *Campo Sujo*, including important metrics. (A) Graphic representation of the annual bipartite network, in which functional/taxonomic groups are represented by the colour yellow for social bees, red for solitary and cleptoparasitic bees and green for plants. Social bee species names are listed on the right and correspond to the numbers in each node. The size of the nodes indicates the relative frequency of the species. (B) Null model analysis for annual network metrics, in which the violin plots represent the distribution of simulated metric values and the red dots indicate the observed value; all metrics

differed significantly from chance, according to the t-test ($p < 0.001$). (C) Seasonal bee–plant interaction networks, showing the structural variation between periods: (a) rainy–dry transition, (b) dry season, (c) dry–rainy transition, and (d) rainy season.


A)
Modularity
n.s.
0.75
0.70
0.65
0.60
0.55
0.50
0.45
Rainy-dry
Dry
Dry-rainy
Rainy
B)
NODF
n.s.
25
20
15
10
Rainy-dry
Dry
Dry-rainy
Rainy
C)
H2'
n.s.
0.7
0.6
0.5
0.4
0.3
Rainy-dry
Dry
Dry-rainy
Rainy
D)
Weigthed Connectance
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0.10
0.08
0.06
Rainy-dry
Dry
Dry-rainy
Rainy
Values
E)
Bees Niche Overlap
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Rainy-dry
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0.20
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Dry-rainy
Rainy
G)
Robustness - Bees
n.s.
0.70
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0.55
Rainy-dry
Dry
Dry-rainy
Rainy
H)
Robustness - Plants
ab
a
b
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0.60
0.55
0.50
0.45
0.40
Rainy-dry
Dry
Dry-rainy
Rainy
Periods

Figure 3. Temporal dynamics of the topological properties of plant–bee interaction networks in the Cerrado. Seasonal variation is presented for eight network metrics calculated in four climatic periods: rainy–dry transition, dry, dry–rainy transition, and rainy. Boxplots illustrate the distribution of metric values calculated at the plot level per climatic period. The metrics analyzed include: (A) modularity, (B) nesting calculated by NODF, (C) specialization (H_2’), (D) weighted connectance, (E) bee niche overlap, (F) plant niche overlap, (G) bee robustness, and (H) plant robustness. Different letters above the boxplots indicate statistically significant differences between seasons (Tukey's post hoc test, $p < 0.05$), while identical letters indicate no significant difference. Metrics indicated as “n.s.” did not show significant variation throughout the year.

Role of species within the interaction network

In both annual and seasonal networks, none of the bee species were classified as network hubs, with more than 90% of species occupying peripheral positions (Fig. 4 A-E). In the annual network, the social bees *Bombus pauloensis* (Apidae, Bombini), *A. mellifera* (Apidae, Apini), *Paratrigona lineata* (Apidae, Meliponini), and the solitary *Ceratina gossypii* (Apidae, Ceratinini) acted as module hubs, whereas the solitary bees *Exomalopsis fulvofasciata* (Apidae, Exomalopsini), *Augochloropsis smithiana* and *Augochloropsis* sp.2 (Halictidae, Augochlorini), and *Ceratalictus clonius* (Halictidae, Augochlorini) primarily functioned as connectors among modules (Fig. 4). This pattern is consistent with species-level centrality metrics, which showed that social bees exhibited the highest values of weighted closeness (CC), weighted betweenness (BC), and degree (DC). Among these, *P. lineata* (BC = 0.44, CC = 0.016, DC = 44), *A. mellifera* (BC = 0.16, CC = 0.016, DC = 22), and *B. pauloensis* (BC = 0.12, CC = 0.015, DC = 7) were the most central species in the network. However, some differences emerged for solitary bees, with *Paratetrapedia punctata* (Apidae, Tapinotaspidini) (WB = 0.058, WC = 0.012, D = 15), *C. gossypii* (WB = 0.034, WC = 0.012, D = 22), and *Exomalopsis tomentosa* (WB = 0.026, WC = 0.012, D = 20) showing relatively higher centrality values (Table S1).

In the seasonal networks, social bees acted predominantly as module hubs (dry and dry–rainy: *A. mellifera* and *P. lineata;* dry–rainy only: *B. pauloensis* and the solitary *E. tomentosa*) similarly to the annual network. During the dry–rainy transition, the solitary species *P. punctata* and *Ceratalictus clonius* (Halictidae, Augochlorini) played the role of connector species, along with the social species *Trigona spinipes*. In the rainy–dry transition, the module hub was the solitary bee *Epicharis analis* (Apidae, Epicharitini), whereas connectors included *P. lineata*, *A. mellifera*, *Gaesischia belophora* (Apidae, Eucerini), *E. tomentosa*, and *C. clonius*. During the rainy season, only solitary bees assumed the role of module hubs (*Monoeca mourei* (Apidae, Tapinotaspidini)) and connectors (*Augochloropsis smithiana*, *Ceratina minima* (Apidae, Ceratinini)) (Fig. 4). Regarding centrality metrics for annual network, the most central species were *P. lineata* (CC = 0.016; BC = 0.440; DC = 44), *A. mellifera* (CC = 0.016; BC = 0.161; DC = 22) and *B. morio* (CC = 0.015; BC = 0.122; DC = 7) (Table S1), while in the periods, *P. lineata* was the most central species in the dry–rainy (CC = 0.022; BC = 0.588; CD = 14) and rainy–dry (CC = 0.023; BC = 0.571; DC = 22) transitions, *A. mellifera* in the dry period (CC = 0.388; BC = 0.038; DC = 12), and *E. tomentosa* in the rainy period (CC = 0.028; BC = 0.296; DC = 13) .

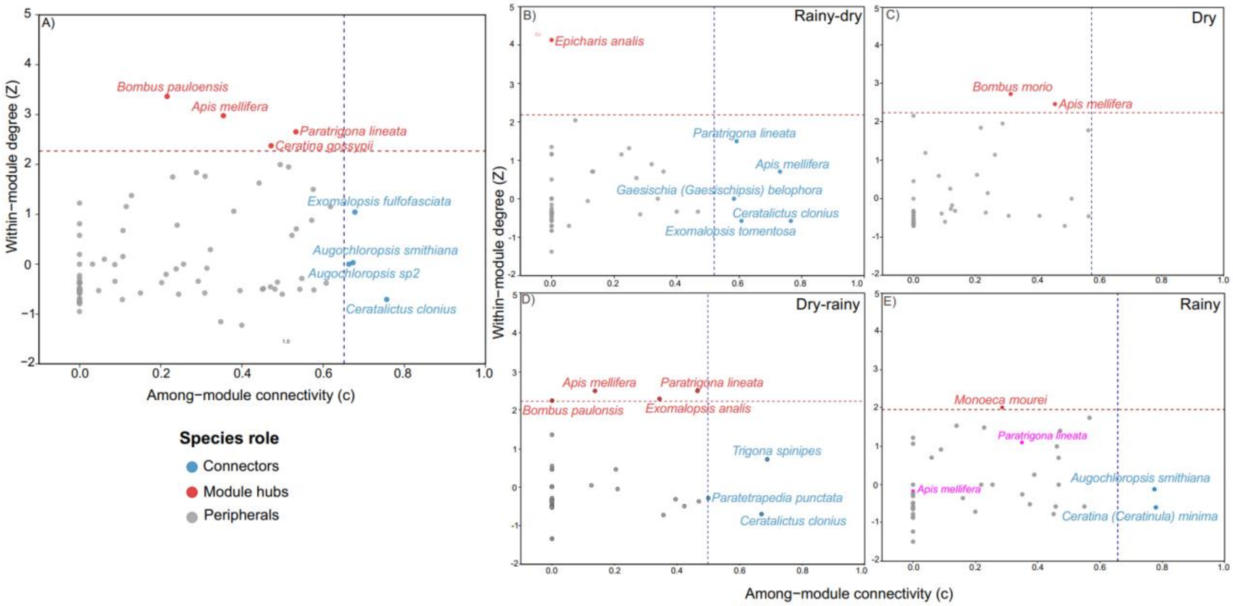

Figure 4. Bee species' role in the A) annual and seasonal (B-E) networks as shown by Z-CScores. Each quadrant shows a different function based on connectivity values between modules (*c* values) and within modules (*z* values). Species roles are represented by the colors: blue (connectors), red (module hubs) and grey (peripherals). For the annual network, the thresholds were c = 0.65 and z = 2.27 for bees and c = 0.65 and z = 2.22 for plants. For the seasonal networks, the values varied

rainy-dry (bees: c = 0.52 and z = 2.18; plants: c = 0.50 and z = 1.20), dry (bees: c = 0.57 and z = 2.25; plants: c = 0.54 and z = 1.86), dry-rainy (bees: c = 0.49 and z = 2.20; plants: c = 0.48 and z = 1.74) and rainy (bees: c = 0.65 and z = 1.97; plants: c = 0.65 and z = 1.79).

Species traits in the interaction network

The Parafit test revealed a significant correspondence between bees and plants in the annual interaction network (ParaFitGlobal = 208.57, $p < 0.001$), indicating that bee species with similar traits tend to interact with a similar group of plants sharing similar traits more frequently than would be expected by chance. This pattern suggests the presence of trait matching at the community level, in which morphological and/or behavioural traits of pollinators and plants influence interaction structure. On the other hand, partial seasonal networks did not show significant congruence between bee and plant traits (rainy-dry: ParaFitGlobal = 18.96, p = 0.856; dry: ParaFitGlobal = 9.78, p = 0.883; dry-rainy: ParaFitGlobal = 6.99, p = 0.644; rainy: ParaFitGlobal = 12.45, p = 0.966), indicating that trait matching emerges as an importante property of the entire network and that, during climatic periods, signs of trait matching are not evident.

The annual RLQ, which was used to test for specific associations between bee characteristics (Q) and plant characteristics (R), indicated that the plant traits do not filter the bees that visit them (Model 2: Obs = 0.676; Std.Obs = 0.356; p = 0.3131), but bees traits that predict who they interact with (Model 4: Obs = 0.676; Std.Obs = 2.326; p= 0.0157). Across the climatic periods, the RLQ analysis did not show significant associations (rainy-dry model 2: Obs = 0.603; Std.Obs = -0.691; p = 0.9714, model 4 Std.Obs = -0.659, p = 0.7249; dry: p = 0.9295, p = 0.9068; dry-rainy: p = 0.9171, p = 0.8418; rainy: p = 0.5238, p = 0.3054). The Fourth-corner analysis for the annual network revealed positive associations between bee body size (ITD) and purple flowers with bilateral symmetry, while the relationship with radially symmetrical flowers was negative. In addition, we observed a negative association between white flowers and buzz-pollinating bees, and a positive association between white flowers and social bees (Figure 5).

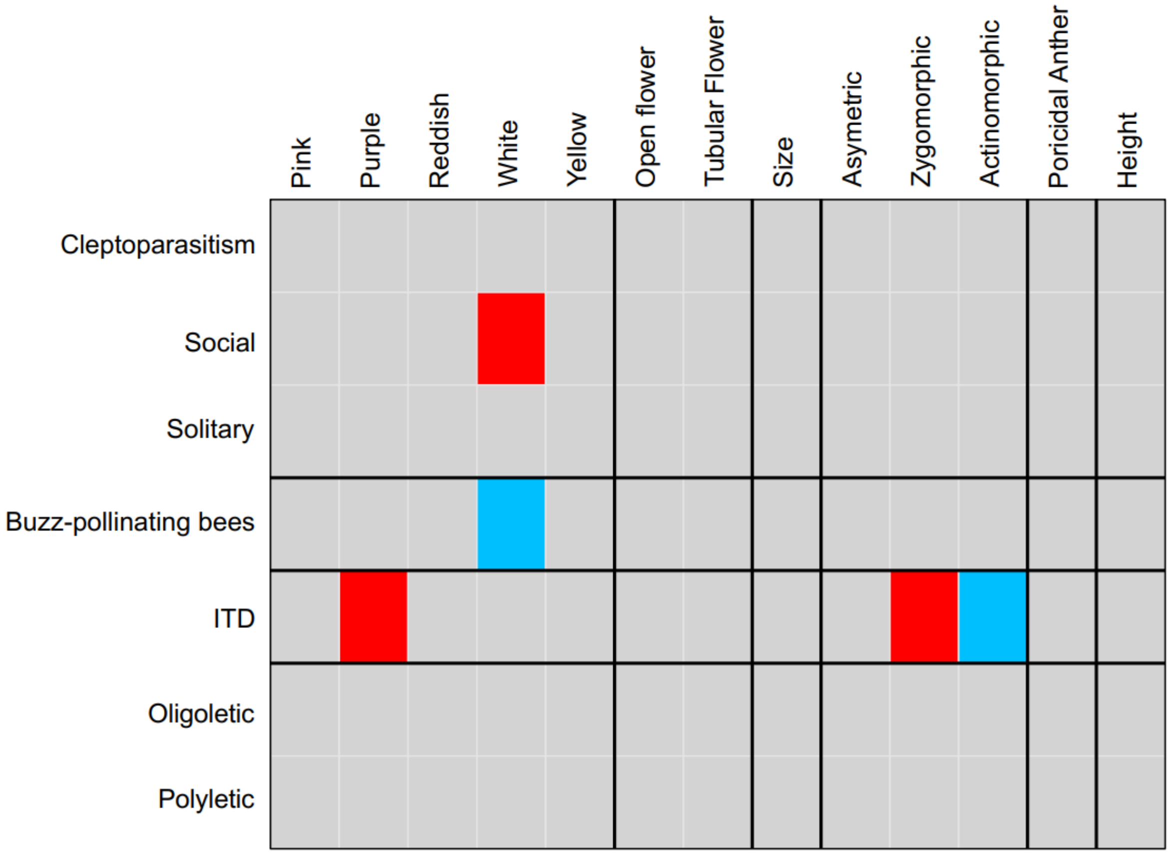

Figure 5. Fourth-corner matrix showing pairwise associations between bee and plant traits. Positive and significant relationships ($p < 0.005$) are shown in red, negative and significant relationships in blue, and non-significant associations in gray.

The NMDS showed that plant and bee community composition varied among periods (Fig. 6). The PERMDISP indicated that the dispersion between groups was homogeneous (bees: F = 1.7275, p = 0.1772; plants: F = 0.7828, p = 0.525), and PERMANOVA detected significant differences between periods (bees: $R^2 = 0.22$, F = 3.57, p-adjusted < 0.001; plants: $R^2 = 0.28$, F = 5.00, p-adjusted < 0.001). Pairwise comparisons indicated that all periods differed significantly from each other, with the largest difference observed between the rainy and dry seasons for both bees (Dry - Rainy: F = 7.42, $R^2 = 0.28$, p-adjusted = 0.006) and plants (Dry - Rainy: F = 5.22, $R^2 = 0.21$, p-adjusted = 0.006), and the transition periods showing moderate differences (Fig. 6). Regarding variations in bee trait composition, the NMDS showed no variation between bee traits over the periods, despite the dominance between traits being dynamic throughout the year (Fig. S2). However, plant trait composition varied only between the dry-rainy and rainy-dry periods (F

= 4.30, R² = 0.18, p-adjusted = 0.030) and between dry-rainy and dry (F = 6.41, R² = 0.24, p-adjusted = 0.006).

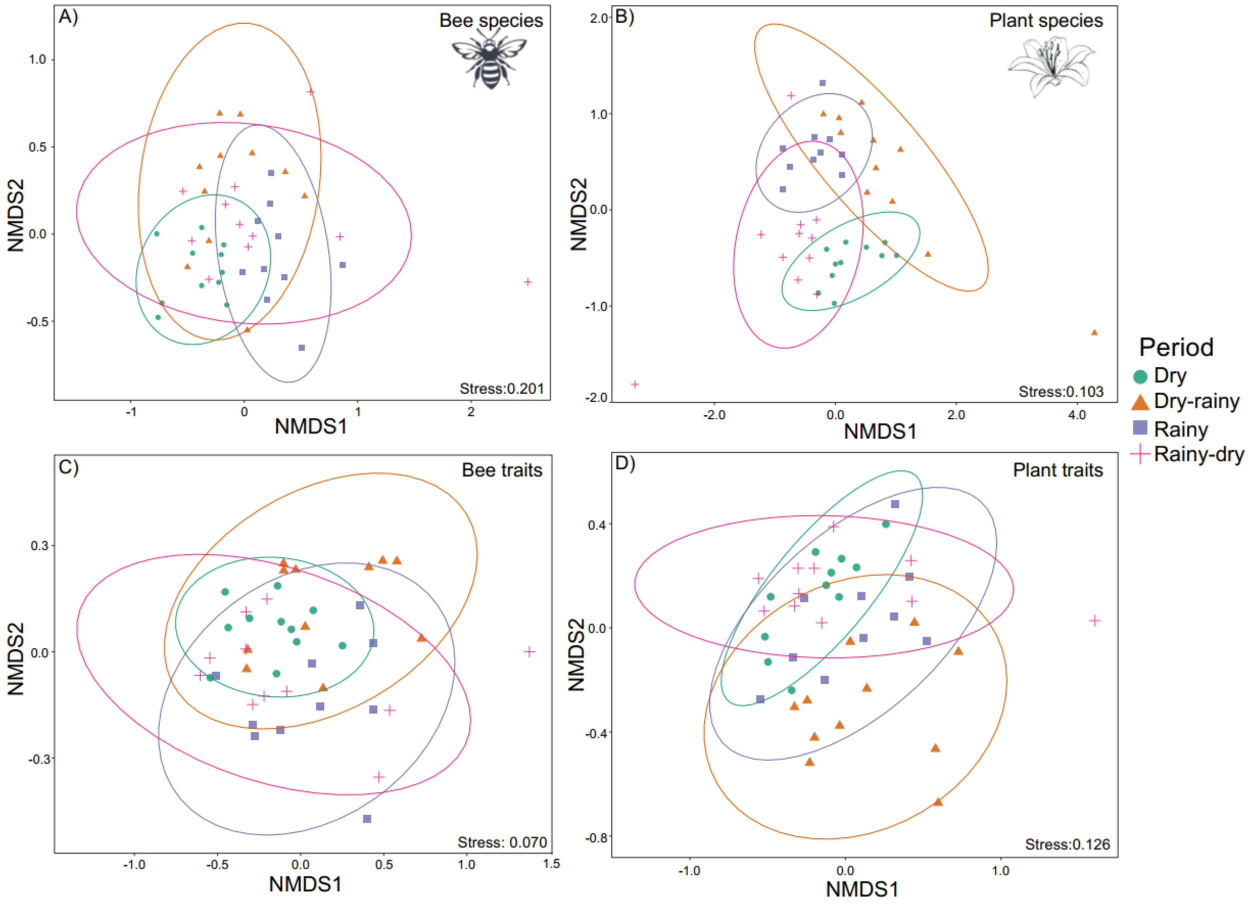

Figure 6. Non-metric multidimensional scaling (NMDS) of the composition of the community of A) bees, B) plants, C) bee traits and D) plant traits. Each point represents one plot per month, and the ellipses represent the periods of the year (dry, rainy, and dry-rainy and rainy-dry transitions), drawn around the centroid of each group to cover 95% of the points. A PERMANOVA revealed significant differences between plants and bees composition all seasons (Table S4). No significant differences in bee trait composition were detected among periods. In contrast, plant traits differed significantly between the dry–rainy and rainy–dry periods and between the dry–rainy and dry periods.

Discussion

We showed that species turnover governs plant-bee interaction across time, but trait-matching was an emergent property at the metanetwork level. Trait-matching regulates plant-bee interaction metanetworks in the Cerrado biome, possibly explaining the highly modular and specialized interaction network previously shown for the entire biome and the whole assemblage of pollinators (Aguiar et al., 2024). However, when climatic periods are analysed separately, the trait-matching gives place to the turnover of species, driven by changes in community composition with functionally redundant species replacing each other across time. As a consequence, different species assume a central role in network cohesion over seasons through the replacement by functionally similar species.

Social bees are the main pollinators in the Neotropical biomes (Biesmeijer & Slaa, 2006, Aguiar et al., 2024, Luna et al., 2024) due to their diversity and abundance, especially in savannas and forests. Indeed, eusocial species such as *P. lineata*, *A. mellifera*, and *T. spinipes* were the most abundant in our annual network. On the other hand, rare species (singletons and doubletons) make up 50% of the community diversity. This supports the idea that the pollination of the diverse Cerrado flora relies on a pool of species with high taxonomic and functional diversity, reflecting the functional complementarity at both sides of the interaction (Fründ et al., 2013). While abundant bee species are usually generalists, rare species presented specialised traits, suggesting complementary roles in ecosystem functions (Coux et al., 2016).

Annual and seasonal plant–bee interaction networks were consistently modular and specialised. These networks typically exhibit low connectance, nestedness and niche overlap, resulting in high specialisation. Temporal variation in network structure follows plant phenological cycles in *Campo Sujo* vegetation. Most herbaceous species bloom during the rainy–dry transition (Batalha & Martins, 2004), while woody species bloom mainly in the late dry season (Mantovani & Martins, 1988; Oliveira & Gibbs, 2000). In contrast, during the rainy season, modularity and specialisation decrease, likely due to reduced floral availability or to sampling effects associated with heavy rainfall, which can limit bee activity and foraging behavior (Roubik, 1989; Lawson & Rands, 2014). Despite year-round flowering, high floral availability promoted bee selectivity and greater network specialisation, whereas low availability leads to broader resource use.

Considering functional traits, we observed species replacement accompanied by the rewiring of interactions among functionally similar species across seasons. Consequently, the identity of central species varied between seasons. *Paratrigona lineata* was central in both transition periods, but it was replaced by *A. mellifera* in the dry season, and *E. tomentosa* in the rainy season as the most central species. The centrality pattern reflected the functional role of species in the network, with social species acting mainly as intra- and intermodular connectors, while solitary species contributed more significantly to the connection between modules. The central role of social bees in most seasons is associated with a high frequency of interactions (Maia et al., 2019) due to the large abundance of individuals and the ability of colony recruitment to explore resources with higher abundance and/or quality (Lindauer & Kerr, 1960; von Frisch, 1967; Grüter, 2020). In contrast, during the period of heavy rains, the network was predominantly structured by solitary species (65% of interactions), reflecting greater resource heterogeneity and more homogeneous distribution of interactions. As the foraging of social species is strongly influenced by the amount of resources even at large distances (Martins et al., 2023), this pattern may also indicate that social bees preferred to forage in adjacent forested areas or had a reduction in foraging activity due to heavy rains.

The main structural mechanism of the annual network was the correspondence of characteristics, whereas in seasonal networks, the structure was influenced by species turnover. Given the great floral diversity available, trait matching emerges as a central factor in the establishment of interactions, especially mediated by resource accessibility. Tubular and zygomorphic flowers, which are structurally more complex, tend to impose greater restrictions on visitors, favoring larger bees with longer tongues, while open, shallow, and actinomorphic flowers are more accessible to smaller, generalist bees (Alves-dos-Santos et al., 2016; Shimizu et al., 2014; Stang et al., 2006, 2009). We observed a positive association between the body size of bees and zygomorphic and purple flowers, and a negative association with actinomorphic flowers, possibly related to greater competition in these generalist flowers, often dominated by aggressive social species (Dworschak & Blüthgen, 2010, Lichtenberg et al., 2010). Smaller bees tend to require more time to access resources in complex flowers, which may lead them to prefer flowers with generalist morphology (Balfour et al., 2015), while larger bees tend to be specialized (Raiol et al., 2010). The positive correlation between social bees and white flowers may be associated with the unspecialised floral morphology described for the Myrtaceae family, which typically includes small, white, polystemonous flowers (Vasconcelos et al., 2018). This suggests that small white flowers may be indicative of generalist floral traits in other plant families.

Taken together, our results suggest that the structure and persistence of interaction networks are primarily sustained by mechanisms of species turnover, in which the matching of characteristics emerges as a fundamental property of interactions. The high dynamism observed shows that the replacement and reorganization of bee species over time does not compromise the stability of the network but, on the contrary, reinforces its robustness through the diversity of functional strategies. In this context, functional diversity is essential for understanding how interactions are established and maintained, since different traits modulate the choices and constraints between plants and pollinators. Furthermore, the observed patterns may reflect, at least in part, the effects of species abundance, phenological overlap, and sampling artifacts, which were not directly assessed. In addition, the complementary roles of social and solitary bees emphasize that, despite occupying different roles in the network, both groups are fundamental to its maintenance, ensuring the stability of interactions even in the face of variations in species composition.

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Supplementary material

Table S1. Community structure and centrality metrics of bee species sampled in the Cerrado (*Campo Sujo*) area. The species are organized by taxonomic families. For each species, the absolute abundance (FREQ) and network metrics calculated from the plant-pollinator interaction matrix are presented: Degree (number of direct connections with plant species); Betweenness Centrality (W.BET) (importance of the species as a bridge connecting different modules of the network); Closeness Centrality (W.CLO) (proximity of the species to all others in the network); and *d'* (complementary specialization index, which measures the level of exclusivity of a species' interactions in relation to resource availability). Species with high centrality values and low *d'* generally act as generalist connectors, while species with high *d'* and low degree represent functional specialists or rare species.

Identification	FREQ	W.BET	W.CLO	Degree	*d'*
Andrenidae					
Oxaea flavescens	18	0.012	0.011	5	0.607
Apidae					
Ancylocelis nigricornis	3	0.000	0.004	2	0.486
Ancylocelis romeroi	10	0.000	0.008	2	0.870
Apis mellifera	224	0.161	0.016	22	0.710
Arhysoceble sp.	1	0.000	0.002	1	0.321
Bombus (*Fervidobombus*) *brevivillus*	24	0.007	0.013	8	0.324
Bombus (*Fervidobombus*) *morio*	31	0.122	0.015	7	0.455
Bombus (*Fervidobombus*) *pauloensis*	18	0.006	0.011	7	0.437

Centris (*Aphemisia*) *mocsary*	1	0.000	0.000	1	1.000
Centris (*Centris*) *aenea*	1	0.000	0.002	1	0.000
Centris (*Centris*) *flavifrons*	1	0.000	0.002	1	0.329
Centris (*Centris*) *nitens*	3	0.000	0.003	3	0.684
Centris (*Centris*) *spilopoda*	1	0.000	0.002	1	0.365
Centris (*Hemisiella*) *tarsata*	5	0.000	0.006	3	0.207
Centris (*Heterocentris*) *analis*	1	0.000	0.002	1	0.000
Centris (*Melacentris*) *obsoleta*	1	0.000	0.002	1	0.000
Centris (*Melacentris*) sp.1	2	0.000	0.004	1	0.142
Centris (*Odontoxys*) *auriger*	1	0.000	0.002	1	0.000
Centris (*Odontoxys*) *flammigera*	1	0.000	0.002	1	0.000
Centris (*Odontoxys*) *violacea*	1	0.000	0.000	1	1.000
Centris (*Trachina*) *fuscata*	7	0.000	0.008	2	0.388
Centris (*Trachina*) sp.1	1	0.000	0.002	1	0.000
Centris (*Xanthemisia*) *lutea*	5	0.000	0.007	2	0.197
Centris (*Xanthemisia*) sp.1	4	0.000	0.006	2	0.218
Ceratina (*Ceratinula*) *minima*	17	0.001	0.010	14	0.372
Ceratina (*Crewella*) *gossypii*	38	0.034	0.012	22	0.380

Ceratina (*Crewella*) *paraguayensis*	4	0.000	0.006	3	0.174
Ceratina (*Neoclavicera*) sp.1	13	0.000	0.009	9	0.548
Ceratina sp.6	2	0.000	0.003	1	0.593
Ctenioschelus goryi	1	0.000	0.002	1	0.000
Doeringiella (*Pseudopeolus*) *carinata*	1	0.000	0.002	1	0.000
Epicharis (*Epicharana*) *flava*	1	0.006	0.008	4	0.525
Epicharis (*Epicharis*) *bicolor*	2	0.000	0.004	2	0.100
Epicharis (*Epicharitides*) *iheringi*	6	0.000	0.002	1	0.500
Epicharis (*Triepicharis*) *analis*	10	0.000	0.007	4	0.655
Eufriesea sp.1	5	0.000	0.007	1	0.276
Eufriesea sp.2	1	0.000	0.002	1	0.000
Euglossa (*Euglossa*) *securigera*	1	0.000	0.002	1	0.206
Eulaema (*Apeulaema*) *nigrita*	1	0.000	0.002	1	0.365
Exomalopsis (*Exomalopsis*) *analis*	13	0.000	0.010	9	0.373
Exomalopsis (*Exomalopsis*) *auropilosa*	2	0.000	0.002	2	0.659
Exomalopsis (*Exomalopsis*) *fulvofasciata*	19	0.011	0.011	14	0.339
Exomalopsis (*Exomalopsis*) *minor*	7	0.000	0.008	4	0.406

Exomalopsis (*Exomalopsis*) *tomentosa*	34	0.026	0.012	20	0.284
Exomalopsis (*Exomalopsis*) *ypiranguensis*	3	0.000	0.005	1	0.686
Gaesischia (*Gaesischiopsis*) *belophora*	4	0.000	0.004	3	0.287
Geotrigona mombuca	2	0.000	0.004	2	0.183
Hopliphora velutina	1	0.000	0.002	1	0.000
Leurotrigona muelleri	1	0.000	0.002	1	0.321
Melipona (*Melikerria*) *quinquefasciata*	2	0.000	0.004	1	0.211
Melissodes (*Ecplectica*) *sexcincta*	2	0.000	0.003	2	0.383
Melissoptila richardiae	11	0.008	0.009	5	0.468
Mesoplia rufipes	1	0.000	0.002	1	0.206
Monoeca mourei	5	0.001	0.005	4	0.497
Monoeca pluricincta	8	0.004	0.007	4	0.336
Monoeca schizacantha	1	0.000	0.002	1	0.409
Paratetrapedia punctata	31	0.058	0.012	15	0.362
Paratrigona lineata	244	0.440	0.016	44	0.464
Partamona cf. *combinata*	7	0.000	0.008	3	0.394
Rhathymus unicolor	2	0.000	0.002	2	0.426

Scaptotrigona depilis	6	0.000	0.005	4	0.545
Tetragona clavipes	18	0.022	0.010	14	0.427
Tetrapedia diversipes	1	0.000	0.002	1	0.500
Tetrapedia sp.1	1	0.000	0.002	1	0.450
Tetrapedia tereza	5	0.000	0.005	4	0.490
Trigona hyalinata	2	0.000	0.004	1	0.915
Trigona spinipes	80	0.035	0.014	20	0.642
Trigonisca intermedia	3	0.000	0.005	3	0.644
Trigonisca meridionalis	1	0.000	0.002	1	0.664
Tropidopedia flavolineata	1	0.000	0.002	1	0.500
Tropidopedia punctifrons	3	0.000	0.005	3	0.325
Xanthopedia aff. *larocai*	2	0.000	0.004	2	0.333
Xylocopa (*Nanoxylocopa*) *ciliata*	8	0.000	0.007	6	0.427
Xylocopa (*Stenoxylocopa*) *nogueirai*	1	0.000	0.002	1	0.626
Colletidae					
Colletes meridionalis	3	0.000	0.004	2	0.485
Halictidae					
Augochloropsis smithiana	14	0.001	0.009	12	0.463

Augochloropsis sp.2	4	0.000	0.005	4	0.457
Augochloropsis sp.3	3	0.000	0.005	2	0.525
Augochloropsis sp.4	1	0.000	0.002	1	0.664
Augochloropsis sp.5	2	0.000	0.004	2	0.285
Augochloropsis sp.6	2	0.000	0.002	2	0.514
Augochloropsis sp.8	1	0.000	0.002	1	0.247
Augochloropsis sp.9	4	0.000	0.006	4	0.497
Ceratalictus clonius	15	0.000	0.010	12	0.223
Lasioglossum (*Dialictus*) sp.1	26	0.022	0.011	10	0.524
Lasioglossum (*Dialictus*) sp.2	2	0.000	0.004	1	0.420
Lasioglossum (*Dialictus*) sp.3	2	0.000	0.002	2	0.457
Lasioglossum (*Dialictus*) sp.5	2	0.000	0.002	2	0.559
Pseudagapostemon sp.	1	0.000	0.002	1	0.069
Pseudagochlora graminea	1	0.000	0.002	1	0.626
Rhinocorynura crotonis	2	0.000	0.004	1	0.463
Rhinocorynura inflaticeps	5	0.000	0.007	3	0.401
Temnosoma sp.	1	0.000	0.002	1	0.000
Thectochlora cf. *alaris*	5	0.000	0.006	4	0.154

Megachilidae					
Coelioxys (*Glyptocoelioxys*) sp.1	1	0.000	0.002	1	0.465
Coelioxys sp.2	2	0.000	0.004	1	0.529
Coelioxys tolteca	1	0.000	0.002	1	0.465
Epanthidium aureocitum	4	0.000	0.006	3	0.299
Epanthidium tuberculatum	1	0.000	0.002	1	0.386
Grafanthidium sp.	3	0.000	0.005	1	0.670
Larocanthidium bilobatum	1	0.000	0.002	1	0.566
Larocanthidium fasciatum	5	0.000	0.007	5	0.245
Megachile (*Austrosarus*) *frankieana*	8	0.000	0.007	6	0.290
Megachile (*Leptorachis*) *aureiventris*	5	0.000	0.005	5	0.448
Megachile (*Pseudocentron*) *rubricatus*	13	0.006	0.009	9	0.345
Megachile (*Pseudocentron*) sp.1	6	0.017	0.006	4	0.464
Megachile (*Pseudocentron*) sp.2	4	0.000	0.005	3	0.365
Megachile (*Pseudocentron*) sp.3	1	0.000	0.002	1	0.329
Megachile (*Pseudocentron*) sp.4	2	0.000	0.004	1	0.142
Megachile (*Pseudocentron*) sp.5	1	0.000	0.002	1	0.711

Table S2. Structural parameters and statistical significance of plant-pollinator interaction networks for the annual network and climatic periods. For each network, the observed values of topological metrics are presented, compared to estimates generated by null models. The columns comprise: the observed values; the mean and standard deviation of the null models; the t-statistic value and the p-value. Observed values that differ significantly from what would be expected by chance ($p < 0.05$) indicate deterministic biological processes structuring the interactions. The metrics include NODF, modularity, weighted connectance, H_2’, niche overlap and robustness of bees (HL) and plants (LL). The null model analysis was performed using the algorithm Patefield, preserving the abundance margins of the original matrix.

Metrics	Observed	Mean null	Std_null	p-value
Annual				
NODF	18.011	31.622	1.73	< 0.001
Modularity	0.546	0.219	0.006	< 0.001
w.connectance	0.04	0.079	0.002	< 0.001
H2	0.423	0.113	0.007	< 0.001
niche.overlap.HL	0.091	0.116	0.008	< 0.002
niche.overlap.LL	0.109	0.269	0.017	< 0.001
robustness.HL	0.693	0.726	0.007	< 0.001
robustness.LL	0.656	0.697	0.005	< 0.001
Rain-dry				
NODF	19.296	30.909	2.627	< 0.001
Modularity	0.623	0.36	0.019	< 0.001
w.connectance	0.054	0.086	0.004	< 0.001
H2	0.48	0.135	0.016	< 0.001
niche.overlap.HL	0.175	0.175	0.017	0.952
niche.overlap.LL	0.129	0.258	0.034	< 0.001
robustness.HL	0.64	0.685	0.009	< 0.001
robustness.LL	0.581	0.631	0.008	< 0.001

Dry				
NODF	18.962	37.985	3.07	< 0.001
Modularity	0.552	0.283	0.017	< 0.001
w.connectance	0.0742	0.103	0.0023	< 0.001
H2	0.509	0.122	0.016	< 0.001
niche.overlap.HL	0.128	0.212	0.024	< 0.002
niche.overlap.LL	0.132	0.43	0.051	< 0.001
robustness.HL	0.687	0.72	0.011	< 0.001
robustness.LL	0.595	0.632	0.009	< 0.001
Dry-rain				
NODF	13.305	27.426	2.519	< 0.001
Modularity	0.557	0.395	0.029	< 0.001
w.connectance	0.073	0.095	0.0024	< 0.001
H2	0.485	0.149	0.023	< 0.001
niche.overlap.HL	0.083	0.144	0.018	< 0.001
niche.overlap.LL	0.158	0.351	0.048	< 0.001
robustness.HL	0.663	0.696	0.01	< 0.021
robustness.LL	0.534	0.567	0.008	< 0.004
Rain				
NODF	23.493	32.113	2.361	< 0.001
Modularity	0.521	0.396	0.019	< 0.001
w.connectance	0.092	0.116	0.002	< 0.001
H2	0.359	0.11	0.004	< 0.001
niche.overlap.HL	0.123	0.167	0.011	< 0.001
niche.overlap.LL	0.105	0.162	0.015	< 0.001
robustness.HL	0.666	0.696	0.006	< 0.001
robustness.LL	0.637	0.68	0.007	< 0.001

Table S3. Generalized Linear Model (GLM) coefficients for network metrics between climatic periods. The coefficients represent changes in network structure following the chronological order of climatic periods, using the Rain-dry transition period (Intercept) as a reference. For the other periods (Dry: Dry; DryRain: Dry-Rain Transition; Rain: Rain), the Estimate values represent the deviation from the Intercept mean. The Standard Error (Std. Error), the t-statistic, and the associated probability (Pr(>|t|)) are presented. Values of P < 0.05 indicate that the metric in that specific period differs significantly from the reference period.

Metrics/Variable	Estimate	Std. Error	t value	p
Modularidade				
(Intercept)	0.650	0.032	20.292	0.0000
Dry	-0.073	0.045	-1.600	0.1355
DryRain	-0.068	0.045	-1.490	0.1620
Rain	-0.035	0.045	-0.773	0.4547
NODF				
(Intercept)	2.486	0.174	14.315	0.0000
Dry	0.130	0.246	0.528	0.6071
DryRain	0.134	0.246	0.547	0.5946
Rain	0.355	0.246	1.445	0.1740
H2				

(Intercept)	0.520	0.069	7.559	0.0000
Dry	0.060	0.097	0.617	0.5489
DryRain	0.083	0.097	0.848	0.4130
Rain	-0.088	0.097	-0.899	0.3861
Niche overlap HL				
(Intercept)	-1.984	0.202	-9.815	0.0000
Dry	-0.179	0.286	-0.625	0.5437
DryRain	-0.223	0.286	-0.781	0.4502
Rain	0.000	0.286	0.000	1.0000
Niche overlap LL				
(Intercept)	0.123	0.016	7.731	0.0000
Dry	0.018	0.022	0.781	0.4499
DryRain	0.053	0.022	2.343	0.0372
Rain	-0.025	0.022	-1.116	0.2864
Robustness HL				

(Intercept)	-0.523	0.037	-14.028	0.0000
Dry	0.061	0.053	1.163	0.2674
DryRain	0.041	0.053	0.783	0.4487
Rain	0.049	0.053	0.936	0.3677
Robustness LL				
(Intercept)	0.515	0.016	31.415	0.0000
Dry	0.030	0.023	1.294	0.2200
DryRain	-0.040	0.023	-1.725	0.1101
Rain	0.025	0.023	1.078	0.3021
W.connectance				
(Intercept)	-2.690	0.106	-25.386	0.0000
Dry	-0.101	0.150	-0.676	0.5121
DryRain	0.193	0.150	1.288	0.2221
Rain	0.240	0.150	1.602	0.1351

Table S4. Pairwise PERMANOVA comparisons of taxonomic composition and functional trait abundance between climatic periods. Values represent F statistics and corrected significance (P-adj) for differences between pairs of climatic periods (e.g., Dry vs. Rainy). The analyses were divided into: (1) Bee species composition; (2) Plant species composition; (3) Abundance of bee functional traits; and (4) Abundance of plant functional traits. Dissimilarity distances were calculated using Bray-Curtis. Values of $P < 0.05$ indicate that communities or functional spaces are significantly different between the compared periods.

Plants Species	F	R²	p_adjusted
Dry - Dry_rain	5.468335	0.214711	**0.006**
Dry - Rain	7.419736	0.280841	**0.006**
Dry - Rain_dry	3.757082	0.158146	**0.006**
Dry_rain - Rain	3.477999	0.154729	**0.006**
Dry_rain - Rain_dry	4.985817	0.199546	**0.006**
Rain - Rain_dry	5.215455	0.215377	**0.006**
Bees Species			
Dry - Dry_rain	4.506403	0.183887	**0.006**
Dry - Rain	5.224807	0.21568	**0.006**
Dry - Rain_dry	3.641241	0.154021	**0.01**

Dry_rain - Rain	3.196288	0.144001	**0.006**
Dry_rain - Rain_dry	2.752004	0.120957	**0.006**
Rain - Rain_dry	2.625665	0.121414	**0.006**
Plant traits			
Rain - Dry_rain	2.159581	0.102062	0.456
Rain - Rain_dry	1.655445	0.080146	0.888
Rain - Dry	2.374873	0.111106	0.342
Dry_rain - Rain_dry	4.299346	0.176933	**0.03**
Dry_rain - Dry	6.412394	0.24278	**0.006**
Rain_dry - Dry	0.638977	0.03096	1
Bee traits			
Rain -Dry_rain	2.071511	0.098309	0.75
Rain -Rain_dry	0.957176	0.047961	1
Rain - Dry	3.939261	0.171726	0.162
Dry_rain - Rain_dry	2.164453	0.097654	0.768

Dry_rain - Dry	4.298536	0.176905	0.192
Rain_dry - Dry	1.238375	0.058308	1

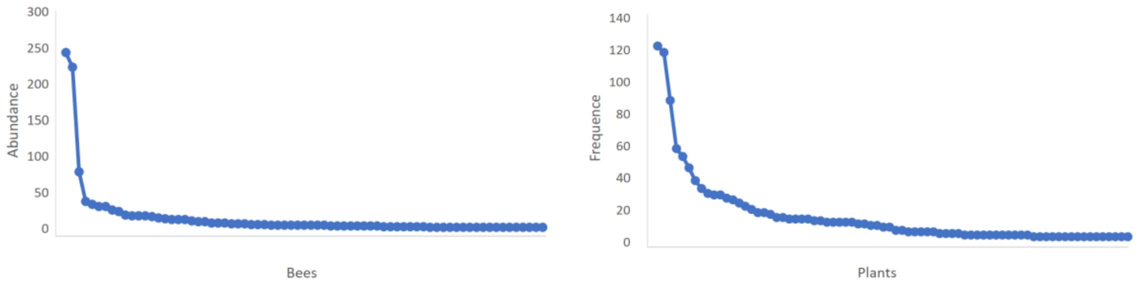

Figure S1. Rank-Abundance curves for the sampled bee and plant communities. On the vertical axis, the absolute abundance for bees (left) and the frequency of interactions for plants (right) are shown. On the horizontal axis, species are ordered from most abundant to least abundant.

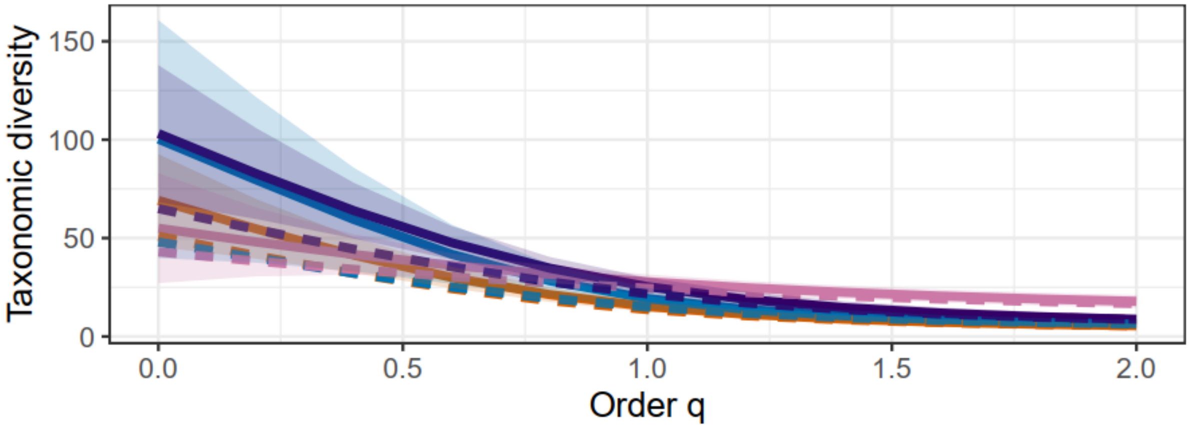

Figure S2. Taxonomic diversity profiles using Hill numbers for bee communities in different climate periods. The graph shows estimated diversity as a function of order q. When q = 0, the value corresponds to species richness (S), q = 1 represents the exponential of the Shannon index, and q = 2 corresponds to the inverse of the Simpson index. The solid lines represent asymptotic estimates, while the shaded areas indicate 95% confidence intervals.

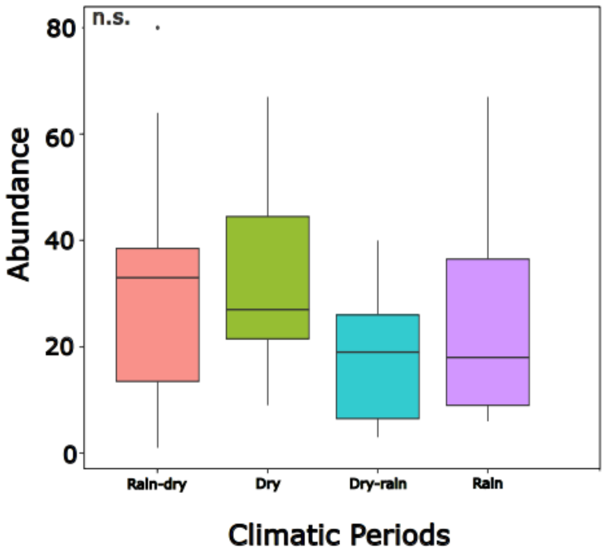

Fig. S3. Average relative abundance of bee species by climate period (rain–dry transition, dry, dry–rain transition, and rain) in the Cerrado. Each boxplot represents the variation in abundance calculated monthly per plot, with each climate period consisting of three months. The horizontal lines inside the boxes indicate the median, the lower and upper edges of the boxes represent the first and third quartiles, respectively, and the lower and upper whiskers indicate the minimum and maximum values. The differences between climatic periods were not significant, as indicated by ANOVA (F = 1.92; p = 0.1235).

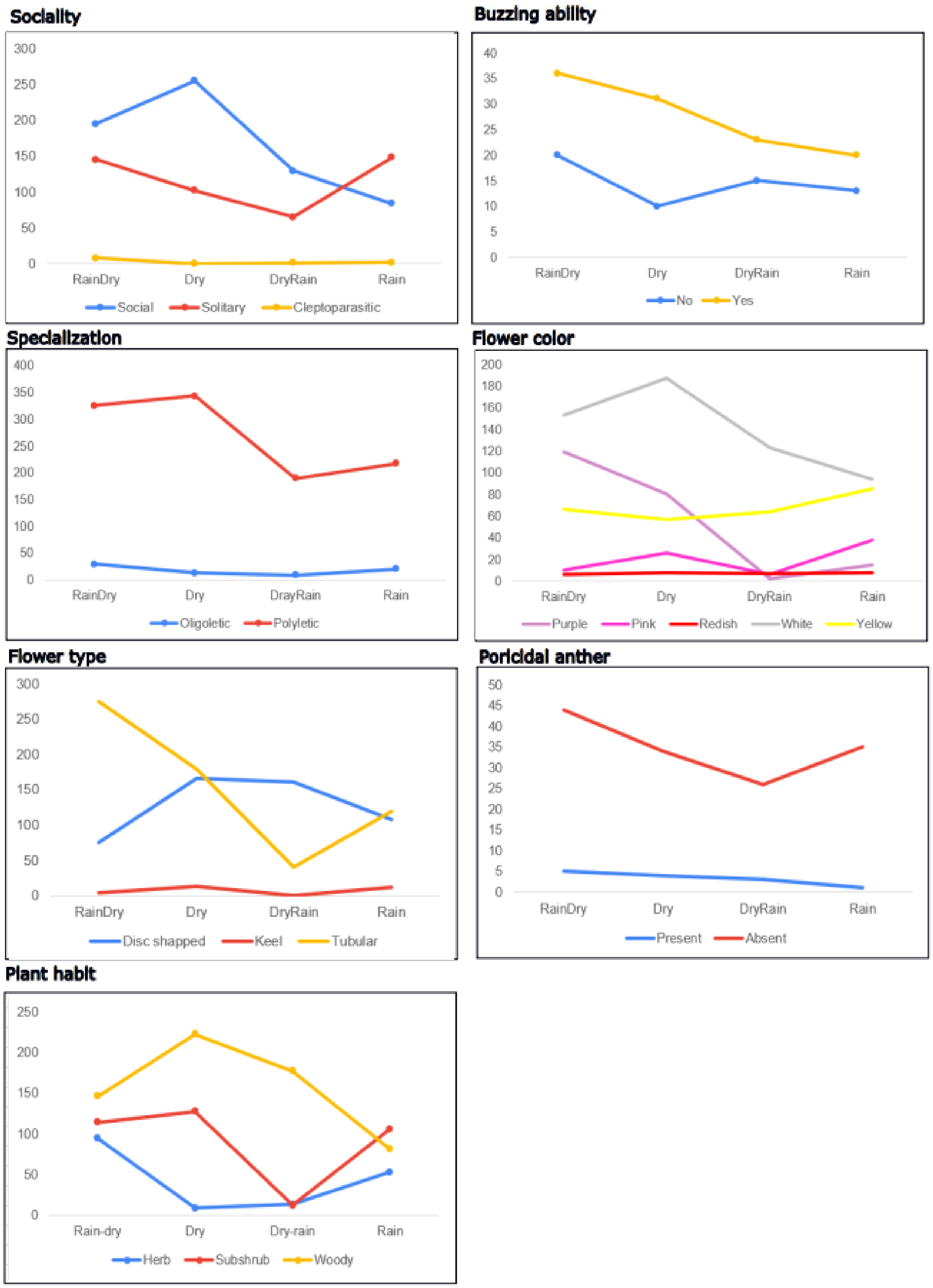

Fig S4. Frequency distribution of functional traits of bees and plants across climatic periods. The lines represent the relative abundance of each functional trait category for each climatic period.

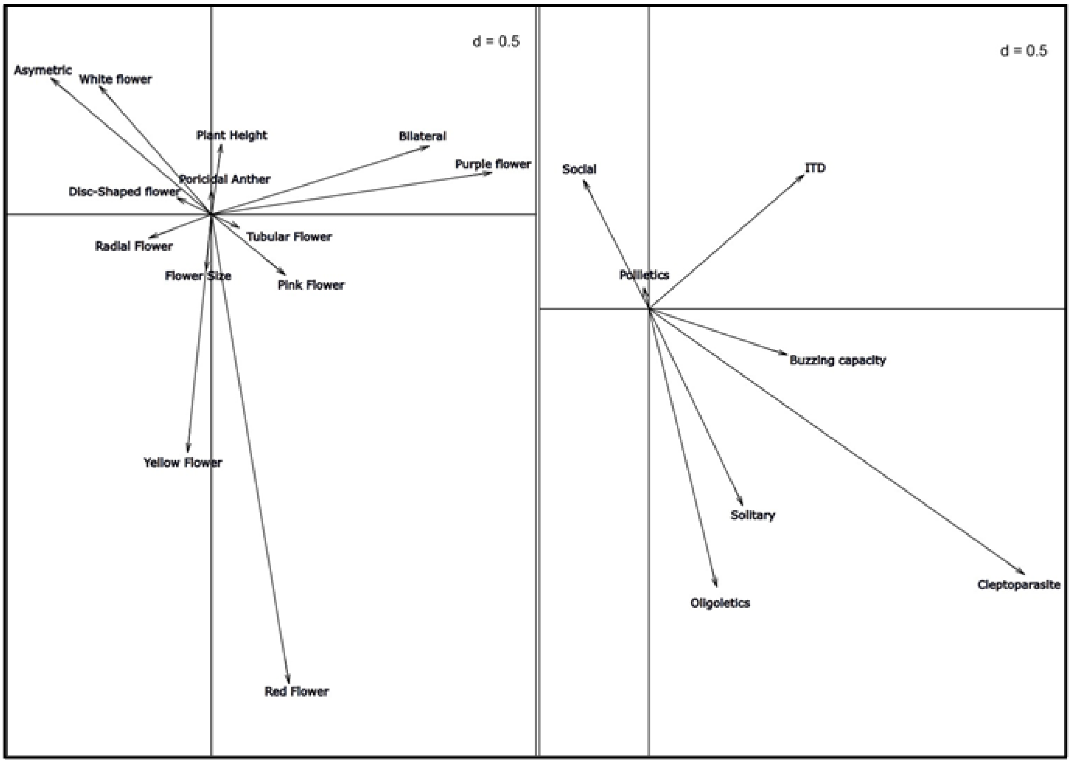

Figure S5.Relationship between the functional traits of plants and bees. Ordering of plant traits (A) and bee traits (B) in the RLQ biplot space, where the size of the vectors represents the contribution of the trait to community structure and the direction indicates a positive relationship between traits, while the opposite indicates a negative relationship. d = 0.5 indicates the scale unit of the axes.

Chapter 2

Floral traits associated to different foraging strategies in stingless bees

Abstract

Eusocial bees are important pollinators of tropical areas, including forest trees and agricultural crops, and are economically and culturally important throughout the tropical Americas. Stingless bees are often classified as generalist pollinators, but the mechanisms underlying their resource use patterns remain poorly understood, particularly in highly seasonal ecosystems. There are several factors that influence which species of plants bees will favor when foraging for food, including abundance of the species in the area, distance from the nest, flowering phenology, and characteristics of the flower. Considering this, we investigate how floral characteristics shape plant-bee interactions involving stingless bees in the Brazilian Cerrado. Using resources collected directly from the nests of bees kept in breeding boxes and identifying the pollen and honey stored in the nests, we mapped the plant species visited by three species of stingless bees: *Tetragonisca angustula*, *Scaptotrigona postica* and *Melipona rufiventris*. Based on this information, we investigated the functional traits of the most visited plant species in order to assess whether there is a preferential pattern of floral resource use. Our results show that, despite interacting with a wide range of plant species, stingless bees concentrate their foraging activity on a subset of floral resources. This selective use of resources is associated with floral traits such as symmetry, color, and resource. Differences in body size and foraging strategies among stingless bees further modulate interaction patterns, with smaller species exploiting a broader range of floral types and larger species showing more constrained interaction patterns. Social behaviors, such as recruitment communication, amplify these patterns by reinforcing the use of highly rewarding and temporally abundant resources. By highlighting the role of floral traits and social foraging behavior, this chapter provides a mechanistic understanding of how stingless bees structure their interactions within plant–pollinator networks

Key-words: stingless bees, floral traits, resource use, foraging behavior, generalism.

Introduction

Bees are among the main pollinators of terrestrial ecosystems, playing a central role in maintaining plant diversity and the functioning of natural systems, especially in the Neotropical region, where dependence on biotic pollination is high (Ollerton et al. 2011; Potts et al. 2016, Tong, Ye-zu et al., 2023). In this context, social bees stand out for their high contribution to pollination flows, due to their abundance and intense foraging activity (Maia et al., 2019; Klein et al. 2007). In Brazil, the main tribes of social bees include the native Bombini, and Meliponini and the exotic Apini represented by the honeybee *Apis mellifera*. Meliponini, also known as stingless bees, constitute the most diverse group of social bees in the world, with the highest concentration of species in the Neotropical region, especially in Brazil (Grüter 2020).

Stingless bees are major pollinators of tropical areas, including forest trees and crops, and have economic and cultural importance in all tropical Americas (Martins et al., 2025; Silva & Paz, 2012). In addition to their ecological importance, these bees are economically and socioculturally relevant, especially in the context of meliponiculture and environmental education initiatives (Silva & Paz, 2012). They visit more than a hundred plant species in a range varying from hundreds of meters to 2 km from their nests (Bueno et al 2023). Due to the permanence of their nests and the high number of individuals per colony, social bees are traditionally considered highly generalist, with a wide trophic niche breadth. This generalism is associated with the need to collect and store large amounts of floral resources to maintain the colony over time, especially during periods of scarcity, which results in the exploitation of a wide diversity of plant species (Roubik 2023, Roubik 1989). We question the extent of this generalist behavior and suggest the existence of a pattern of preferred flowers, usually associated with open, small, whitish flowers with abundant resources and that flower in mass, i.e. display a huge number of flowers over a short period of time (Ramalho 2004).

Generalism can coexist with preference patterns, expressed by a greater intensity of use of certain floral resources (Vázquez et al., 2009; Blüthgen et al., 2006). There are several factors that influence which species of plants bees will favor when foraging for food, including abundance of the species in the area, distance from the nest, flowering phenology, and characteristics of the flower (i.e. pollination syndrome, Dellinger, 2020). The choice of flowers may be related to the quantity and quality of the resource offered, as well as its accessibility, so that some plant species concentrate much of the pollinator foraging effort, while others are exploited more sporadically (Fenster et al. 2004). Thus, preference emerges not as exclusivity, but as disproportionate use of resources within a broad spectrum of interactions. Because these factors depend on the flora of the region and period of the year, it is difficult to compare species preferences across studies conducted in different locations.

Stingless bees are a particularly suitable model for investigating these patterns due to their high ecological diversity, wide variation in nesting behaviors, and occupation of different habitats (Grüter 2020). Although many species are associated with forest environments, they can forage in open areas and travel long distances in search of resources (Martins et al. 2023). They are usually considered generalists (Bueno et al. 2023) but, as a general rule, they seem to prefer white flowers with a dish-like shape and abundant resources (Ramalho 2004).

Given this scenario, the objective of the present study is to investigate whether stingless bees show some preference for certain sets of floral characteristics. To this end, we evaluated different floral attributes, such as color, plant habit, and resource type, of 30 plants mostly visited by three stingless bee species in an area of Cerrado vegetation, which were identified through DNA metabarcoding of pollen stored in nests. We hypothesized that stingless bees prefer hermaphroditic or monoecious small-whitish protandrous flowers with abundant resources, flowers in mass (large amounts of flowers over a short period of time) and a high pollen supply, possibly associated with tree species. We also hypothesized that this pattern can change depending on body size and foraging behavior presented by different stingless bees: smaller species can visit a broader range of flowers, but only the largest can efficiently visit, for example, buzz-pollinated flowers; forage recruiters, like *Melipona*, will be more associated to canopy mass flowering trees. In this sense we aim to not classify plants associated with stingless bees, but to evidence which traits matter most regarding stingless bees flower choice (Ollerton et al. 2009).

Methods

Study area

The study was conducted at the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE/RECOR) (15°56′41″ S, 47°53′07″ W). Together with the Brasília Botanical Garden and the Experimental Farm of the University of Brasília, the reserve comprises the Environmental Protection Area of the Gama and Cabeça de Veado river basins (APA). RECOR covers approximately 1,931ha and includes eight of the eleven vegetation types of the Cerrado biome, ranging from open formations to gallery forests (IBGE, 2011). The regional climate is classified as tropical savanna (Aw, Köppen classification), with two well-defined seasons: a dry and cooler winter and a hot and rainy summer. Fieldwork was carried out from September 2019 to December 2020, encompassing the transition from the dry to the rainy season, a period characterized by intense flowering, particularly of woody species (Mantovani & Martins, 1988; Oliveira & Gibbs, 2000). The selected vegetation type was dense savanna woodland (cerradão), since these three species usually nest in pre-opened cavities, found in forested regions (Silva et al., 2013).

Installing the nests

In this study, 18 nests belonging to three species of stingless bees *Scaptotrigona postica* (8), *Melipona rufiventris* (3), and *Tetragonisca angustula* (7), were installed in the field and maintained from July 2019 to December 2020. Although the nests were established in July, sampling began in September 2019 to allow colonies sufficient time to acclimate and collect resources in the new area. Every 15 days, pollen and nectar samples were collected from each nest and stored for subsequent identification of plant species using metabarcoding, enabling the reconstruction of the floral resources visited by the bees. The Meliponini species were selected because they differ markedly in body size: *T. angustula* is the smallest species (intertegular distance, ITD = 1.1 mm), *Scaptotrigona postica* is intermediate in size (ITD = 1.7 mm), and *M. rufiventris* is the largest (ITD = 2.6 mm). All three species are commonly managed by stingless beekeepers, which facilitated access to the colonies and made them suitable model species for this study. Nests were installed within the same area, with a minimum distance of 1 m between them, ensuring that colonies were exposed to similar surrounding floral resources. Each nest was mounted approximately 1 m above ground on wooden posts fixed firmly into the soil. The posts were inserted into pre-dug holes and stabilized with compacted soil. A wooden support structure attached to the top of each post allowed nests to be secured using screws and wire. To protect colonies from direct sunlight and rainfall, each nest was covered with a small roof.

Pollen and honey sampling

Each nest was assigned a unique identification code, and all samples were labeled accordingly. Resource sampling was carried out every 15 days. During each sampling event, nest boxes were carefully opened, and pollen and nectar (pot-honey) were collected using a small sterilized metal spatula, with a separate spatula used for each nest to avoid cross-contamination. To ensure that the collected pollen originated exclusively from the study area and not from resources gathered prior to nest installation, only recently collected pollen pots were sampled. These were identified based on the lighter color and softer texture of the wax. Alternatively, pollen was collected from pots that were completely full and still open, indicating that they were actively being provisioned and had not yet been sealed. The same criteria were applied to pot-honey sampling, with care taken to collect only freshly stored resources. All samples were placed in sterile Falcon tubes, transported to the laboratory, and stored under refrigeration until DNA extraction. Sample preparation for DNA metabarcoding involved weighing and macerating the material with liquid nitrogen. DNA extraction from honey samples was performed using the NucleoSpin Food kit from Macherey-Nagel (Düren, Germany), while pollen samples were processed using the NucleoSpin Plant II kit from Macherey-Nagel (Düren, Germany). ITS2 region was amplified, normalized, quantified and sequenced using Illumina according to the protocol described in Sickel et al. (2015). Sequencing analysis and the determination of Amplicon Sequence Variants (ASV) was performed using the bioinformatic pipeline available at https://github.com/chiras/metabarcod ing_ pipeline and the results published in our previous paper (Martins et al. 2023).

Functional Traits.

To characterize the plants visited by bees, we selected the 30 most visited plant species based on sequence frequency. We chose floral characteristics considered relevant to plant-bee interactions, related to attractiveness and the type of resource offered by flowers (Garibaldi et al., 2015; Peralta et al., 2020). We considered floral symmetry, as it is associated with different levels of generalization or specialization of flowers, in addition to floral color and the type of resource available. In addition, we evaluated plant habits (herbaceous, subshrub, or arboreal). Plants that were not identified at the species level had their characteristics disregarded. The characteristics of the plants were taken from the Flora and Funga do Brasil and Specieslink databases, following methods presented in Chapter 1.

Results

A total of 104 plant species belonging to 39 families and 81 genera were visited by bees. The family with the highest number of species was Myrtaceae with 14 species, followed by Fabaceae (8), Euphorbiaceae (7), and Asteraceae, Malpighiaceae, and Melastomataceae, all with 6. Of the 104 plant species visited, 28 were identified only at the genus level and 4 at the family level, so that 72 species were determined. The bee species that visited the highest number of plants was *Tetragonisca angustula* (71), followed by *Scaptotrigona postica* (52) and *Melipona rufiventris* (49) (Fig. 1), with 2 species shared between the three species.

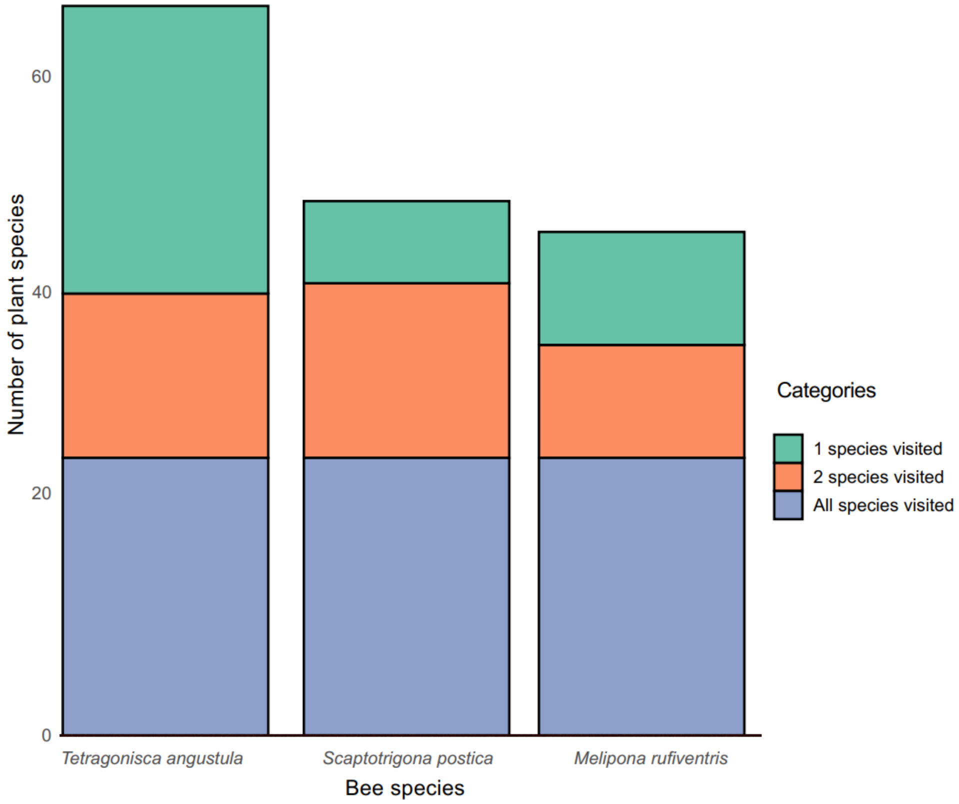

Figure 1 – Frequency histogram showing the number of plant species visited by each bee species. The different colors represent plant species shared by all three bee species, visited by two species, and unique plant species visited by only one species.

The 30 plant species most frequently used by bees were distributed across 16 plant families. Myrtaceae was the most visited family, comprising eight species, followed by Melastomataceae and Euphorbiaceae, each represented by three species (Table 1). Among these 30 taxa, four were identified to the genus level and one to the family level. Only species identified at the species level were included in trait analyses (n=25), as floral traits are species-specific and may vary substantially among genera within speciose families. Regarding floral morphology, 20 species had open flowers and four had tubular flowers, indicating that most species impose relatively low restrictions on resource accessibility. Half of the species exhibited white flowers, followed by green and yellow flowers, and 22 species lacked nectar guides. In terms of floral rewards, 11 species offered pollen only, 10 provided both pollen and nectar, and the remaining species also offered alternative resources such as oils or resins. Finally, regarding plant habit, 17 species were trees and eight were shrubs.

Table 1. List of the 30 species and morphotypes of plants most visited by the stingless bee species *Tetragonisca angustula*, *Scaptotrigona postica*, and *Melipona rufiventris*. The floral resources abbreviations represent P = pollen, PN = pollen and nectar, PO = pollen and oil, PNR = pollen, nectar, and resin. Plants that have not been identified to species level are marked with NA.

Plant ID	**Flower type**	**Major color**	**Nectar guides**	**Rewards**	**Habit**
Anacardiaceae					
Toxicodendron succedaneum	Open	Green	Absent	PNR	Tree
Tapirira guianensis	Tubular	Yellow	Absent	PN	Tree
Asteraceae					
Baccharis dracunculifolia	Tubular	Cream	Absent	PN	Shrub
Chloranthaceae					
Hedyosmum brasiliense	Open	Green	Absent	P	Tree
Clusiaceae					
Clusia criuva	Open	White	Absent	PR	Tree
Euphorbiaceae					
Mabea fistulifera	Tubular	Reddish	Absent	PN	Tree
Croton conduplicatus	Open	White	Absent	PN	Shrub
Maprounea guianensis	Tubular	White	Absent	P	Tree
Fabaceae					
Stryphnodendron spc	NA	NA	NA	NA	NA

Loranthaceae					
Struthanthus/Psittacanthus spc	NA	NA	NA	NA	NA
Malpighiaceae					
Byrsonima basiloba	Open	Yellow	Absent	PO	Shrub
Byrsonima pachyphylla	Open	Yellow	Absent	PO	Tree
Melastomataceae					
Leandra polystachya	Open	White	Absent	P	Shrub
Miconia hirtella	Open	White	Absent	PN	Tree
Miconia leucocarpa	Open	White	Absent	P	Tree
Miconia stenostachya	Open	White	Absent	P	Shrub
Myrtaceae					
Blepharocalyx salicifolius	Open	White	Absent	P	Tree
Eucalyptus spc	NA	NA	NA	NA	NA
Myrcia guianensis	Open	White	Absent	P	Tree
Myrcia linearifolia	Open	White	Absent	P	Shrub
Myrcia pinifolia	Open	White	Absent	P	Shrub
Myrcia tomentosa	Open	White	Absent	P	Tree
Syzygium cumini	Open	White	Absent	PN	Tree
Myrtaceae spc	NA	NA	NA	NA	NA
Nyctaginaceae					
Guapira graciliflora	Open	Green	Absent	PN	Tree
Phyllanthaceae					
Richeria grandis	Open	Green	Absent	PN	Tree
Piperaceae					
Piper aduncum	NA	green	NA	P	Tree
Primulaceae					
Myrsine spc	NA	NA	NA	NA	NA
Rosaceae					
Rubus urticifolius	Open	White	Present	PN	Shrub
Sapindaceae					
Matayba guianensis	Open	White	Absent	PN	Tree

Discussion

Our results indicated that, although the three social bee species studied exhibit a broad dietary breadth, plant resources are not exploited homogeneously. Instead, a restricted subset of plant species concentrates most visits for pollen, nectar and other resources, suggesting the existence of preferences within an overall generalist foraging strategy. These frequently visited plants shared a suite of floral traits typically associated with generalized pollination systems, such as white coloration, open and radially symmetrical flowers, and the provision of easily accessible rewards, primarily pollen and nectar.

Floral color emerged as an important attribute structuring visitation patterns. The predominance of white-flowered species among the most frequently visited plants corroborates the results obtained in the first chapter of this dissertation, in which social bees were positively associated with white flowers. Tall tropical trees commonly bear small, light-colored and open flowers, a floral syndrome typically associated with pollination by generalist insects (Bawa et al. 1985; Delmas et al. 2019; Swart et al., 2023). This pattern contrasts with that observed for larger and solitary bees, which tend to be more strongly associated with zygomorphic flowers and more specialized floral architectures, as also documented in Chapter 1. The dominance of Myrtaceae species may be related to the relatively unspecialized floral morphology characteristic of Myrtaceae, which has small, white, polystemone flowers, offering abundant and easily accessible pollen, characteristics that are consistent with generalized pollination systems (Vasconcelos et al. 2018).

Despite their broad food spectrum, social bees visited some plant species much less frequently than others, indicating that resource availability and reward quantity likely modulate foraging decisions. Mass-flowering plants that offer large amounts of pollen and/or nectar tend to attract a disproportionate number of visits, especially when combined with recruitment behavior, which can quickly concentrate foraging effort in highly rewarding areas (Lindauer & Kerr, 1960; von Frisch, 1967; Grüter, 2020). This mechanism may also explain the higher visitation rates observed for tree species, as they typically produce large floral displays and, consequently, greater total resource availability compared to shrubs or herbs.

The predominance of flowers that present only pollen as reward or a combination of pollen and nectar among the most visited species further highlights the central role of pollen as a key resource for social bees. A preference for flowers with high-quality pollen has already been observed in bees of the genus Bombus (Vaudo et al., 2016) and of the subfamily Meliponini (Adler et al., 2025). Pollen is essential for larval development and colony maintenance, and its availability is often one of the main factors determining the foraging decisions of stingless bees.

Therefore, our findings corroborate the idea that generalist species have some degree of selectivity (Nicholls & Hempel de Ibarra 2017). In line with this perspective, our findings support the idea that generalism in social bees does not imply homogeneous use of floral resources. Instead, foraging patterns emerge from the combined effects of floral characteristics, resource availability, and social behavior, such as recruitment, which can rapidly concentrate foraging effort on a limited set of highly rewarding plant species.

Some plant families stand out as the most important floral sources for the three species in the area in the rainy season. Among the 20 most frequently found plant species in honey and pollen samples, they belong to the following families: Myrtaceae, Loranthaceae, Anacardiaceae, Phyllantaceae, Sapindaceae, Melastomataceae, Euphorbiaceae, Primulaceae, Nyctaginaceae, Rosaceae, Asteraceae, Malpighiaceae, Cloranthaceae, Piperaceae, corroborating findings forms several prior studies showing a preference of stingless bees for those families (e.g. Bueno et al. 2023, Ramalho 2004, Aleixo et al. 2017, Elliot et al. 2021). Those plant families are also common components of tropical flora (Flora and Funga do Brasil 2026), therefore, if Meliponini preference reflects a bias from general abundance or a particular set of traits presented by flowers of those plant families, it deserves further investigation.

From our data and literature knowledge (Ramalho 2004), we suggest that some patterns of floral exploitation by stingless bees exist, and we assume a "pollination syndrome" linked to these pollinators. We acknowledge the artificiality in syndromes classification in spite of their utility in understanding plant-pollinator evolution (Waser et al. 1996, Fenster et al. 2005). Plants in this "stingless bee syndrome" are usually hermaphroditic or monoecious, have small-whitish protandrous flowers with abundant pollen or nectar and, most importantly, flower in mass, i.e produce a large amount of flowers over a short period of time (Ramalho 2004). In the Atlantic Rainforest, woody plants account for up to 90% of total resources source for stingless bees, and these bees correspond to 80% of bees visiting the upper canopy stratum (Ramalho 2004). In Cerrado savanna, herbaceous plants showed higher importance for stingless bees (38%, against

22% shrubs and 26% trees), which reflects the savanna phytophysiognomy, where herbs are preponderant (Klink et al. 2020).

We intend to further develop the analyses presented in this chapter by comparing the plant species most frequently visited by stingless bees with those that were flowering during the same periods but were not visited. Throughout the study, systematic surveys of flowering plant species were conducted in the surroundings of the experimental area where the nests were installed. The next step will therefore be to contrast the functional traits of preferred versus non-visited plant species, allowing us to more explicitly identify the traits associated with floral selection and to disentangle preference from availability.

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Concluding remarks

This dissertation investigated how bees interact with floral resources in the Cerrado, integrating trait-based and network approaches to understand interaction dynamics and patterns of generalism and selectivity. By relating community-level patterns to species traits, the two chapters provide complementary insights into the mechanisms that structure plant-pollinator networks.

In Chapter 1, we showed that interactions between plants and bees may be shaped by two mechanisms: species turnover within networks across climatic periods, and trait-matching, which is an emergent property of the overall network. Some traits were matched, such as large bees and zygomorphic flowers, suggesting that different groups of pollinators follow distinct trait-matching rules within the same ecological context. We also found that the stability of interaction networks, despite temporal variation, is maintained by the turnover of functionally similar species. Furthermore, it is important to note that these observed patterns may be influenced in parallel by abundance, phenological overlap, and sampling artifacts that were not tested for comparison purposes. In Chapter 2, we saw that a wide variety of food does not imply homogeneous use of resources. Although stingless bees interact with many plant species, their foraging efforts are concentrated on a subset of them. This selective use of resources reflects the combined effects of floral characteristics, resource availability, and social behaviors such as recruitment communication.