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# Floral preferences of carpenter bees (Apidae: Xylocopini: *Xylocopa*) from Maranhão, Northeast Brazil

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**ABSTRACT**

The current study aimed to recognize the floral resources used by bees of the genus *Xylocopa* in transition physiognomies. We compiled the information available from biological collections and analyzed metrics of dystrophic interaction. We listed 2547 records of *Xylocopa* in flowers, across twelve identified bee species. The bees were collected from 109 plant species, belonging to 77 genera and 36 families. An interaction network was constructed based on 193 interactions. In which there was a significant correlation between the abundance of bees collected and the richness of plants visited. The most generalist bees were *X. cearensis* and *X. frontalis*, and the plants with the most records were *Chamaecrista hispidula* and *C. ramosa*. Significant seasonality was observed in the total number of individuals. On the other hand, there was a weak similarity among *Xylocopa* species according to plant species, despite the clear relationship of the bees according to physiognomies. The interaction network proved to be highly nested, indicating a functional partitioning that allows several species to occur in the same environment. The contribution made by the current work for its regional scope stands out, dealing with areas that have distinct characteristics.

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Solitary bees; pollination; plant-pollinator; interaction network; ecotone

## Introduction

Large carpenter bees, also known as mamangava bees, are represented by the genus *Xylocopa* Latreille, 1802 (Michener 2007). These bees are of medium to large size, usually nest in dead wood, and are characterized by solitary behavior with cooperatively breeding (Gerling et al. 1989; Danforth et al. 2019). The species in this genus are widely distributed around the world, with the greatest diversity found in tropical zones (Hurd & Moure 1963), with approximately 480 species distributed in 31 subgenera (Plant & Paulus 2016; Lucia et al. 2020).

*Xylocopa* species are dependent on the floral resources and nesting substrates (Hurd 1978; Sazima & Sazima 1989). Their body size, life cycle and long foraging distances make them essential pollinators (Silva et al. 2019; Harano & Hrncir 2023), especially for botanical species that produce large flowers, such as *Bertholletia* spp (Cavalcante et al. 2023) and *Passiflora* spp (Barrera et al. 2021).

Because of this service provision, especially with respect to the productive increase in crops with high economic value in Brazil (Giannini et al. 2015), some studies have been conducted to research and conserve large carpenter bees, such as *X. frontalis* and *X. grisescens* (Pereira & Garófalo 2010; Giannini et al. 2020; Araújo et al. 2021; Farias-Silva & Freitas 2021; Costa et al. 2022). These and all other species of the genus, are considered polyletic, meaning that they potentially visit a wide variety of plant species in search of food (Keasar 2010; Lucia et al. 2017; Villamizar et al. 2020).

In Northeast Brazil, several works have identified plant species used by *Xylocopa* in dune and restinga areas (Silva & Martins 1999; Viana et al. 2002; Viana & Kleinert 2006; Albuquerque et al. 2007; Pigozzo et al. 2007; Ramalho & Rosa 2010; Santos et al. 2013; Figueiredo et al. 2013). However, little is known about the use of floral resources in other ecosystems, such as savannas, forests, and, especially, in transitional areas.

The State of Maranhão (MA) is located in the Eastern Amazon, where it is represented by the convergence of the humid vegetation of the ombrophilous forest and the dry and open vegetation of the savanna,

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characterized by the Brazilian Cerrado. These convergences have created a great diversity of ecosystems, including different types of physiognomies, leading to the region representing a point of biogeographic interest (Eiten 1994).

The records of *Xylocopa* spp. in MA are derived from some structured surveys (Rebêlo 1995; Rêgo et al. 2000; Albuquerque et al. 2007; Oliveira et al. 2010; Gostinski et al. 2016; Neves et al. 2021) and case studies (Oliveira et al. 2016; Pinto et al. 2020), mostly concentrated in coastal areas, and not all report information on the associated plant species. Although other surveys have been carried out in the different physiognomies of MA (Rêgo & Albuquerque 2012), a more comprehensive analysis of the resources exploited by species of the genus *Xylocopa* in these environments is still needed.

Therefore, considering that as well as knowledge of taxonomy and distribution, biotic interactions have been pointed out as an important gap to be filled in ecological research (Giannini et al. 2012; Hortal et al. 2015), the current study aimed to identify the floral resources used by *Xylocopa* species in different physiognomies of MA. As specific objectives, the study aimed to [1] quantify and qualify the interactions exerted by bees; [2] provide general information on the types of resources, habits (vertical stratification), and seasonal patterns involved in the interactions; and [3] analyze the degree of similarity of bees according to the resources used and the physiognomies studied.

## Materials and methods

### *Study area*

Maranhão is a northeastern Brazilian state located between 01°01′ – 10°21′ S and 41°48′ – 48°50′ W (IBGE 2012). The topography varies with latitude, with the mid-north characterized by plains and coastal formations, and the mid-south by the presence of plateaus, uplands, and tablelands. The climate varies with longitude, with a tropical hot climate type – Aw (Koeppen 1948), divided into a humid equatorial zone in the western portion; a semi-humid tropical equatorial zone in the central portion; and a semi-arid tropical equatorial zone in the eastern portion (IBGE 2012; NUGEO 2021). The combination of these characteristics is reflected in the direct influence of adjacent biomes (Amazon, Cerrado, and Caatinga), which promote the establishment of different types of vegetation cover or transitional physiognomies (IBGE 2012).

Originally, the Ombrophylous Forest occupied approximately 30.4% of the territory, concentrated in the western part of the state, but in recent decades it has suffered serious impacts due to the agricultural frontier and urban expansion (Martins & Oliveira 2011). Currently, the remnants of primary vegetation characteristic of the Amazon are concentrated in indigenous lands and protected areas (MapBiomas 2022).

The Park Savanna is characterized by shrub vegetation and occupies the entire central-southern part of MA (43.2% of the territory). It consists of the complexity of the Cerrado *stricto sensu*, where it can assume both formations associated with water bodies and humid forest, as well as drier formations. The vegetation has high diversity and environmental heterogeneity (Silva et al. 2008) and is considered fundamental for the maintenance of populations of different animal groups (Barreto 2007). The Steppic Savanna is a variation of this physiognomy that occupies a small area in the east of the state (0.5%) and corresponds to the typical elements of the Caatinga, where the vegetation is resistant to the warmer climate and water deficit (IBGE 2012). The contact areas or enclaves are characterized by the Deciduous Seasonal Forest (10%), which occupies the central-eastern part of the state, where there is a strong presence of Babassu palm trees (*Attalea speciosa* Mart.) and large discontinuous areas (mosaics) adapted to climatic transitions (Barreto et al. 2019). These elements, combined with the pedological characteristics of the northern coast, make up the Pioneer Formations (4.09%), which can occur under marine (Dunes and Restinga), fluviomarine (Mangroves), and fluvial or lacustrine influence (Flooded Fields) (NUGEO 2021). The typical vegetation of these areas includes a high diversity of herbaceous and liana plants, which are considered important environmental stabilizers, as restingas have been identified as one of the most threatened ecosystems today (Serra et al. 2016; Amorim et al. 2023).

### *Data collection*

Information on the distribution and floral resources of *Xylocopa* spp. was obtained directly from the labels of individuals deposited at the Coleção de Abelhas da Universidade Federal do Maranhão (LEACOL – UFMA), where most of the bee records for Maranhão are found (Ferreira et al. 2020). These data were compared with the inventories conducted in the state, which were based on the list of plant species visited by bees. Although some of these inventories were not formally published, the information is available in specialized literature such as technical reports, monographs, dissertations, and thesis (Ferreira et al. 2020). Occasional collections were also considered if they contained information on provenance, date, and associated botanical species.

Records were categorized by phytophysiognomy, according to the classification of the Environmental Information Database (BDiA 2021), with additional information on provenance (municipality), date (collection interval), richness (number of *Xylocopa* species), dominance (*Xylocopa* species with the greatest number of individuals), and relative interaction (observed interactions of *Xylocopa* spp. in relation to the total number of bees).

Some taxonomic inconsistencies were corrected based on the original descriptions of each *Xylocopa* species, through the identification keys proposed by Schlindwein et al. (2003), Marchi and Alves-dos-Santos (2013), Lucia et al. (2014), Lucia et al. (2015), Mawdsley (2018), Villamizar et al. (2020), Mérida-Rivas et al. (2022) and by comparison with the material deposited at the Coleção Entomológica Danúncia Urban, Universidade Federal da Integração Latino-Americana, Foz do Iguaçu, PR (CEDU) and the Coleção de Abelhas da Universidade Federal do Maranhão, São Luís, MA (LEACOL).

The listed plants were classified according to habit, resource, pollination syndrome, and origin, using as a reference: Faegri and van der Pijl (1979) and Almeida et al. (2022) generically, in addition to the online bases RCPol (2013) and Flora do Brasil (2020). The classification system used was APG IV (2016), and the revision and updating of species names was based on the database provided by IPNI (1999).

## Data analysis

A bipartite interaction network between bees and visiting plants was constructed using R Core Team software, version 4.2.3 (R development core team 2019), with the bipartite package (Dormann 2022). The following metrics describing a trophic interaction network were calculated: [1] connectance (C), which measures the proportion of observed interactions (IO) to the total possible interactions (IP), where $C = IO \times 100/IP$ (Pigozzo & Viana 2010), and [2] average degree (k), which corresponds to the average number of observed interactions as a function of bee (A) and plant (P) richness, where $kA = IO/A$ and $kP = IO/P$ (Blüthgen et al. 2008). To assess the degree of nestedness of the network, the N and NODF (Nestedness metric based on Overlap and Decreasing Fill) indices were calculated using Aninhado software, version 3.0.3 (Guimaraes & Guimarães 2006). The N index was obtained from the T index (temperature), which is inversely proportional to the degree of nestedness: $N = (100\text{-}T)/100$. This measure varies from 0 to 1, with values closer to 1 indicating greater nesting and values closer to 0 indicating the opposite (Bascompte et al. 2003). The NODF index, on the other hand, considers the overlapping and decreasing filling of a binary matrix and indicates the number of unexpected presences and absences, with values varying from 0 to 100 (Almeida-Neto et al. 2008). For this calculation, 1000 simulations were performed.

In addition, we evaluated the relationship between the abundance of each bee species and the number of interactions per plant species using an R-squared correlation plot ($R^2$). The trend line was plotted based on series-logarithmic where it best fits the input data.

To evaluate the seasonality of *Xylocopa* spp. we used the Rayleigh (Z) uniformity test (Zar 1999) to analyze bee activity, based on the date of occurrence of the interactions. In this calculation, the index r is presented as a measure of unimodal clustering on a set of points within a circle. A low value of r indicates that the points are uniformly distributed around the circle, while a high value indicates that the points are clustered in one or more directions, i.e. a seasonal pattern (Morellato et al. 2000). Circular statistics were performed using Oriana – Circular Statistics software, version 4.02 (Kovach 2011b).

The similarity between *Xylocopa* species as a function of plant species used as resources and physiognomies was calculated with the Sorensen index or Coefficient of Association (CA), which is defined as the ratio between twice the number of species common to both samples (c) and the total sum of the number of species in both samples (a + b), where $CA = 2c/a + b \times 100$. This index can range from 0 to 1, where 0 indicates no similarity between the samples and 1 indicates total similarity, i.e. when the two samples share exactly the same species. For this cluster analysis, only binary data (presence and absence) were used to avoid biases caused by uneven sampling in the different physiognomies. The similarity dendrogram was generated using the software MVSP - MultiVariate Statistical Package, version 3.22 (Kovach 2011a).

## Results

In total, we listed 2547 records of *Xylocopa* on flowers in Maranhão over a 40-year interval (1982-2022), through 15 structured surveys (77.2% of individuals), seven case studies (20.5%), and 16 occasional collections (2.3%) (Table 1). From these records, we identified three subgenera and 12 bee species: *Xylocopa*

**Table 1.** Records of species of the genus *Xylocopa* collected from plants in Maranhão State, deposited at the Coleção de Abelhas da Universidade Federal do Maranhão (LEACOL – UFMA). PH – physiognomies: SS – steppic Savanna; DS – deciduous seasonal Forest; FF – flooded Fields; *am – X.* (*Neoxylocopa*) *amazonica, au – X.* (*N.*) *aurulenta, ce – X.* (*N.*) *cearensis, fr – X.* (*N.*) *frontalis, gr – X.* (*N.*) *grisescens, hi – X.* (*N.*) *hirsutissima, Ni – X.* (*N.*) *nigrocincta, tt – X.* (*N.*) *transitoria, ma – X.* (*Schonnherria*) *macrops, mu – X.* (*S.*) *muscaria, su – X.* (*S.*) *subcyanea, st – X.* (*Stenoxylocopa*) sp.; S – richness; D – dominant species: P% – relative frequency of plants visited in surveys; REF – references.

| PH | | Municipalities | Collectors | Year | S | D | P% | REF |
|---|---|---|---|---|---|---|---|---|
| Ombrophylous Forest | | Alcântara | Araújo & Gonçalves | 1992–1993 | 2 | *Fr* | 7.6 | 1 |
| | | Buriticupu | Pereira, C.Q.B.** | 1999 | 1 | *Ce* | – | 2 |
| | | Carutapera | Ferreira, L.A.C.** | 2014 | 3 | *Fr* | – | 3 |
| | | Cururupu | Dos Anjos, J.V. | 2015–2016 | 1 | *Fr* | 11.1 | 4 |
| | | São Luís | Brenha & Rebêlo | 1982–1983 | 4 | *Fr* | 15.7 | 5 |
| | | | Cruz & Sodré | 1999–2000 | 4 | *Mu* | 14.8 | 6 |
| | | | Apocalypse & Rodrigues | 1991–1992 | 5 | *Fr* | 15.6 | 7 |
| | | | Machado & Botão* | 2005 | 1 | *Ce* | – | 8 |
| | | | Ferreira, L.A.C.** | 2022 | 4 | *Ce* | – | 9 |
| Park Savanna | | Balsas | Jesus & Silva | 2006–2007 | 6 | *Gr* | – | 10 |
| | | Barreirinhas | Brito & Mendonça | 1991–1992 | 4 | *Fr* | 75.0 | 11 |
| | | | Serra, B.D.V.* | 2005–2006 | 3 | *Fr* | – | 12 |
| | | Caxias | Pinho, A.N.** | 2009 | 1 | *Hi* | – | 13 |
| | | Chapadinha | Brito & Rêgo** | 1994 | 1 | *Am* | – | 14 |
| | | | Barbosa & Pinto** | 2011 | 1 | *Ni* | – | 15 |
| | | Formosa da Serra Negra | Araújo & Brito | 2011–2012 | 2 | *Gr* | 2.56 | 16 |
| | | Grajaú | Ferreira, L.A.C.** | 2022 | 1 | *Fr* | – | 17 |
| | | São João dos Patos | Ferreira, L.A.C.** | 2022 | 1 | *Fr* | – | 18 |
| | | Urbano Santos | Mendes & Ramos** | 2003 | 2 | *Mu* | – | 19 |
| | | | Serra, B.D.V.* | 2005–2006 | 2 | *Fr* | – | 20 |
| SS | | Barão de Grajaú | Ferreira, L.A.C.** | 2022 | 1 | *Hi* | – | 21 |
| DS | | Codó | Ferreira, L.A.C.** | 2022 | 1 | *Ce* | – | 22 |
| | | Colinas | Ferreira, L.A.C.** | 2022 | 1 | *Fr* | – | 23 |
| | | Imperatriz | Ferreira, L.A.C.** | 2022 | 1 | *Ce* | – | 24 |
| | | Timon | Ferreira, L.A.C.** | 2022 | 2 | *Hi* | – | 25 |
| Pioneer Formations | Dunes | São José de Ribamar | Oliveira & Mendonça | 2005–2006 | 3 | *Ce* | 66.6 | 26 |
| | | | Ferreira, L.A.C.** | 2016 | 2 | *Ce* | – | 27 |
| | | | Santana, I.B.P.A.* | 2017 | 2 | *Fr* | – | 28 |
| | | São Luís | Albuquerque & Ferreira | 1993–1994 | 4 | *Ce* | 63.6 | 29 |
| | Restinga | Barreirinhas | Gostinski & Carvalho | 2009–2010 | 5 | *Ce* | 20.3 | 30 |
| | | | Silva, F.M.A.* | 2009–2010 | 4 | *Fr* | – | 31 |
| | | | Silva, O.** | 2011 | 1 | *Su* | – | 32 |
| | | | Oliveira, F.S.* | 2015 | 2 | *Ce* | – | 33 |
| | | | Pinto, R.S.* | 2017 | 4 | *Ce* | – | 34 |
| | | Raposa | Souza & Martins | 1999–2000 | 2 | *Ce* | 46.1 | 35 |
| | | Tutóia | Neves JR & Barros | 2017–2018 | 4 | *Ce* | 73.6 | 36 |
| | FF | Anajatuba | Araújo & Carvalho | 2008–2009 | 4 | *Ce* | – | 37 |
| | | | Oliveira, F.S.* | 2008–2009 | 4 | *Fr* | – | 38 |
| | | Vitória do Mearim | Ferreira & Santos | 1991–1992 | 5 | *Mu* | 40.0 | 39 |

Note. *Case studies; ** Occasional collections; Publications with botanical data: 5 – Rebêlo (1995); 11 – Albuquerque and Mendonça (1996); 12, 20 – Serra and Drummond (2006); 29 – Albuquerque et al. (2007); 33 – Oliveira et al. (2016); 34 – Pinto et al. (2020); 35 – Silva et al. (2001); 36 – Neves et al. (2021); 38 – Oliveira (2014); 39 – Rêgo et al. (2000); Publications without botanical data: 10 – Rêgo et al. (2007); 30 – Gostinski et al. (2016); 26 – Oliveira et al. (2010); Unpublished data: 1, 4, 6, 7, 8, 10, 16, 28, 31, 37.

(*Neoxylocopa*) *amazonica* Enderlein, 1913; *X.* (*N.*) *aurulenta* (Fabricius, 1804); *X.* (*N.*) *cearensis* Ducke, 1910; *X.* (*N.*) *frontalis* (Olivier, 1789); *X.* (*N.*) *grisescens* Lepeletier, 1841; *X.* (*N.*) *hirsutissima* Maidl, 1912; *X.* (*N.*) *nigrocincta* Smith, 1854; *X.* (*N.*) *transitoria* Pérez, 1901; *X.* (*Schonnherria*) *macrops* Lepeletier, 1841; *X.* (*S.*) *muscaria* (Fabricius, 1775); *X.* (*S.*) *subcyanea* Pérez, 1901; and *X.* (*Stenoxylocopa*) sp., distributed in 23 municipalities. The physiognomies with the highest *Xylocopa* abundance values were Dunes (44.7%) and Restinga (30.6%); and the highest richness values were Park Savanna (75%) and Ombrophylous Forest (58.3%).

Bees were collected visiting 109 plant species, distributed in 77 genera and 36 botanical families (Table 2). The most representative families were Fabaceae (34 spp.), Malvaceae (8 spp.) and Asteraceae and Convolvulaceae (5 spp. each). Another 17 families were represented by only one species. Within this richness, 87% are native plants, of which 9.2% are considered endemic to Brazil, and the others are of exotic origin, naturalized (6.4%) or cultivated (2.7%).

The vertical stratification consisted of herbaceous plants (28.7%), shrubs (27.7%), trees (17.5%), lianas (16.6%), and subshrubs (7.4%). Regarding the availability of the resources offered, almost half of the visited plants offer nectar as the main attraction (49%), followed by pollen (23.1%) and the combination of these two resources (20.3%), while floral oils were offered by only 4.6% of the species. As for the pollination

**Table 2.** Floral resources used by species of the genus *Xylocopa* in Maranhão State, deposited at the Coleção de Abelhas da Universidade Federal do Maranhão (LEACOL – UFMA). Habit: tr – tree, sh – shrub, ss – subshrub, hb – herbs, cr – creeper; resource: ne – nectar, Po – pollen, ol – Oil; syndrome: Mel – melitophilia, psi – psicophilia, Myo – myophilia, Chi – chiropterophily, orn – ornithophily; origin: nv – native, nz – naturalized, ct – cultivated; *Xylocopa* species: *am* – *X.* (*Neoxylocopa*) *amazonica*, *au* – *X.* (*N.*) *aurulenta*, *ce* – *X.* (*N.*) *cearensis*, *fr* – *X.* (*N.*) *frontalis*, *gr* – *X.* (*N.*) *grisescens*, *hi* – *X.* (*N.*) *hirsutissima*, *Ni* – *X.* (*N.*) *nigrocincta*, *tr* – *X.* (*N.*) *transitoria*, *ma* – *X.* (*Schonnherria*) *macrops*, *mu* – *X.* (*S.*) *muscaria*, *su* – *X.* (*S.*) *subcyanea*, *st* – *X.* (*Stenoxylocopa*) sp.; REF – references in table 1.

| | | | | | | *Xylocopa* species | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CODE/Family/*Botanical Species* | | Habit | Resource | Syndrome | Origin | *Am* | *Au* | *Ce* | *Fr* | *Gr* | *Hi* | *Ni* | *Tr* | *Ma* | *Mu* | *Su* | *St* | REF |
| | **Amaranthaceae** | | | | | | | | | | | | | | | | | |
| 1 | *Alternanthera tenella* Colla | Hb | Po | Mel | Nv | | | x | | | | | | | | | | 26 |
| | **Anacardiaceae** | | | | | | | | | | | | | | | | | |
| 2 | *Anacardium occidentale* L. | Tr | Po+Ne | Mel | Nv | | | x | | | | x | | | | | | 10, 11, 30, 35, 36 |
| | **Apocynaceae** | | | | | | | | | | | | | | | | | |
| 3 | *Allamanda blanchetii* A.DC. | Sh | Ne | Mel | Nv* | | | x | | x | | | | | | | | 11 |
| 4 | *Funastrum clausum* (Jacq.) Schltr. | Cr | Po | Mel+Psi | Nv | | | x | | | | | | | | | | 35 |
| | **Asteraceae** | | | | | | | | | | | | | | | | | |
| 5 | *Centratherum punctatum* Cass. | Hb | Ne | Mel | Nv | | | | | | | x | | | | | | 39 |
| 6 | *Lepidaploa arenaria* (Mart. ex DC.) H.Rob. | Ss | Ne | Mel | Nv* | | | x | | | | x | | | | | | 29 |
| 7 | *Lepidaploa rufogrisea* (A.St.-Hil.) H.Rob. | Sh | Ne | Mel | Nv* | | | x | | | | x | | | | | | 30, 38 |
| 8 | *Praxelis kleinioides* (Kunth) Sch. Bip. | Hb | Ne | Mel | Nv | | | | x | | | | | | | | | 6 |
| 9 | *Tilesia baccata* (L.) Pruski | Sh | Ne | Mel | Nz | | | x | | | | | | | | | | 29 |
| | **Bignoniaceae** | | | | | | | | | | | | | | | | | |
| 10 | *Adenocalymma subincanum* Huber | Cr | Ne | Mel | Nv | | | x | x | | | | | | | | | 7 |
| 11 | *Fridericia platyphylla* (Cham.) L.G.Lohmann | Sh | Ne | Mel | Nv | | | x | | | | | | | | | | 29 |
| 12 | *Tecoma stans* (L.) Juss. Ex Kunth | Sh | Ne | Mel | Nz | | | x | x | | x | x | x | | | | | 6, 9, 17, 18, 21, 22, 23, 24, 25 |
| | **Bixaceae** | | | | | | | | | | | | | | | | | |
| 13 | *Bixa orellana* L. | Sh | Po | Mel | Nv | | | | x | x | | x | | | | | | 4, 6, 20 |
| | **Boraginaceae** | | | | | | | | | | | | | | | | | |
| 14 | *Euploca polyphylla* (Lehm.) J.I.M.Melo & Semir | Hb | Ne | Mel | Nv | | | x | | | | | | x | | | | 29, 35, 36 |
| 15 | *Varronia multispicata* (Cham.) Borhidi | Sh | Po+Ne | Mel | Nv* | | | | | | | | | | x | | | 1 |
| | **Bromeliaceae** | | | | | | | | | | | | | | | | | |
| 16 | Bromeliaceae sp. | – | – | – | – | | | | | | | | | | | | x | 10 |
| | **Burseraceae** | | | | | | | | | | | | | | | | | |
| 17 | *Protium heptaphyllum* (Aubl.) Marchand | Sh | Ne | Mel+Chi | Nv | | | x | | | | | | | | | | 29, 35 |
| | **Caryocaraceae** | | | | | | | | | | | | | | | | | |
| 18 | *Caryocar cuneatum* Wittm. | Tr | Po+Ne | Chi+Psi | Nv* | | | x | | x | | | | | | | | 11 |
| | **Chrysobalanaceae** | | | | | | | | | | | | | | | | | |
| 19 | *Hirtella racemosa* Lam. | Sh | Ne | Psi | Nv | | | | | | | | | | x | | | 6 |
| | **Convolvulaceae** | | | | | | | | | | | | | | | | | |
| 20 | *Ipomoea asarifolia* (Desr.) Roem. & Schult | Hb | Po+Ne | Mel | Nv | | | | | | | x | | | | | | 37 |
| 21 | *Ipomoea maurandioides* Meisn. | Cr | Po+Ne | Mel | Nv | | | x | | | | | | | | | | 36 |
| 22 | *Ipomoea mauritiana* Jacq. | Cr | Ne | Mel | Nv | | | x | | | | | | | | | | 29 |
| 23 | *Ipomoea pes-caprae* (L.) R.Br. | Hb | Ne | Mel | Nv | | | x | | | | | | | | | | 26, 35 |
| 24 | *Jacquemontia tamnifolia* (L.) Griseb. | Cr | Po+Ne | Mel | Nv | | | x | | | | | | | | | | 36 |
| | **Euphorbiaceae** | | | | | | | | | | | | | | | | | |
| 25 | *Cnidoscolus urens* (L.) Arthur | Hb | Ne | Mel+Psi | Nv | | | x | | | | | | | | | | 26 |
| 26 | Euphorbiaceae sp. | – | – | – | – | | | | | | | | | | | x | | 19 |
| | **Fabaceae** | | | | | | | | | | | | | | | | | |
| 27 | *Ancistrotropis peduncularis* (Kunth) A. Delgado | Cr | Ne | Mel | Nv | | | x | | | | | | x | | | | 36 |
| 28 | *Andira surinamensis* (Bondt) Splitg. ex Amshoff | Tr | Ne | Mel | Nv | | | x | | | | | | | | | | 36 |
| 29 | *Bauhinia* sp. | Sh | Ne | Mel+Psi | Nz | | | | x | | | | | | | | | 10 |
| 30 | *Bowdichia* sp. | Tr | Ne | Mel | Nv | | | | | x | | | | | | | | 11 |
| 31 | *Calopogonium* sp. | Hb | Ne | Mel | Nv | | | x | x | | | | | | | | | 9 |
| 32 | *Canavalia rosea* (Sw.) DC. | Cr | Ne | Mel | Nv | | | x | x | | | | x | | | | | 26, 29 |
| 33 | *Canavalia* sp. | Hb | Ne | Mel | Nv | | | | x | | | | | | | | | 36 |

(*Continued*)

**Table 2.** (Continued).

| | | | | | | *Xylocopa* species | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | CODE/Family/*Botanical Species* | Habit | Resource | Syndrome | Origin | *Am* | *Au* | *Ce* | *Fr* | *Gr* | *Hi* | *Ni* | *Tr* | *Ma* | *Mu* | *Su* | *St* | REF |
| 34 | *Cassia* sp. | Tr | Po | Mel | Nv | | | | x | x | | | | | | | | 11 |
| 35 | *Cenostigma bracteosum* (Tul.) Gagnon & G.P.Lewis | Tr | Ne | Mel | Nv* | | | x | x | x | | x | | | | | | 30, 31, 38 |
| 36 | *Centrosema brasilianum* (L.) Benth. | Cr | Ne | Mel | Nv | | | x | | | | | | | | | | 3, 12 |
| 37 | *Centrosema plumieri* (Turpin ex Pers.) Benth. | Cr | Ne | Mel | Nv | | | | x | | | | | | | | | 10 |
| 38 | *Centrosema* sp. | Cr | Ne | Mel | Nv | | | x | | | | | | | | | | 28, 29 |
| 39 | *Chamaecrista diphylla* (L.) Greene | Ss | Po | Mel | Nv | | | | | | | | | | x | | | 39 |
| 40 | *Chamaecrista hispidula* (Vahl) H.S.Irwin & Barneby | Ss | Po | Mel | Nv | | | x | x | | | | | | x | | | 26, 29 |
| 41 | *Chamaecrista ramosa* (Vogel) H.S.Irwin & Barneby | Ss | Po | Mel | Nv | | | x | x | x | x | | | x | | x | | 10, 35, 36 |
| 42 | *Crotalaria retusa* L. | Hb | Ne | Mel | Nz | | x | x | x | x | | x | | | | | | 5, 28, 29, 35, 39 |
| 43 | *Crotalaria* sp. | Hb | Ne | Mel | Nv | | | | x | | | | | | | | | 1 |
| 44 | *Dioclea* sp. | Cr | Ne | Mel | Nv | | | | x | | | | | | | | | 4 |
| 45 | *Dioclea virgata* (Rich.) Amshoff | Cr | Ne | Mel | Nv | | | | x | | | x | x | | | | | 5, 7, 39 |
| 46 | Fabaceae sp. | – | – | – | – | | | x | | x | | | | | | | | 10, 37 |
| 47 | *Galactia jussiaeana* Kunth | Ss | Ne | Mel | Nv | | | x | | | | | | | | | | 29 |
| 48 | *Hymenaea parvifolia* Huber | Tr | Po+Ne | Chi | Nv | | | x | | | | | | | | | | 30 |
| 49 | *Macroptilium atropurpureum* (Sessé & Moc. ex DC.) Urb. | Cr | Ne | Mel | Nz | | | x | | | | | | | | | | 29 |
| 50 | *Macroptilium lathyroides* (L.) Urb. | Hb | Ne | Mel | Nv | | | | x | | | | | | | | | 39 |
| 51 | *Parkia platycephala* Benth. | Tr | Ne | Chi | Nv* | | | | | x | | | | | | | | 11 |
| 52 | *Pueraria phaseoloides* (Roxb.) Benth. | Hb | Ne | Mel | Nz | | | x | | | | | | | | | | 39 |
| 53 | *Senna alata* (L.) Roxb. | Sh | Po | Mel | Nv | | | x | x | | | x | | | x | | | 5, 39 |
| 54 | *Senna latifolia* (G.Mey.) H.S.Irwin & Barneby | Sh | Po | Mel | Nv | | | | x | x | | | | | | | | 5 |
| 55 | *Senna obtusifolia* (L.) H.S.Irwin & Barneby | Ss | Po | Mel | Nv | | | x | | | | x | | | | | | 37, 39 |
| 56 | *Senna occidentalis* (L.) Link | Sh | Po | Mel | Nv | | | x | | | | | | | | | | 37 |
| 57 | *Senna reticulata* (Willd.) H.S.Irwin & Barneby | Sh | Po | Mel | Nv | | | | x | | | | | | x | | | 39 |
| 58 | *Senna silvestris* (Vell.) H.S.Irwin & Barneby | Sh | Po | Mel | Nv | | | | | x | | | | | | | | 16 |
| 59 | *Senna* sp. | Sh | Po | Mel | Nv | x | | | x | | | | | | | | | 4 |
| 60 | *Vatairea sericea* (Ducke) Ducke | Tr | Po+Ne | Mel | Nv | | | x | x | x | | | | | x | | | 11 |
| | **Gentianaceae** | | | | | | | | | | | | | | | | | |
| 61 | *Coutoubea spicata* Aubl. | Hb | Po | Mel | Nv | | | x | | | | x | x | | x | | | 6, 7 |
| | **Humiriaceae** | | | | | | | | | | | | | | | | | |
| 62 | *Humiria balsamifera* (Aubl.) A.St.-Hil. | Tr | Ne | Mel | Nv | | | | x | | | | | | | | | 30 |
| 63 | *Humiria balsamifera* var. *floribunda* (Mart.) Cuatrec. | Tr | Ne | Mel | Nv | | | x | x | x | | x | | | | | | 34 |
| | **Hypericaceae** | | | | | | | | | | | | | | | | | |
| 64 | *Vismia guianensis* (Aubl.) Choisy | Sh | Po+Ne | Mel | Nv | | | | | | | | | | x | | | 1 |
| | **Lamiaceae** | | | | | | | | | | | | | | | | | |
| 65 | *Marsypianthes chamaedrys* (Vahl) Kuntze | Hb | Ne | Mel | Nv | | | x | | | | | | | | | | 29 |
| 66 | *Mesosphaerum suaveolens* (L.) Kuntze | Hb | Ne | Mel | Nv | | | | | | | | | | x | | | 39 |
| | **Lecythidaceae** | | | | | | | | | | | | | | | | | |
| 67 | *Gustavia augusta* L. | Tr | Po | Mel | Nv | | | x | | | | | | | | | | 29 |
| | **Loganiaceae** | | | | | | | | | | | | | | | | | |
| 68 | *Spigelia anthelmia* L. | Hb | Po+Ne | Mel | Nv | | | x | | | | | | | | | | 36 |
| | **Loranthaceae** | | | | | | | | | | | | | | | | | |
| 69 | *Phthirusa* sp. | Hb | Ne | Mel | Nv | | | x | | | | | | | | | | 2, |
| 70 | *Psittacanthus robustus* (Mart.) Mart. | Hb | Ne | Orn+Chi | Nv | | | | x | | | | | | | | | 16, 30 |
| | **Lythraceae** | | | | | | | | | | | | | | | | | |
| 71 | *Cuphea mimuloides* Cham. & Schltdl. | Hb | Ne | Mel | Nv | | | x | | | | | | | | | x | 30 |
| 72 | *Cuphea* sp. | Hb | Ne | Mel | Nv | | | x | | | x | | | | | | | 13, 30 |
| | **Malpighiaceae** | | | | | | | | | | | | | | | | | |
| 73 | *Banisteriopsis nummifera* (A.Juss.) B.Gates | Cr | Po+Ol | Mel | Nv | | | | | | | | | | x | | | 7 |

*(Continued)*

**Table 2.** (Continued).

| | CODE/Family/*Botanical Species* | Habit | Resource | Syndrome | Origin | *Xylocopa* species | | | | | | | | | | | | REF |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | *Am* | *Au* | *Ce* | *Fr* | *Gr* | *Hi* | *Ni* | *Tr* | *Ma* | *Mu* | *Su* | *St* | |
| 74 | *Byrsonima crassifolia* (L.) Kunth | Tr | Po+Ol | Mel | Nv | | | x | | | | x | x | | | | | 6, 36 |
| 75 | *Malpighia glabra* L. | Tr | Po+Ol | Mel | Ct | | | | x | | | | | | | | | 37 |
| | **Malvaceae** | | | | | | | | | | | | | | | | | |
| 76 | *Eriotheca globosa* (Aubl.) A.Robyns | Tr | Po+Ne | Mel | Nv | | | | x | x | | x | | | | | | 5 |
| 77 | *Eschweilera decolorans* Sandwith | Tr | Ne | Mel | Nv | | | x | x | | | | | | | | | 11 |
| 78 | *Gossypium* L. | Sh | Po+Ne | Mel | Nv | | | | | | | | | | | x | | 32 |
| 79 | *Hibiscus sabdariffa* L. | Sh | Po+Ne | Mel | Nz | | | x | | | | | | | | | | 8 |
| 80 | Malvaceae sp. | – | – | – | – | | x | | | | | x | | | x | | | 39 |
| 81 | *Pavonia cancellata* (L.) Cav. | Hb | Po+Ne | Mel | Nv | | | | | | | | | | x | | | 39 |
| 82 | *Sida acuta* Burm.f. | Ss | Po+Ne | Mel | Nv | | | | x | | | | | | | | | 4 |
| 83 | *Sida* sp. | Ss | Po+Ne | Mel | Nv | | | | | | | x | x | | | | | 6 |
| | **Melastomataceae** | | | | | | | | | | | | | | | | | |
| 84 | *Comolia villosa* (Aubl.) Triana | Sh | Po | Mel | Nv | | | x | | | | | | | | | | 30 |
| 85 | *Mouriri acutiflora* Naudin | Tr | Po+Ol | Mel | Nv | | | x | x | | | x | | | x | | | 30, 37, 39 |
| 86 | *Mouriri guianensis* Aubl. | Sh | Po+Ol | Mel | Nv | | | x | | x | | | | | | | | 33 |
| | **Myrtaceae** | | | | | | | | | | | | | | | | | 39 |
| 87 | *Myrtus* sp. | Sh | Ne | Mel+Myo | Ct | | | | | | x | | | | | | | 10 |
| | **Ochnaceae** | | | | | | | | | | | | | | | | | |
| 88 | *Ouratea hexasperma* (A.St.-Hil.) Baill. | Tr | Po | Mel | Nv | | | x | x | x | | | | | x | | | 11, 36 |
| 89 | *Ouratea racemiformis* Ule | Tr | Po | Mel | Nv* | | | x | x | | | x | x | | x | | | 6, 30 |
| 90 | *Ouratea semiserrata* (Mart. & Nees) Engl. | Sh | Po | Mel | Nv* | x | | | | | | | | | | | | 14 |
| 91 | *Ouratea* sp. | Sh | Po | Mel | Nv | | | | | | | x | | | x | | | 15, 19 |
| | **Oxalidaceae** | | | | | | | | | | | | | | | | | |
| 92 | *Oxalis juruensis* Diels | Sh | Po+Ne | Mel | Nv | | | | | | | | | | x | | | 39 |
| | **Passifloraceae** | | | | | | | | | | | | | | | | | |
| 93 | *Passiflora acuminata* DC. | Cr | Ne | Mel | Nv | | | | | | | x | | | | | | 37 |
| 94 | *Passiflora edulis* Sims | Cr | Ne | Mel | Nv | | | | x | | | | | | | | | 3 |
| 95 | *Passiflora foetida* L. | Cr | Ne | Mel | Nv | | | x | x | | | | | | | | | 26, 29 |
| 96 | *Passiflora* sp. | Cr | Ne | Mel | Nv | | | x | x | | | | | | | | | 27, 35 |
| | **Polygalaceae** | | | | | | | | | | | | | | | | | |
| 97 | *Asemeia hirsuta* (A.St.-Hil. & Moq.) J.F.B.Pastore & J.R.Abbott | Hb | Ne | Mel | Nv* | | | x | | | | | | | | | | 29 |
| | **Rubiaceae** | | | | | | | | | | | | | | | | | |
| 98 | *Borreria verticillata* (L.) G.Mey. | Hb | Po+Ne | Mel+Psi | Nv | | | x | x | | | | | x | x | | | 4, 7, 29, 35, 36 |
| 99 | *Diodia* sp. | Hb | Ne | – | – | | | x | | | | | | | | | | 28 |
| 100 | *Mitracarpus* sp. | Hb | Po+Ne | Mel+Psi | Nv | | | x | | | | | | | | | | 35 |
| | **Sapindaceae** | | | | | | | | | | | | | | | | | |
| 101 | *Pseudima frutescens* (Aubl.) Radlk. | Sh | Ne | Mel | Nv | | | x | | | | | | | | | | 29 |
| | **Sapotaceae** | | | | | | | | | | | | | | | | | |
| 102 | *Manilkara* sp. | Sh | Ne | Mel | Nv | | | x | | | | | | | | | | 36 |
| | **Solanaceae** | | | | | | | | | | | | | | | | | |
| 103 | *Solanum jamaicense* Mill. | Sh | Po | Mel | Nv | | | x | x | | | | | | x | | | 37 |
| 104 | *Solanum nudum* Dunal | Sh | Po | Mel | Nv | | | x | x | | | | | | | | | 29 |
| 105 | *Solanum subinerme* Jacq. | Sh | Po | Mel | Nv | | | x | | | | x | | | | | | 5 |
| | **Talinaceae** | | | | | | | | | | | | | | | | | |
| 106 | *Talinum* sp. | Hb | Po | Mel | Nv | | | x | | | | | | | | | | 26 |
| | **Turneraceae** | | | | | | | | | | | | | | | | | |
| 107 | *Piriqueta cistoides* (L.) Griseb. | Hb | Po+Ne | Mel | Nv | | | x | x | | | x | | | | | | 26, 30, 35, 38 |
| 108 | *Turnera melochioides* Cambess. | Hb | Po+Ne | Mel | Nv | | | x | | | | | | | | | | 29, 36 |
| 109 | *Turnera ulmifolia* L. | Hb | Po+Ne | Mel | Ct | | | | x | | | | | | | | | 37 |
| | **Total interactions** | **n** | | | | 2 | 2 | 67 | 41 | 17 | 4 | 24 | 7 | 4 | 20 | 3 | 2 | |
| | | **%** | | | | 1.8 | 1.8 | 61.5 | 37.6 | 15.6 | 3.7 | 22 | 6.4 | 3.7 | 18.3 | 2.8 | 1.8 | |

*endemic species to the Brazilian territory according to Flora do Brasil (2020).

syndromes, most plants present melitophilia as the main system (85.1%), the others present a combination of melitophilia with other pollinating insects (7.4%) and chiropterophily (2.7%).

The interaction network (Figure 1) consisted of 12 bee species and 109 plant species, resulting in 1308 possible interactions, however, only 193 interactions were observed, resulting in a connectance of 14.7%. The generalist bee species were *X. cearensis* (61.5% of all observed plants), *X. frontalis* (37.6%), and *X. nigrocincta* (22%). In contrast, *X. aurulenta* and *X. amazonica* visited only two plant species each, representing only 1.8% of the total. In addition, five other *Xylocopa* species visited less than 10 plant species.

The most visited plants in terms of bee abundance were *Chamaecrista hispidula* (Vahl) H.S.Irwin & Barneby (9.9% of individuals), *Chamaecrista ramosa* (Vogel) H.S.Irwin & Barneby (9.2%), and *Passiflora foetida* L. (7.8%); in terms of species richness, the highest values were found for *Chamaecrista ramosa* (50% of species), and *Tecoma stans* (L.) Juss. Ex Kunth, and *Crotalaria retusa* L. (41.6% each).

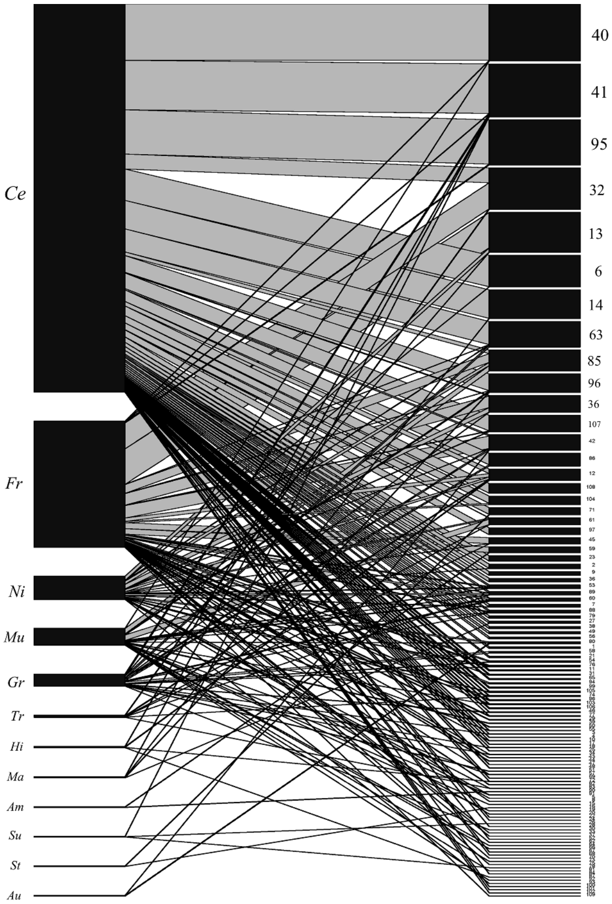


**Figure 1.** Bipartite interaction network: interactions between *Xylocopa* species (left) and plants (right) in transition areas of MA. The vectors represent the interactions between these species. The thickness of the vectors is proportional to the relative abundance of the visiting bees.

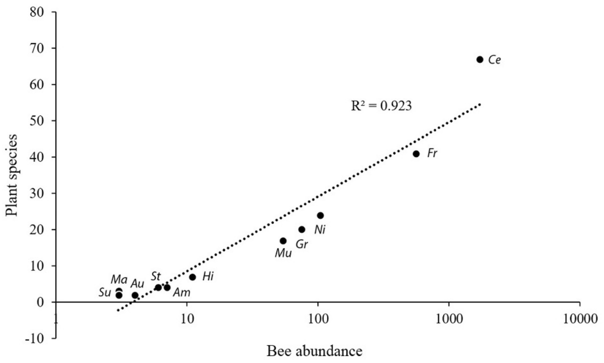
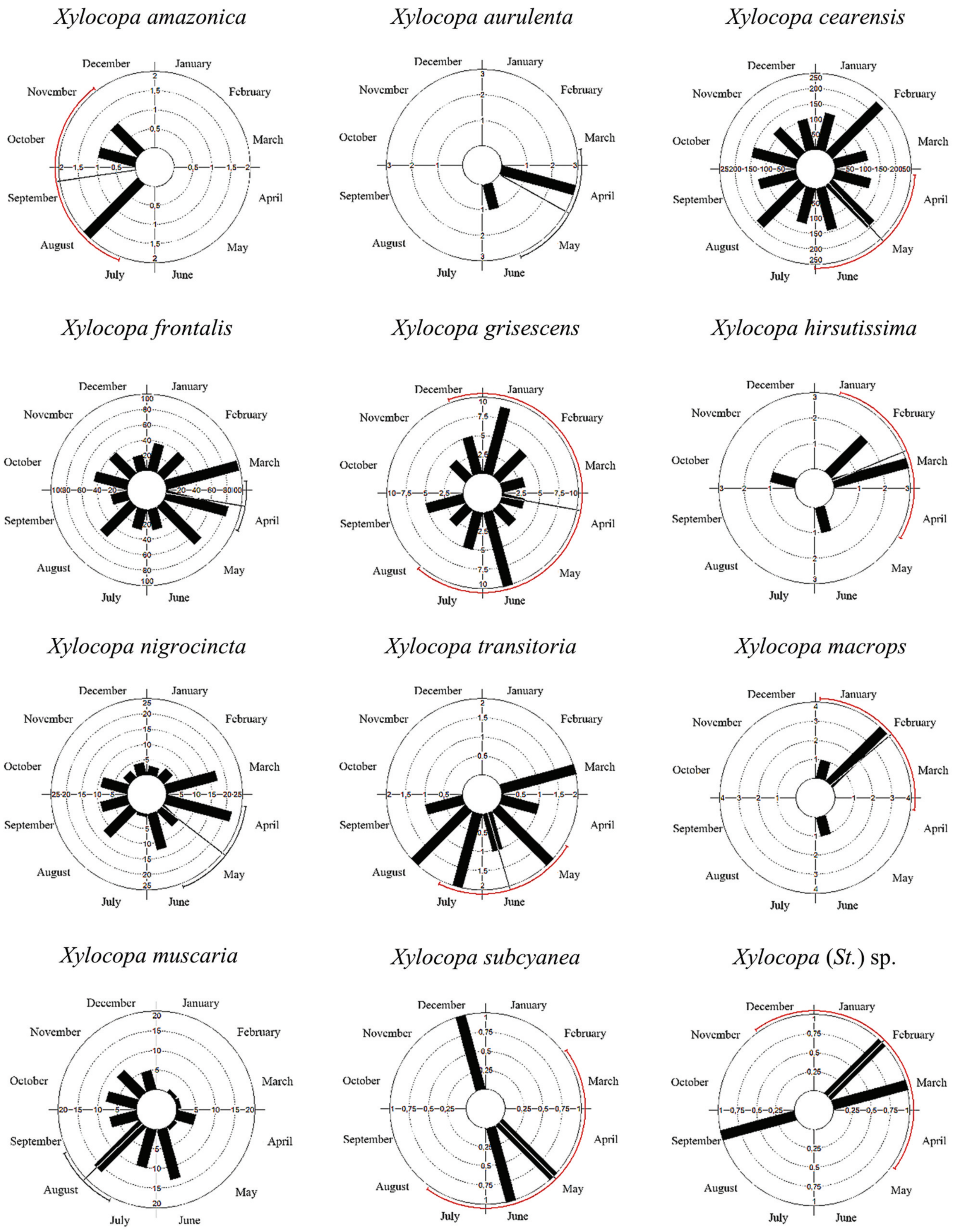


**Figure 2.** Relation between the number of individuals and the species of plants visited by *Xylocopa* spp. recorded in Maranhão State, Brazil. Species abbreviations in table 2.

The average degree of visiting bees to plants (kA) was 16.08 and the average degree of plants to bees (kP) was 1.77. The interaction network showed a high nestedness degree, $N = 0.90$ and NODF = 36.1. In addition, the correlation graph (Figure 2) showed a clear relationship between the abundance of bee species collected and the number of visited plant species, according to the $R^2$ value = 0.923.

The seasonality of the bee species is presented with a circular distribution histogram (Figure 3), which showed the low number of species active throughout the year. The Rayleigh test indicated a significant distribution in relation to the total number of individuals (Z = 19.33), with May presenting the average range of interactions. The species with the most significant results were *X. frontalis* (Z = 28.54) and *X. muscaria* (Z = 16.10) (Table 3). The species *X. subcyanea* and *Xylocopa* sp. showed low significance in the Z test due to the limited samples.

The similarity between *Xylocopa* species according to the plant species visited (Figure 4A) showed a 40% similarity between two groups: *X. transitoria* with *X. nigrocincta*, and *X. frontalis* with *X. cearensis*, respectively, while the other species showed 70% or more similarity. Similarity between *Xylocopa* species according to physiognomic forms (Figure 4B) showed that eight of the 12 species had more than 60% similarity, with two well-defined groups (CA = 1): *X. muscaria* with *X. nigrocincta*, and *X. frontalis* with *X. cearensis*. Among species with the highest number of records, *X. muscaria* is the most dissimilar species when we consider the proportion of plants visited per physiognomy.



*Xylocopa amazonica*

*Xylocopa aurulenta*

*Xylocopa cearensis*

*Xylocopa frontalis*

*Xylocopa grisescens*

*Xylocopa hirsutissima*

*Xylocopa nigrocincta*

*Xylocopa transitoria*

*Xylocopa macrops*

*Xylocopa muscaria*

*Xylocopa subcyanea*

*Xylocopa* (*St.*) sp.

**Figure 3.** Circular distribution histogram of *Xylocopa* species collected from plants in Maranhão State, Brazil. The standard deviation is represented by the line at the top of the vector.

**Table 3.** Rayleigh test of uniformity (Z) applied to *Xylocopa* species recorded from plants in Maranhão State, Brazil.

| *Xylocopa* species | Mean vector (μ) | Month | Length of mean vector (R) | Rayleigh test (Z) |
|---|---|---|---|---|
| Total number | 122.801° | May | 0.087 | 19.33** |
| *X. amazonica* | 261.738° | September | 0.789 | 2.489 |
| *X. aurulenta* | 118.898° | April | 0.912 | 3.325* |
| *X. cearensis* | 136.835° | May | 0.044 | 3.323* |
| *X. frontalis* | 99.448° | April | 0.226 | 28.54** |
| *X. grisescens* | 100.182° | April | 0.09 | 0.434 |
| *X. hirsutissima* | 67.631° | March | 0.563 | 2.221 |
| *X. nigrocincta* | 127.848° | May | 0.249 | 6.401* |
| *X. transitoria* | 163.713° | June | 0.549 | 3.310* |
| *X. macrops* | 49.792° | February | 0.739 | 3.273* |
| *X. muscaria* | 226.117° | August | 0.463 | 16.109** |
| *X. subcyanea* | 135° | May | 0.337 | 0.341 |
| *X.* sp. | 45° | February | 0.337 | 0.341 |

*$p < 0.05$; **$p < 0.001$.

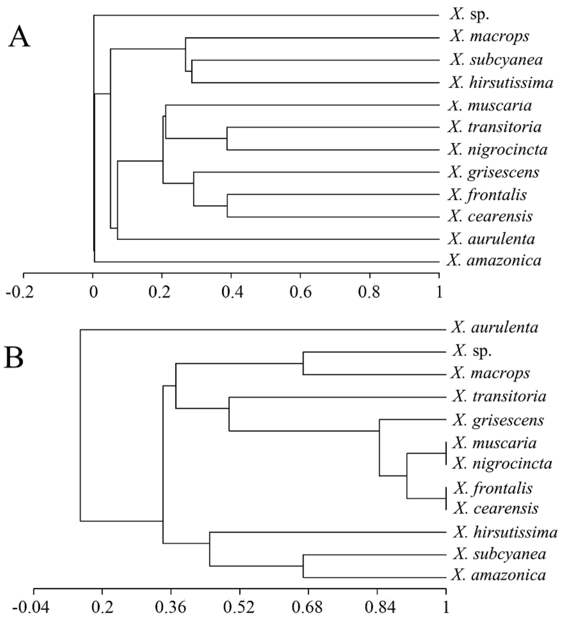


**Figure 4.** Sorensen similarity between (A) *Xylocopa* species according to plants visited and (B) *Xylocopa* species according to physiognomies in MA, Brazil.

## Discussion

The genus *Xylocopa* is well represented in Maranhão and was present in all surveys previously conducted in this territory, including those that were not included in our analysis due to lack of botanical information (Rebêlo et al. 2003; Rêgo et al. 2007; Ferreira et al. 2019) or due to individuals not being deposited in LEACOL (Ducke 1908; Gottsberger et al. 1988) and which, therefore, could not be verified. However, the distribution of abundance proved to be very uneven, since most of these works were carried out in the northern and northeastern part of MA (Rebêlo et al. 2003), and bee communities in the dunes and restingas areas were dominated by the species *X. cearensis* (Silva et al. 2001; Albuquerque et al. 2007; Oliveira et al. 2010; Gostinski et al. 2016; Neves et al. 2021). The dominance of *X. cearensis* has also been observed in other areas of Brazil with the same phytophysiognomic characteristics (Viana et al. 2002; Silva & Viana 2002; Pigozzo et al. 2007; Ramalho & Rosa 2010; Figueiredo et al. 2013; Silva et al. 2019).

On the other hand, *Xylocopa* richness was slightly higher in park savannas (Rêgo et al. 2007), despite the deficit of systematized sampling in this physiognomy. In this context, occasional or incremental collections play an important role in filling sampling gaps (Huybrechts et al. 2022). In our study, 66% of the richness was concentrated in only 2.3% of the individuals recorded by this method.

*Xylocopa* species were observed to visit several botanical families with a high proportion of mellitophilous species, including Fabaceae, Malvaceae, and Asteraceae. These families represent a significant part of the diversity of the Brazilian flora (BFG 2021) and are important for maintaining biodiversity and ecosystem functioning (Bawa 1990; Frankie et al. 2005). In the transitional areas of Maranhão, most of the plants visited by *Xylocopa* bees are of native origin, indicating that the historical relationship between native species still prevails over exotic or invasive species, even in areas of high urban occupation (Almeida et al. 2022; Amorim et al. 2023).

However, some exotic plant species can be very attractive, especially to generalist bees, due to mass flower production or the density of individuals that dominate the environment (Silva et al. 2007; Stout & Morales 2009). In our records, *Tecoma stans*, a plant native to Mexico and the southern USA, attracted five of the 12 *Xylocopa* species present in MA. However, three of these species (*X. frontalis*, *X. grisescens*, and *X. nigrocincta*) were found to be nectar robbers in a study of their floral visitors (Silva et al. 2007). On the other hand, for *Crotalaria retusa*, a native Asian plant commonly found in tropical coastal areas (Riet-

Correa et al. 2011; Amorim et al. 2023), *X. frontalis* and *X. grisescens* were shown to be effective pollinators (Jacobi et al. 2005).

Among the ten Brazilian native and endemic plants visited by *Xylocopa* in MA, the most representative were *Lepidaploa arenaria* and *Asemeia hirsuta* in dune areas (Albuquerque et al. 2007) and *Cenostigma bracteosum* in restinga. Endemic species are generally adapted to the specific environmental and climatic conditions of their area of occurrence, as well as to the species to which they are related, and often function as key-species in local ecosystems (Martins 2002; Gögler et al. 2009; Miranda et al. 2015).

Another fundamental component in maintaining ecological relationships is environmental heterogeneity, which refers to the diversity of conditions and resources within ecosystems (Palmer & Dixon 1990; Tamme et al. 2010). In the case of plants, variation in floral resources along vertical strata can generate a complementarity effect among local pollinators (Almeida et al. 2022), in some cases avoiding niche overlap (Araújo et al. 2021). In MA, the stratification of resources was variable, and plants with herbaceous and subshrub habits stood out, attracting 47.2% of individuals, mainly among small to medium-sized species, while tree-sized species attracted just under 15% of individuals, regardless of bee size. This same frequency was observed in dune (Gottsberger et al. 1988) and Cerrado (Gottsberger & Silberbauer-Gottsberger 2018) areas, respectively, and overall, this difference may be influenced by the availability and type of resources provided (Almeida et al. 2022).

According to our results, nectariferous plants formed the largest group of species and were visited more uniformly than polliniferous plants. In the latter, a very high visitation frequency was observed, but only in a few plant species, especially in representatives of the genera *Chamaecrista*, *Bixa* and *Senna*. The collection of protein through pollen usually involves some specialization on the part of the pollinating organism (Linsley 1958). In the case of bees, especially solitary bees, the most common strategy is collection by vibration, also known as 'buzz pollination' (Buchmann 1983; Vallejo-Marín 2019; Rosi-Denadai et al. 2020).

For some highly generalist carpenter bee species, the offered resource is only optional and seems to be consumed for convenience, according to the degree of local competition (Araújo et al. 2021). The interactions between *Xylocopa* species and plants in the MA were found to be heterogeneous, due to the concentration of many plant species visited by few bees and vice versa. Although this is a regional dataset, this pattern has also been observed in local studies (Pinto et al. 2020; Neves et al. 2021). The asymmetry observed in the interaction network, where five bee species visited more than the average number of plants, was mainly caused by *X. cearensis* and *X. frontalis*. This type of dominance is an expected characteristic of bipartite networks of mutualistic interactions (Pigozzo & Viana 2010; Diniz & Buschini 2015).

According to the correlation of the number of bee individuals per plant species, there is no evidence of specialization in the use of floral resources for any *Xylocopa* species, either by visiting a large number of plant species or by the small number of individuals analyzed, as is the case for *X. amazonica*, *X. subcyanea*, and *X. aurulenta*.

Only when we consider exclusive data from structured surveys can we analyze, for example, the effects generated by seasonal and geographic patterns on some species (Biesmeijer et al. 2005; Teixeira et al. 2007).

Our results revealed that more than half of the *Xylocopa* species in MA reached some level of significance with respect to seasonality. Some species, such as *X. cearensis*, *X. frontalis*, and *X. grisescens*, had regular records throughout the year, indicating possible multivoltinism, when there is overlap between generations (Ramalho et al. 2004), while other species, even those with a reasonable number of records, such as *X. muscaria*, showed a partitioned frequency over the months.

In general, *Xylocopa* species were more frequent between the months of February and June, a period marked by the highest rainfall in the state. This event is probably related to the availability of poricid flowers in coastal regions, also verified by Viana et al. (2002). The pollen supply provided by species of the genus *Chamaecrista* throughout the rainy season corroborates the study of Almeida et al. (2022), in which the authors discuss the temporal relationship of this resource as a complement to the abundant nectariferous species in the dry season.

Considering the *Xylocopa*-plant interactions according to the different types of resources, vertical stratification, and seasonal patterns, low similarity was found among most of the bees, indicating that on average they compete for only 25% of the resources. This is the case even among the most similar species in terms of physiognomy, such as *X. frontalis* and *X. cearensis*, which overlapped strongly in the dunes/restinga environments, and *X. muscaria* and *X. nigrocincta* in the flooded fields.

The nestedness, observed by the significant values of the N and NODF indices, indicates the presence of a functional partitioning, in which the establishment of interactions between the less abundant bee species adjusts to the secondary resources of the most abundant species, thus supporting the permanence of both in the same environment (Bascompte & Jordano 2007; Pigozzo & Viana 2010; Pinto et al. 2020).

Although sampling biases are inherent in the historical data available and should be interpreted with caution, we can conclude from the analysis of the most abundant species that the diversity of floral resources is a crucial factor for *Xylocopa* populations, the transitional areas of the MA can assume an important function as a stronghold for restricted species. The conservation of these natural environments is therefore essential for the protection and conservation of these pollinators.

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No potential conflict of interest was reported by the authors.

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