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Range and trophic niche overlap of two sympatric species of floral oil collecting bees in a fragment of dry forest

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Plant-pollinator interactions constitute complex mutualistic relationships responsible for the maintenance of the reproduction of flowering plants in different biomes. The genus *Centris* stands out as one of the main groups of pollinators in the Neotropical region. These bees have a close relationship with floral oil-producing plants, using this resource in the construction of their nests and/or larval feeding. The aim of the present study was to compare the resources exploited by *Centris perforator* and *Centris xanthomelaena* and assess the established trophic relationships of these two species in a fragment of dry forest (Caatinga domain). For such, direct observations were made at the flowers and analyses were performed of the pollen load on the body of female bees and the content of the larval provisions in the nests. A strong association was found between the two bee species and plants with poricidal anthers of the genus *Chamaecrista*, which accounted for more than half of the larval diet in both species. Samples of the pollen load of *C. xanthomelaena* exhibited a greater diversity of pollen types. While *Rhaphiodon echinus* was a constant source of nectar for *C. xanthomelaena*, *C. perforator* females collected nectar from plants of short, rapid flowering, such as *Cenostigma microphyllum* and *Tabebuia aurea*. *Malpighia emarginata* was the main source of floral oil for both species. However, *C. xanthomelaena* also interacted with *Angelonia cornigera* and *Krameria* sp. to obtain this resource. The similarity in the trophic niche of the species was 57% in the subsamples of pollen on the body of females and 46% for larval provision. The results showed that areas of native vegetation are essential for bee populations in regions with agricultural activity, ensuring a regular supply of ecological resources for these bees.

KEYWORDS

solitary bee, *Centris*, diet range, Caatinga, plant-pollinator interactions

1 Introduction

For an estimated 90% of flowering plants, including diverse species of crops, depend on the pollination service provided by animals (Ollerton et al., 2011). The mutualistic relationships established between plants and pollinators are critical to the maintenance of ecosystems and are likely one of the most important animal-plant interactions (Klein et al., 2007; Ollerton et al., 2011). Bees (Apiformes) play a central role in this context, with solitary species constituting an important component of the community of pollinating insects (Roubik, 1992). The stability of these interactions is susceptible to anthropogenic changes and can be negatively impacted by numerous factors, such as habitat fragmentation (Aizen and Feinsinger, 2003; Xiao et al., 2016). Thus, studies on plant-pollinator interactions can contribute to the understanding of the dynamics of ecosystems.

The guild of oil-collecting bees and the plants that produce this resource was first studied by Vogel in 1974 and soon drew the attention of other authors (Vogel, 1974; Neff and Simpson, 1981; Buchmann, 1987; Cocucci, 1991; Vogel and MaChado, 1991; Neff and Simpson, 2017). The collection of floral oil by bees evolved independently in groups belonging to six different tribes, with Centridini, Tapinostapidiini and Tetrapediini representatives of the Neotropical region (Renner, 2006; Alves-dos-Santos et al., 2007; Moure et al., 2007). Females of these bees have morphological adaptations on the forelegs and/or middle legs that enable oil collection from structures named elaiophores, which may be trichomal or epithelial (Vogel, 1974; Neff and Simpson, 1981; Buchmann, 1987). Some of these species are adapted to oil collecting from a specific type of elaiophore, whereas others are able to exploit this resource from both types (Neff and Simpson, 1981). Floral oil collected by females is a resource of high energy value mixed with pollen and nectar in larval provision and/or used as a lining for brood cells (Vogel, 1974; Simpson et al., 1977; Cane et al., 1983; Buchmann, 1987; Sabino et al., 2019).

Within the tribe Centridini, the genus *Centris* Fabricius is composed of 14 subgenera and approximately 332 species distributed in the Neotropical region (Silveira et al., 2002; Moure et al., 2007; Vivallo, 2020, Vivallo, 2022a, Vivallo, 2022b; Vivallo et al., 2023). *Centris* females can nest on different substrates, but ground nesting is the predominant habit in this genus (Coville et al., 1983; Camillo et al., 1995; Aguiar et al., 2005; Martins et al., 2020a). Various morphological, physiological and behavioral characteristics make *Centris* bees stand out as the main pollinators of plants with mass flowering and species of economic interest, such as the West Indian cherry (*Malpighia emarginata* DC.) (Frankie et al., 1983; Schlindwein, 2000; Vilhena and Augusto, 2007; Vilhena et al., 2012; Silva et al., 2017). However, available information on the floral resources necessary to maintain natural populations of *Centris* species remains scarce, especially for ground-nesting species. For instance, the pollen content of larval provisions was analyzed for *Centris* (*Centris*) *flavifrons* (Fabricius) (Rêgo et al., 2006; Dórea et al., 2017), *Centris* (*Centris*) *caxienseis* Ducke (Ribeiro et al., 2008); *Centris* (*Melacentris*) *conspersa* Mocsáry (Rocha-Filho et al., 2017), *Centris* (*Paracentris*) *burgdorfi* Friese (Sabino et al., 2019) and *Centris* (*Melacentris*) *collaris* Lapeletier (Rocha-Filho et al., 2018), which correspond to approximately 2% of the species of the genus.

Although data on plants visited by bees are traditionally obtained through direct observations of flowers (e.g., Aguiar et al., 2003), palynology become increasingly important in this scenario, providing more detailed information on the interactions between bees and plants (Silva et al., 2020). A grain of pollen serves as an important taxonomic marker (Erdtman, 1960); thus, analyses can be performed of the pollen deposited on the scopa/corbicula of females, the provisions stocked in the brood cells and even larval feces (Dórea et al., 2010a, Dórea et al., 2010b; Silva et al., 2017).

As most floral visits by bees have the objective of collecting resources for feeding the offspring, palynological analyses of the provisions in nests can provide more in-depth information on the true spectrum of plants visited by females throughout their lives (Dórea et al., 2017; Silva et al., 2017). With regards to solitary bees, however, palynology has been used for provisions of few species, mainly due to the difficulty in finding the nests, especially of those that nest in the ground (Sabino et al., 2019). An alternative to the use of larval provisions has been found in the analysis of the pollen load on females, as the pollen collected from anthers is directed to the scopa/corbicula, transported to the nest and offered as larval provision. However, grains of pollen can also remain adhered to different parts of the body of females and are responsible for the reproduction of plants through the pollination process (Rech et al., 2014). Analyses of the pollen load adhered to the body of females has proved to be equally efficient for determining the trophic niche of these species, even in the absence of the nests (Silva et al., 2010, Sabino et al., 2019).

Centris (*Relicthemisia*) *xanthomelaena* Moure and Castro and *Centris* (*Trachina*) *perforator* Smith are two species broadly distributed in the Caatinga domain (dry forest) of Brazil (Zanella, 2000; Vivallo, 2020) and abundant in the study area. *Centris* *xanthomelaena* nests in a dense aggregation while *C. perforator* nests widely scattered (Martins et al., 2020a, Martins et al., 2020b), and occur in a sympatric manner. Considering the overlap in the period of activity, the principal aim of the present study was to compare the floral resources exploited by *C. perforator* and *C. xanthomelaena* and assess the trophic relationships established between the two species in a fragment of the Caatinga domain.

2 Materials and methods

2.1 Study area

The sampling area of the study is located in a fragment of the Caatinga situated on the Campus of Agrarian Sciences of Universidade Federal do Vale do São Francisco (UNIVASF) (9° 19'44,2"S, 40°33'30,1W) in the municipality of Petrolina, state of Pernambuco, Brazil (Figure 1A). The Caatinga is one of the phytogeographical domains of Brazil. It has a high level of endemism and is classified as a wooded steppe savanna (Andrade-Lima, 1981). The climate in the region is considered semiarid, dry and warm (BSh according to the Köppen classification), with low rainfall (annual average of 433 mm) and two well-defined seasons: dry from May to October and rainy from November to April. The annual average temperature is 24.8°C (Alvares et al., 2013).

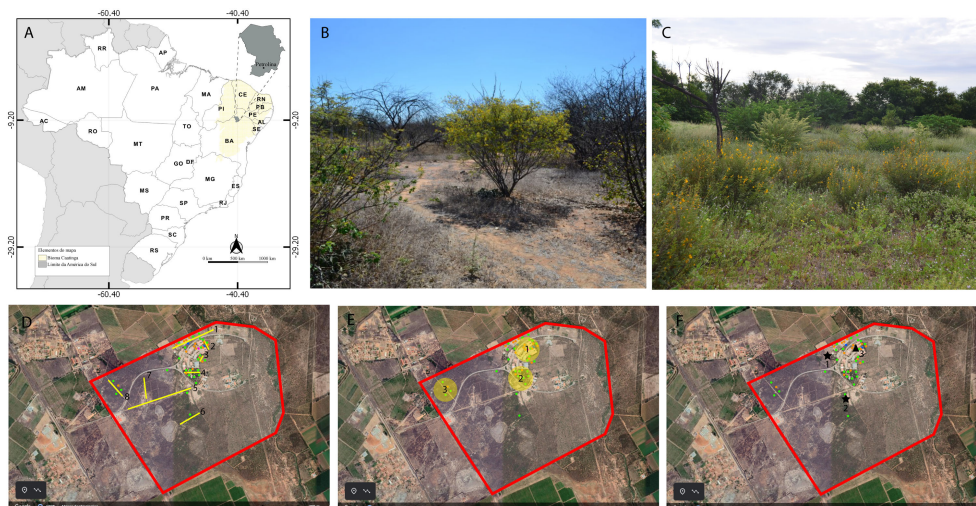


FIGURE 1

(A) Study area where samples were collected in the Caatinga environment, (B) open shrub layer with *Cenostigma microphyllum* blooming during the dry season, (C) herbaceous layer with the presence of *Chamaecrista*, (D–F) aerial view delimiting the Caatinga fragment area (red line): (D) transects traveled (the lines in yellow) to observe the plants visited by the species, (E) places where pollen load collections were carried out, (F) places where the brood cell samples were obtained (★ 1 and 2 represent the aggregations of *C. xanthomelaena* and ▲ represents the main nesting site for *C. perforator*).

The area is in the Senator Nilo Coelho Irrigation Project (C1), which is one of the main fruit farming centers in Brazil (Bustamante, 2009). Orchards of plants of agricultural interest surround the area, such as mangos (*Mangifera indica* L.), grapes (*Vitis vinifera* L.), coconut trees (*Cocos nucifera* L.) and acerola (West Indian cherry) (*Malpighia emarginata* DC.) (Figure 1).

The vegetation in the area is classified as low Caatinga (Andrade-Lima, 1981), with a predominance of bush vegetation, such as *Cenostigma microphyllum* (Mart. ex G. Don) Gagnon and G.P.Lewis and *Senegalia tenuiflora* (L.) Britton and Rose (Figure 1B), as well as an herbaceous stratum composed mainly of species of Lamiaceae, Leguminosidae, Malvaceae and Rubiaceae (Figure 1C), with the presence of large trees being rare.

2.2 Sampling

Monthly samples of bees were collected between November 2017 and October 2018 to record plants visited by the species. Collections were performed on two consecutive days from 6:00 to 17:00 h, totaling 22 hours per month, in eight preestablished transects of different distances (Figure 1D). One collector carefully inspected each flowering plant for maximum five minutes and both female and male bees were caught randomly with an insect net during visits to the flowers. Whenever possible, the resource collected by the bee was observed. To avoid recapture, bees were marked on the thorax with a nontoxic pen (UniPosca®) and released. Specimens of both species were sacrificed, mounted and deposited in the Entomological Collection of the UNIVASF Entomology Lab.

To characterize the composition of the pollen load on the females, monthly visits were performed in two perimeters

(Figure 1E) on two consecutive days between the years 2018 and 2021. In this period, a maximum of five samples were collected per month based on the presence of females, totaling 60 samples (30 for each species). Females with pollen adhered to the scopa were caught with an insect net during flight. The pollen on the scopa was removed using a rinsing process following the method proposed by Silva et al. (2010) and transferred to 15-ml Falcon test tubes containing 1.5 ml of distilled water. The females were then dried with paper towel, marked on the thorax with nontoxic pens (UniPosca®) of different colors to avoid recapture and released. The pollen removed was stored in 70% alcohol until acetolysis.

To understand the composition of the larval diet, samples of larval provisions were collected from 60 brood cells (30 from each species) from 30 nests of *C. xanthomelaena* and 27 nests of *C. perforator* (Figure 1F) between the years 2017 and 2021. Due to the low availability of *C. perforator* nests, no minimum number of samples per month was established for this species. Additionally, more than one brood cell was used of the nests built by two *C. perforator* females that had more than 12 cells/nest, with cells selected from different stages of construction of the nests. All samples were collected from fresh provisions soon after the conclusion of the nests by the females and stored in 70% alcohol until acetolysis.

2.3 Pollen analysis

The pollen samples were submitted to chemical treatment (acetolysis), as proposed by Erdtman (1960). At the end of the process, slides were mounted for optical microscopic analysis. Four slides were mounted with Kisser glycerol gelatin (Kisser, 1935) for each sample. After mounting, qualitative analysis was performed for

the identification of the pollen types on each slide and quantitative analysis was performed, with counts of 1000 grains of pollen per sample (250 per slide) (Montero and Tormo, 1990). Pollen types that appeared at a frequency of less than 0.01% were considered contaminants and excluded from the quantitative analysis.

Based on the quantitative analysis, the frequency of occurrence was calculated for the different types of pollen in each sample and mean frequencies were calculated for each type among the samples (Villanueva-Gutiérrez and Roubik, 2004; Silva, 2009). The percentage of each pollen type was determined and categorized using the classification proposed by Jones and Bryant (1996): very frequent (> 50% of all pollen on the slide), frequent (20 to 50%), infrequent (10 to 20%) and rare (< 10%).

In the period from 2018 to 2019, monthly monitoring was performed of plants in bloom in the study area (UNIVASF Campus of Agrarian Sciences), with a total of 153 species sampled. A reference slide collection was created of the pollen obtained from the flowers of the species, following the method proposed by Erdtman (1960). The pollen collection contributed to a more precise identification of the pollen types in the samples from the bees. Vouchers of the plants were identified by specialists and deposited in the Vale do São Francisco Herbarium.

2.4 Data analysis

The Shannon-Weaver diversity index (H') (Shannon, 1948) was used to assess the diversity of plants that composed the diet, considering the richness and abundance of pollen types. The uniformity of the floral resources was tested by calculating Pielou's evenness index (J') (Pielou, 1977). The dominance (D) of pollen types was determined using the Berger-Parker index (Magurran, 2004). The number of the most important pollen types in the diet of the species was calculated from the apparent S (apparent $S = e^{H'}$). The analysis of trophic niche overlap of the two species was performed using the Jaccard similarity index (S_j) and the proportion of plant species in the diets was determined using the percentage similarity index (PS). (The formulas are available in the Supplementary Data 1).

The bipartite package of the R program 3.4.1 (R Core Team, 2017) was used for the representation of interaction networks in Eulerian graphs. To visualize the relationship of the plants on the genus level and the bee species, a weighted network was created through the analysis of quantitative matrices using the Pajek program version 5.13 (De Nooy et al., 2018) and the 'Kamada-Kawai free' method, making the subgroups and centrality of each vertex more evident.

3 Results

3.1 Floral visits

A total of 433 individuals of the two species were collected: 209 specimens of *Centris perforator* and 224 specimens of *Centris xanthomelaena* (Table 1). Together both species visited 32 plant

species (*C. perforator* = 22 species and *C. xanthomelaena* 19 species). Leguminosae was the botanical family with the largest number of interactions ($n = 274$), the majority of which involved the subfamily Caesalpinioideae ($n = 226$). Lamiaceae was the family with the second largest number of interactions ($n = 104$), despite the small number of species recorded in the area.

Centris perforator females interacted with the flowers of 19 plant species and males visited 14 species. The largest part of the pollen sources used for larval feeding was nearly exclusively from plants of the family Leguminosae, with *Chamaecrista* and *Senna* as the genera with the largest number of visits ($n = 73$ and 24, respectively). *Cenostigma microphyllum* (Mart. ex G.Don) Gagnon and G.P.Lewis was the main source of nectar visited by both male and females of *C. perforator*. However, *Rhaphiodon echinus* (Nees and Mart.) Schauer and *Libidibia ferrea* (Mart. ex Tul.) L.P. Queiroz also received a number of visits by males of the species. The only source of floral oil visited by the females was *Malpighia emarginata*, which was also used sporadically as a source of pollen. During the flowering period of *Tabebuia aurea* (Silva Manso) Benth. and Hook.f. ex S.Moore (September–November), nectar collecting by both males and females seems to concentrate on this plant.

Females of the species *C. xanthomelaena* interacted with the same number of plants as those of *C. perforator* ($n = 19$). However, *C. xanthomelaena* males restricted their visits to smaller number of plants ($n = 9$). Females restricted pollen collecting to four species of *Chamaecrista* (L.) Moench ($n = 69$), followed by *Zornia brasiliensis* Vogel ($n = 6$). Both males and females were regularly seen visiting *R. echinus*, which was the main species visited by females to collect nectar. During pollen collection, females also interacted with *R. echinus*, *Malpighia emarginata* and *Angelonia cornigera* Hook.f. were the two oil sources visited by the females. Table 1 displays the complete list of plants on which males and females of both species were observed or collected.

3.2 Pollen sources

For both sample types (pollen load on females and larval provisions), 47 pollen types were found, corresponding to at least 16 families and 26 genera of plants (Table 2).

3.2.1 *Centris perforator*

The qualitative analyses of the pollen load from females ($n = 30$) revealed the presence of 25 pollen types belonging to seven botanical families, six of which could not be identified (Figure 2). The greatest richness of pollen types was found in the family Leguminosae ($n = 15$ species). The pollen types with the greatest representativeness were *Senna martiana*, *Chamaecrista repens* and *Chamaecrista hispidula*, which together accounted for 78.1% of the pollen types represented in the samples and were the three main sources of pollen visited by the females (Table 2). Other pollen types that had representation greater than 1% were *Malpighia emarginata*, *Chamaecrista calycioides*, *Chamaecrista amiciella*, *Cenostigma microphyllum* and *Tabebuia aurea*, which were classified as rare pollens, accounting together for 18.54% of the pollen types found in the samples. *Cenostigma microphyllum* and *T.*

TABLE 1 Plants visited by females and males of *Centris perforator* and *Centris xanthomelaena* in a fragment of Caatinga in the municipality of Petrolina, PE, Brazil, and main resource offered (P = pollen; N = nectar; O = floral oil).

| Family/Plant species | Plant type | <i>Centris perforator</i> | | <i>Centris xanthomelaena</i> | | Resource offered |
|---------------------------------|------------|---------------------------|--------|------------------------------|--------|------------------|
| | | Male | Female | Male | Female | |
| Apocynaceae | | | | | | |
| <i>Allamanda puberula</i> | shrubs | 5 | – | – | – | N |
| Bignoniaceae | | | | | | |
| <i>Tabebuia aurea</i> | Tree | 12 | 4 | – | – | N/P |
| Euphorbiaceae | | | | | | |
| <i>Cnidoscolus quercifolius</i> | shrubs | – | – | – | 2 | N/P |
| <i>Cnidoscolus urens</i> | shrubs | 2 | – | 4 | 1 | N/P |
| <i>Jatropha mutabilis</i> | shrubs | – | – | – | 1 | N/P |
| Lamiaceae | | | | | | |
| <i>Hyperia salzmännii</i> | shrubs | – | – | 8 | 1 | N/P |
| <i>Marsypianthes chamaedrys</i> | herbaceous | – | – | 3 | 2 | N/P |
| <i>Rhaphiodon echinus</i> | herbaceous | 10 | 2 | 29 | 49 | N/P |
| Leg-Caesalpinioideae | | | | | | |
| <i>Caesalpinia microphylla</i> | Tree | 3 | – | – | – | N/P |
| <i>Cenostigma microphyllum</i> | Tree | 19 | 12 | 16 | 7 | N |
| <i>Chamaecrista amiciella</i> | herbaceous | – | 1 | – | 24 | P |
| <i>Chamaecrista calycioides</i> | herbaceous | – | 1 | – | 18 | P |
| <i>Chamaecrista repens</i> | shrubs | – | 40 | – | 22 | P |
| <i>Chamaecrista supplex</i> | herbaceous | – | – | – | 5 | P |
| <i>Libidibia ferrea</i> | Tree | 11 | 3 | – | – | N/P |
| <i>Poincianella bracteosa</i> | Tree | 7 | 1 | – | – | N/P |
| <i>Senna macranthera</i> | Tree | – | 8 | – | – | P |
| <i>Senna martiana</i> | Tree | – | 16 | – | – | P |
| <i>Tamarindus indica</i> | Tree | 4 | 8 | – | – | N/P |
| Leg-Papilionoideae | | | | | | |
| <i>Centrosema</i> sp.1 | Liana | – | 1 | – | – | N/P |
| <i>Dioclea grandiflora</i> | Tree | 3 | 1 | – | – | N/P |
| <i>Luetzelburgia bahiensis</i> | Tree | 2 | – | 3 | 1 | N/P |
| <i>Macroptilium lathyroides</i> | herbs | – | 8 | 5 | 1 | N/P |
| <i>Macroptilium martii</i> | Liana | – | – | 2 | 3 | N/P |
| <i>Zornia brasiliensis</i> | herbaceous | – | – | – | 6 | N/P |
| Malpighiaceae | | | | | | |
| <i>Malpighia emarginata</i> | shrubs | – | 2 | – | 2 | P/O |
| Malvaceae | | | | | | |
| <i>Waltheria albicans</i> | herbaceous | – | – | 4 | 2 | N/P |
| Passifloraceae | | | | | | |
| <i>Passiflora cincinnata</i> | Liana | 6 | 2 | – | – | N/P |

(Continued)

TABLE 1 Continued

| Family/Plant species | Plant type | <i>Centris perforator</i> | | <i>Centris xanthomelaena</i> | | Resource offered |
|-----------------------------------|------------|---------------------------|--------|------------------------------|--------|------------------|
| | | Male | Female | Male | Female | |
| Passifloraceae | | | | | | |
| <i>Passiflora foetida</i> | Liana | – | 2 | – | – | N/P |
| Polygalaceae | | | | | | |
| <i>Polygala cf. violacea</i> | herbaceous | – | – | – | 1 | N/P |
| Plantaginaceae | | | | | | |
| <i>Angelonia cornigera</i> | herbaceous | – | – | – | 2 | P/O |
| Verbenaceae | | | | | | |
| <i>Stachytarpheta microphylla</i> | herbaceous | 1 | – | – | – | N/P |
| Total | | 89 | 120 | 74 | 150 | |

aurea were the main sources of nectar and *M. emarginata* was the only source of floral oil exploited by the species in the sample.

Eighteen pollen types were found in the larval provisions (n = 30), belonging to five botanical families, with Leguminosae again the family with the greatest richness of pollen types (n = 14 species). *Chamaecrista repens* was the predominant pollen type in the samples and, together with the pollen types *Chamaecrista calycioides* and *Senna martiana*, represented the main sources of

pollen, accounting for 88.05% of the pollen types found in the samples (Figure 3, Table 2). *Chamaecrista hispidula* and *Malpighia emarginata* were rare pollen types and the latter was the probable source of floral oil.

3.2.2 *Centris xanthomelaena*

Twenty-seven pollen types from 10 botanical families were found in the pollen loads on the body of the females (n = 30).

TABLE 2 Frequency of pollen types/plants recorded in samples from the body of females and nests of *Centris perforator* and *Centris xanthomelaena*.

| Pollen types/Plant species | Percentage contribution (%) | | | | Resource offered |
|---------------------------------|-----------------------------|------|-------------------------|-------|------------------|
| | <i>C. perforator</i> | | <i>C. xanthomelaena</i> | | |
| | body | nest | body | nest | |
| Amaranthaceae | | | | | |
| <i>Alternanthera</i> sp. | – | – | – | 0,01 | – |
| Bignoniaceae | | | | | |
| <i>Tabebuia aurea</i> | 1,53 | 0,53 | – | – | N/P |
| Curcubitaceae | | | | | |
| sp.1 | 0,02 | – | – | – | – |
| Euphorbiaceae | | | | | |
| <i>Cnidoscolus quercifolius</i> | – | – | – | 0,01 | N/P |
| <i>Cnidoscolus urens</i> | – | – | – | 0,01 | N/P |
| Krameriaceae | | | | | |
| <i>Krameria</i> sp. | – | – | 0,03 | – | P/O |
| Lamiaceae | | | | | |
| <i>Hyptenia salzmannii</i> | – | – | – | 0,01 | N/P |
| <i>Hyptis</i> sp. | 0,01 | – | 0,11 | – | – |
| <i>Rhaphiodon echinus</i> | 0,01 | 0,27 | 10,05 | 10,62 | N/P |

(Continued)

TABLE 2 Continued

| Pollen types/Plant species | Percentage contribution (%) | | | | Resource offered |
|---------------------------------|-----------------------------|-------|-------------------------|-------|------------------|
| | <i>C. perforator</i> | | <i>C. xanthomelaena</i> | | |
| | body | nest | body | nest | |
| Leg.-Caesalpinioideae | | | | | |
| <i>Cenostigma microphyllum</i> | 2,74 | 0,43 | 0,29 | 0,17 | N/P |
| <i>Chamaecrista amiciella</i> | 3,72 | 0,09 | 17,46 | 8,39 | P |
| <i>Chamaecrista calycioides</i> | 5,11 | 19,94 | 32,46 | 46,81 | P |
| <i>Chamaecrista hispidula</i> | 18,67 | 3,56 | 11,24 | 3,57 | P |
| <i>Chamaecrista repens</i> | 28,59 | 51,13 | 10,89 | 13,49 | P |
| <i>Libidibia ferrea</i> | 0,61 | – | – | – | N/P |
| <i>Senegalia tenuifolia</i> | 0,02 | 0,21 | 0,39 | 2,28 | N/P |
| Mimosoideae sp.1 | 0,01 | 2,44 | – | 0,03 | – |
| Mimosoideae sp.2 | 0,35 | – | – | – | – |
| <i>Senna macranthera</i> | 0,95 | 0,03 | – | – | P |
| <i>Senna martiana</i> | 30,84 | 15,97 | – | 8,82 | P |
| Leg.-Papilionoideae | | | | | |
| <i>Cajanus cajan</i> | 0,24 | 0,01 | – | 0,09 | N/P |
| <i>Centrosema</i> sp. | 0,18 | 0,01 | 0,2 | 0,01 | N/P |
| <i>Cratylia mollis</i> | – | 0,01 | 0,05 | 0,04 | N/P |
| <i>Dioclea grandiflora</i> | – | 0,01 | – | – | N/P |
| <i>Macroptilium lathyroides</i> | – | 0,34 | – | 0,15 | N/P |
| <i>Macroptilium martii</i> | 0,9 | – | 0,14 | – | N/P |
| <i>Zornia brasiliensis</i> | 0,02 | – | 2,13 | 1,48 | N/P |
| Leguminosae sp.1 | – | – | – | 0,41 | – |
| Leguminosae sp.2 | – | – | 2,67 | 1,07 | – |
| Malpighiaceae | | | | | |
| <i>Malpighia emarginata</i> | 5,44 | 3,40 | 2,01 | 1,12 | P/O |
| Mal.- Sterculioideae | | | | | |
| <i>Melochia tomentosa</i> | 0,01 | – | 0,33 | 0,18 | N/P |
| <i>Waltheria albicans</i> | 0,01 | – | 0,30 | 0,20 | N/P |
| Myrtaceae | | | | | |
| sp.1 | – | 0,44 | – | – | – |
| Passifloraceae | | | | | |
| <i>Passiflora foetida</i> | 0,01 | – | 0,01 | – | N/P |
| Polygalaceae | | | | | |
| <i>Polygala violacea</i> | – | – | 0,01 | – | N |
| Plantaginaceae | | | | | |
| <i>Angelonia cornigera</i> | – | – | 0,67 | 0,96 | P/O |

(Continued)

TABLE 2 Continued

| Pollen types/Plant species | Percentage contribution (%) | | | | Resource offered |
|------------------------------|-----------------------------|-------------|-------------------------|-------------|------------------|
| | <i>C. perforator</i> | | <i>C. xanthomelaena</i> | | |
| | body | nest | body | nest | |
| Rubiaceae | | | | | |
| <i>Richardia grandiflora</i> | – | – | 0,01 | – | N/P |
| Solanaceae | | | | | |
| <i>Solanum</i> sp. | – | – | 3,32 | – | P |
| Turneraceae | | | | | |
| <i>Turnera subulata</i> | – | – | – | 0,01 | N/P |
| Indeterminate 1 | 0,04 | – | – | – | – |
| Indeterminate 2 | 0,03 | – | – | – | – |
| Indeterminate 3 | 4,08 | – | – | – | – |
| Indeterminate 4 | 0,03 | – | – | – | – |
| Indeterminate 5 | 0,03 | – | – | – | – |
| Indeterminate 6 | 0,01 | – | – | – | – |
| Indeterminate 7 | – | 0,14 | – | – | – |
| S | 29 | 19 | 22 | 25 | – |
| H' | 1,80 | 1,42 | 2,08 | 1,78 | – |
| S apparent | 6,04 | 4,13 | 8,00 | 5,92 | – |
| J' | 0,56 | 0,49 | 0,63 | 0,55 | – |
| D | 0,31 | 0,51 | 0,32 | 0,47 | – |

body = pollen load on females; nest = larval provision. S = species richness; H' = Shannon-Weaver diversity index; apparent S = apparent number of pollen type used; J' = evenness index; D = Berger-Parker dominance index.

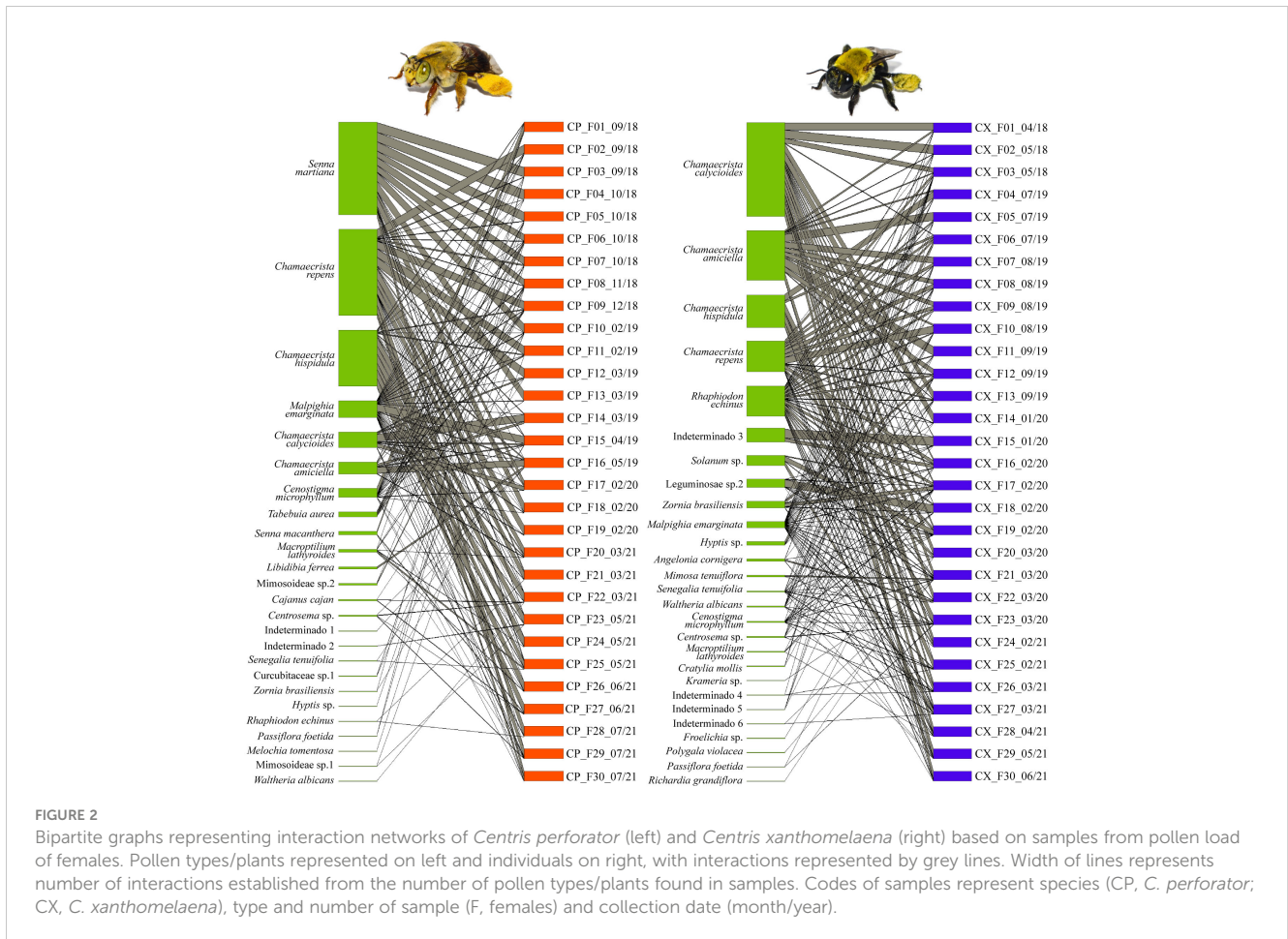
The main sources of pollen corresponded to four pollen types from the genus *Chamaecrista* (Figure 2): *Chamaecrista calycioides*, *Chamaecrista amiciella*, *Chamaecrista hispidula* and *Chamaecrista repens*. *Rhaphiodon echinus* was an infrequent nectar source, but was present in all samples analyzed, corresponding to 10.07% of the diet. *Melochia tomentosa* and *Waltheria albicans* were alternative sources of nectar, which, despite being rare pollen types, were frequent in the samples. Three sources of oil were recorded in the samples: *Malpighia emarginata*, *Angelonia cornigera* and *Krameria* sp. Among the other pollen types found in the samples, only *Solanum* sp. (3.32%), Leguminosae sp.2 and *Zornia brasiliensis* had contributions higher than 1% (Table 2).

Twenty-five pollen types belonging to eight botanical families were found in the larval provisions (n = 30). Once again, the genus *Chamaecrista* was predominant in the sample (Figure 3), accounting for 72.28%: *Chamaecrista calycioides*, *Chamaecrista repens*, *Chamaecrista amiciella* and *Chamaecrista hispidula*. *Senna martiana* was a rare source of pollen, accounting for 8.82% of the sample. *Rhaphiodon echinus* was the most representative source of nectar, corresponding to 10.63% of the pollen grains found. Pollen from two floral oil-producing species was identified with rare frequency in the samples: *Malpighia emarginata* and *Angelonia cornigera* (Table 2).

3.3 Trophic interactions

Centris xanthomelaena use a greater diversity of pollen types ($H'_{\text{nest}} = 2.08$; $H'_{\text{body}} = 1.78$) compared to *C. perforator* ($H'_{\text{nest}} = 1.42$; $H'_{\text{body}} = 1.81$). The number of species considered important in the diet of the immature forms (apparent S) varied with the type of sample, ranging from four to eight (Table 2). Three to nine pollen types were found in each subsample for *C. perforator* ($\bar{X} = 5.4 \pm 1.44$; n = 60), whereas three to 13 pollen types were found in each subsample for *C. xanthomelaena* ($\bar{X} = 7 \pm 2.35$; n = 60).

The two species used plants of the genus *Chamaecrista* as the main source of pollen (Figure 4), diverging on the species level. While *Ch. repens* was used by *C. perforator* as the main source of pollen, *C. xanthomelaena* collected the large portion of pollen from *Ch. calycioides*. Moreover, *Senna martiana* composed a considerable fraction of the larval diet for *C. perforator*. A difference was also found with regards to the sources of nectar, with *Ce. microphyllum* as the main source for *C. perforator* and *R. echinus* as the most important source for *C. xanthomelaena*. The Jaccard index (Sj) revealed 36.8% similarity in the pollen samples from the body of all females and 43.3% in the larval provision samples. The proportions of plant species in the diet (PS) were



similar, with 43.52% overlap in the samples from the body of the females and 47.89% in the samples from the nests.

4 Discussion

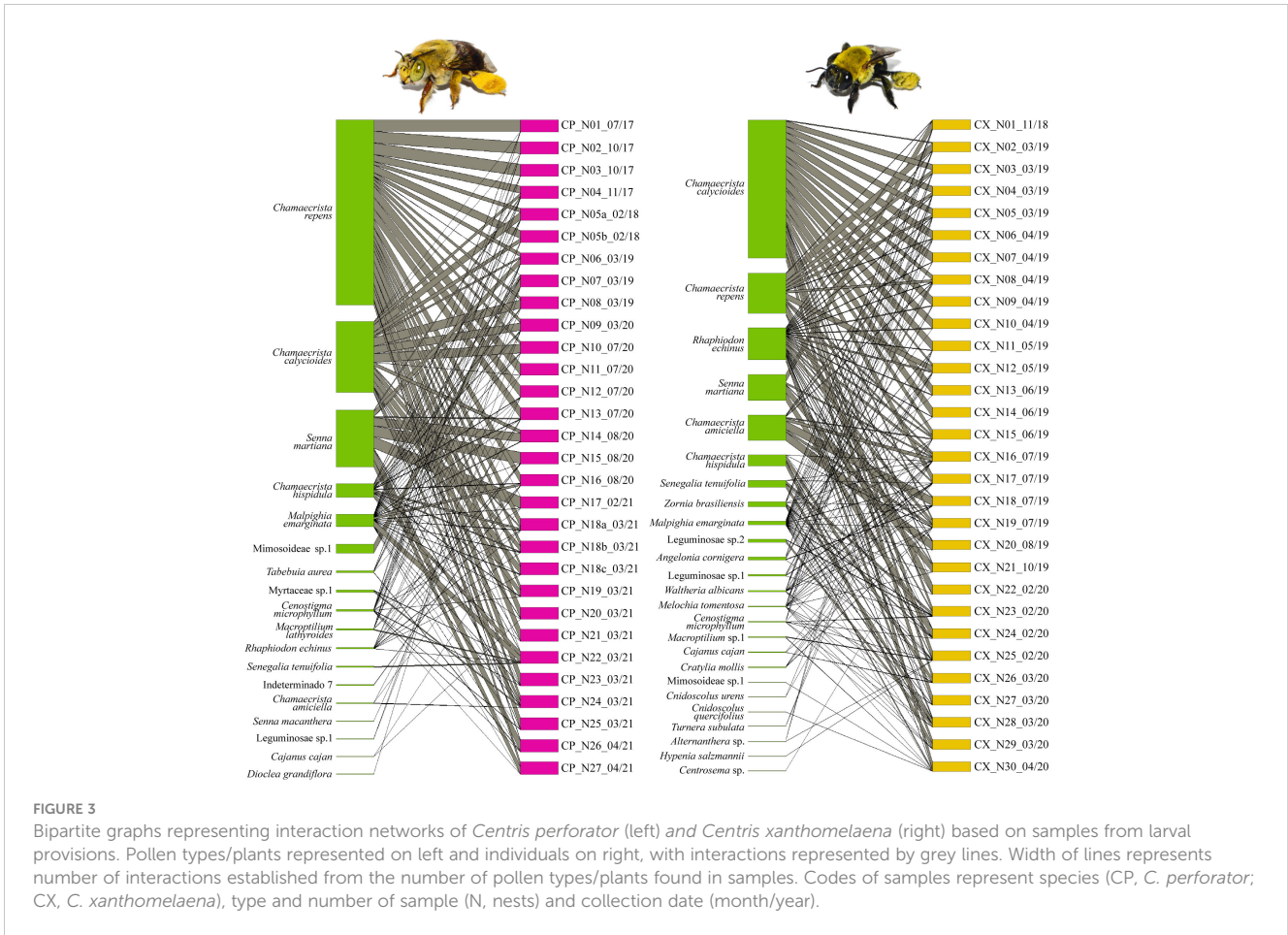
4.1 Trophic niche of species

The analyses of the pollen load on the females and the nests of *Centris perforator* and *Centris xanthomelaena* demonstrated a strong association with plants with poricidal anthers, such as the genus *Chamaecrista*, which corresponded to the largest part of the pollen types and was present in all samples analyzed. Pollen types from at least four species of *Chamaecrista* were identified in the samples, together corresponding to more than 45% of the pollen types found on the scopas and in the nests. Certainly, *Chamaecrista* is the main source of pollen for both species of *Centris*. The results of the present study lend strength to the hypothesis put forth by Aguiar et al. (2003) that species of *Centris* endemic to the Caatinga domain, such as *Centris hyptidis* Ducke and *C. xanthomelaena*, restrict pollen collecting to fewer sources in comparison to more widely distributed species of the genus. The description of pollen sources found in the nests of *Centris analis* (Fabricius), *Centris tarsata* Smith and *Centris trigonoides* Lepelletier studied in an area of the Caatinga demonstrated a strong association with species of Leguminosae,

especially the genera *Chamaecrista* and *Senna* (Aguiar et al., 2003; Dórea et al., 2010a, Dórea et al., 2010b; Dórea et al., 2013; Cruz et al., 2015). Vivallo and Zanella (2021) in a collection of plants visited by *C. xanthomelaena* also pointed to *Chamaecrista* as the only source of pollen recorded to date. Moreover, Sabino et al. (2019) found that *Chamaecrista* was a constant or dominant source of pollen for *Centris burgdorfi* even in different types of vegetation.

The two studied bee species differ regarding to the species *Chamaecrista* exploited for pollen. *Ch. calycioides* was the predominant pollen type in the samples of *C. xanthomelaena* while *Ch. repens* was the dominant pollen types in the samples of *C. perforator*. This difference may be related to the size of the flowers, as *Centris xanthomelaena*, which is smaller, exhibited a preference for smaller *Chamaecrista* flowers (Figure 5), unlike the dominant species in the samples of *C. perforator*, thus diminishing competition among the females (see the details of measurements in Supplementary Table 1, Supplementary Figure 1).

In the Caatinga domain, Leguminosae is the best represented botanical family and is an important resource for various species of bees (Queiroz, 2002). The high availability and proximity of plants in this family to nesting sites optimizes the provisioning phase and, consequently, diminishes the energy expenditure of females in search of resources. Despite being an abundant resource, pollen collection from various species of Leguminosae, especially those of the subtribe Cassiinae, is limited to bees with the capacity to

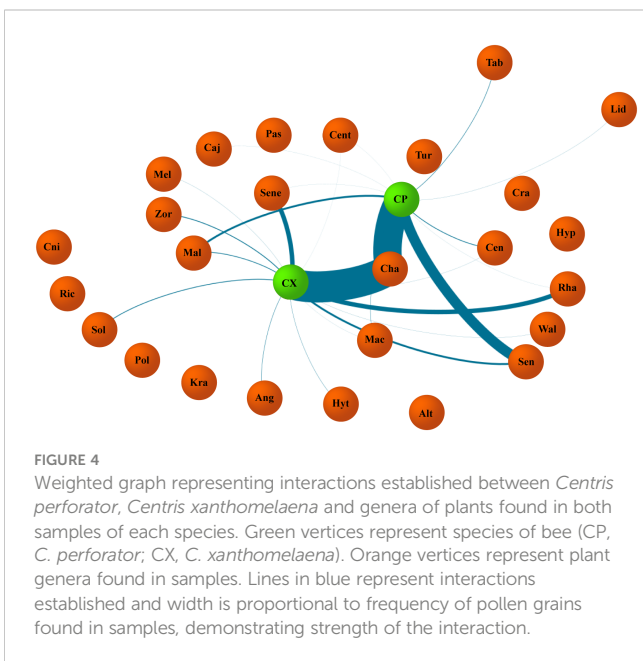


perform collection by vibration, which is known as “buzz pollination”, such as those of the genera *Bombus*, *Centris*, *Epicharis*, *Melipona* and *Xylocopa* (Nunes-Silva et al., 2010). With buzz pollination, pollen is released from the poricidal anthers through the vibration executed by the thoracic muscles of the

bees (Buchmann, 1983). The high protein content of the pollen produced by plants with poricidal anthers may result in the preference on the part of females due to the quality of the resource (Roulston et al., 2000; Vaudo et al., 2020).

Richness in the pollen samples ranged from 18 to 27 species. The diversity indices in the samples of *C. perforator* varied mainly due to the presence of contaminant species, with percentages lower than 1% (12 species) on the body of females. We believe that various of these species were visited for nectar consumption (even the undetermined ones) or only represent contamination during foraging of the females. The number of species and Shannon’s diversity index (H') were lower in the nests of *C. perforator* ($S = 18$; $H' = 1.42$) and the brood cells are evidently supplied with pollen from Leguminosae – Caesalpiniaceae (> 75% *Chamaecrista* + 16% *Senna*), thus explaining a higher dominance index in comparison to pollen from the scopa. The richness of pollen types used by *C. xanthomelaena* was slightly higher in the samples from the scopa than those from the nests. In contrast, dominance was greater in the samples from the brood cells of the two species.

The evenness indices (J') were similar in all samples (difference of less than 10%) and slightly higher in the sample from the nests of the two species of *Centris*. The Jaccard indices (S_j) indicated 36.8% similarity in the samples of pollen from the body of the females of the two species and 43.3% for the samples from nests. The proportions of plants species in the diet (PS) varied, with 43.52% overlap in the samples from the scopas of the females and 47.89% in the samples from the nests of the two species.



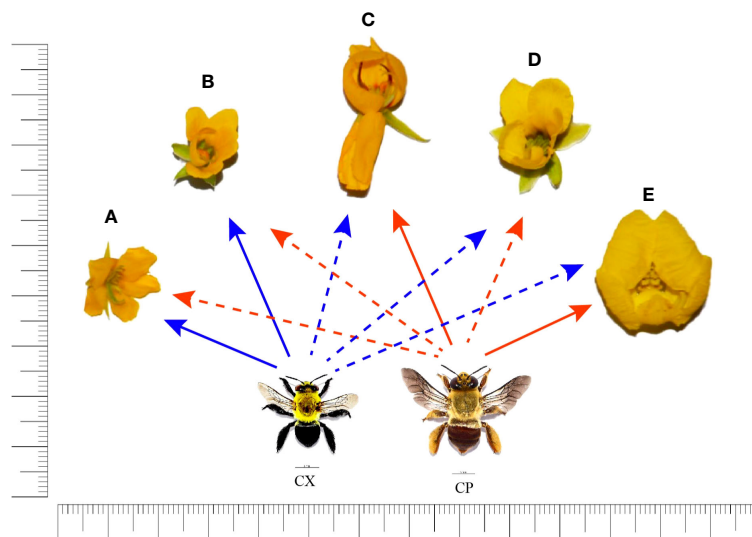


FIGURE 5

Relative sizes of *Chamaecrista* and *Senna* flowers used as a pollen source by *Centris xanthomelaena* (CX) and *Centris perforator* (CP) in their diets. The arrows indicate partial (dashed line) or priority (solid line) use of pollen. (A) *Chamaecrista calycioides*; (B) *Chamaecrista amiciella*; (C) *Chamaecrista repens*; (D) *Chamaecrista hispida*; (E) *Senna martiana*. Scale = 5 mm.

Despite that close similarity in the sources of pollen exploited by the two species of *Centris*, a difference was found in the plants visited to obtain nectar. *Rhaphidodon echinus* was the main source of nectar recorded in all samples of *C. xanthomelaena*, with *M. tomentosa* and *W. albicans* as secondary sources. Apparently, *R. echinus* is an annual source of nectar composing the diet of females and immature forms, even in periods of resource scarcity, and accounted for approximately 10% of the pollen types in the samples. Martins et al. (2020b) found that nectar is one of the constituents of the larval provisions of *C. xanthomelaena* and added together with the oil soon after pollen collection trips. *Rhaphidodon echinus* was also reported as a source of nectar for other species of *Centris* in the Caatinga domain, such as *C. analis* (Dórea et al., 2010a), *C. tarsata* (Dórea et al., 2010b) and *C. trigonoides* (Dórea et al., 2013). Besides being endemic to the Caatinga, *R. echinus* is one of the main plants of the herbaceous stratum in the study area (Harley et al., 2015). Floral visitation data confirm that this herbaceous plant is a key species for the permanence of *C. xanthomelaena* in the area.

The sources of nectar for *C. perforator* were more diverse. The pollen from *Cenostigma microphyllum* appears with greater frequency in the samples, but the main source of nectar alternated with the period of the year. In samples from September to November, *Tabebuia aurea* was the main source of nectar visited by the females. This species has mass flowering in the dry season (Barros, 2001), when resource scarcity naturally occurs.

In the same way as the females, the males of both species diverged in their trophic niche with regards to the main sources of nectar exploited. Males of *C. xanthomelaena* visited flowers of *R. echinus* more intensely, whereas the two main sources of nectar visited by males of *C. perforator* were *Ce. microphyllum* and *T. aurea*. Moreover, males of this species demonstrated territorial behavior at these plants, underscoring their importance for the trophic niche. To maximize reproductive success, patrolling for

virgin females on flowers is one of the tactics employed by males of different species (Paxton, 2005), which would explain the preference of males of *C. xanthomelaena* and *C. perforator* for the main sources of nectar used by the females.

4.2 Interaction with floral oil-producing plants

Bees of the genus *Centris* have a strong association with plants of the family Malpighiaceae (Anderson, 1990) and this interaction is reflected in the source of floral oil exploited by *C. perforator* and *C. xanthomelaena*. The analysis of the samples revealed that *M. emarginata* is the main source of oil used by both species. Despite appearing to be the exclusive source of oil for *C. perforator*, the *C. xanthomelaena* samples indicate that *Agelonia cornigera* and *Krameria* sp. are alternative sources of oil used by the females. Besides floral oil, some studies indicate that Malpighiaceae also furnishes pollen as a reward, such as the genus *Epicharis*, in which pollen loads can contain more than 90% of the pollen from *Byrsonima* (Gaglianone, 2005). However, only two samples of *C. perforator* had *M. emarginata* as the dominant pollen type.

The presence of pollen from *Agelonia cornigera* in the samples occurred simultaneously to the rainy period (February to May), in which peak flowering of this plant also occurred. The flowers were found in sites with sandy soil very close to the nesting sites. In the samples containing pollen from *A. cornigera*, the frequency of grains of pollen from *M. emarginata* was very low or absent.

Although most species of *Centris* are adapted to collect oil from epithelial elaiophores (Vogel, 1974; Neff and Simpson, 1981), some species have morphological modifications that enable collecting oil from flowers with trichomal elaiophores (Vogel, 1974; Simpson et al., 1990; Cocucci, 1991; MaChado et al., 2002). This modified

“four-legged” pattern (Neff and Simpson, 1981) is found in *C. xanthomelaena*, *C. burgdorfi*, *C. tricolor* and all species of the subgenus *Hemisiella* (Taniguchi, 2010), enabling these species to expand their sources of oil (Neff and Simpson, 1981). Sabino et al. (2019) studied three populations of *C. burgdorfi* in different types of vegetation and found plasticity with regards to the sources of oil exploited in flowers with epithelial and trichomal elaiophores of the genera *Krameria* and *Angelonia*, respectively. Although pollen from *Krameria* was found in a low frequency in the samples of *C. xanthomelaena*, no plant belonging to this genus was found within a 500-meter radius of the nesting sites of the species. There are reports of *C. xanthomelaena* serving as an effective pollinator of *Krameria grandiflora*, which also received sporadic visits from *C. perforator* (Carneiro et al., 2019).

4.3 Final remarks

The females of *Centris perforator* and *Centris xanthomelaena* demonstrated high dependence on the vegetation mainly in the herbaceous and shrub strata. These strata are fundamental to the survival and permanence of pollinating agents in agricultural areas (Wolowski et al., 2019), but are constantly eliminated within these areas. Acerola (West Indian cherry) requires pollinators for cross fertilization (Freitas et al., 1999; Sazan et al., 2014), which makes good management practices all the more necessary, ensuring not only productivity, but also the quality of the fruit (Magalhães and Freitas, 2013). As the visits of females of *C. perforator* and *C. xanthomelaena* are directed to the collection of the floral oil in acerola, the possibility of the management of females in orchards depends on the presence of the surrounding herbaceous and shrub strata, ensuring the availability of sources of pollen and nectar essential to the survival and permanence of the populations of the species in the area.

The availability of floral resources is one of the main factors responsible for the regulation and abundance of native bee populations (Roulston and Goodell, 2011), especially those resources that are indispensable to species survival, such as the case of floral oil for *Centris* (Silva et al., 2017). Silva et al. (2019) call attention to the change in the regularity of floral resources in response to climate change events, such as long periods of drought, especially in dry forests like the Caatinga. Consequently, the reduction in these floral resources for bees can cause the decline in these pollinators, thus affecting the biome as a whole (Kearns et al., 1998; Kevan and Imperatriz-Fonseca, 2002). The herbaceous stratum constitutes one of the main groups of plants that can suffer these effects more intensely, especially plants endemic to the Caatinga (Silva et al., 2019). In this scenario, populations of *C. perforator* and *C. xanthomelaena* could be affected, as both species are highly dependent on plants of this stratum, such as the endemic species *Cenostigma microphyllum* and *Raphiodun echinus*.

5 Conclusion

Despite visiting numerous species of plants, few of these species contributed to the major fraction of the diet of immature forms. The

genus *Chamaecrista* is a key group for the maintenance of populations of *Centris perforator* and *Centris xanthomelaena* in the area of the Caatinga domain. However, differences in the trophic niches are found on the species level, thus avoiding interspecific competition. Most females of both species interacted with acerola (West Indian cherry) (*Malpighia emarginata*) only for the collection of floral oil, which underscores the importance of maintaining plants that provide nectar and pollen in areas surround the orchards, especially species with poricidal anthers, like *Chamaecrista*. Lastly, areas of native forest are fundamental to the maintenance of bee populations in zones of agricultural activity, ensuring the regularity of important resources for the feeding of adults and the diet of immature forms.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

HM: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. MD: Formal analysis, Methodology, Writing – original draft, Writing – review & editing. VF: Conceptualization, Writing – original draft, Writing – review & editing. CS: Methodology, Writing – original draft, Writing – review & editing. IA-D-S: Conceptualization, Formal analysis, Investigation, Methodology, Resources, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frbee.2024.1383589/full#supplementary-material>

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