ANNOTATED CHECKLIST OF THE BEES OF BONAIRE, WITH A FOCUS ON HOST PLANTS (ANTHOPHILA)

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Bonaire is an isolated oceanic island at the border of the Guajira-Barranquilla ecoregion which is dominated by tropical dry forest. In this paper we present an overview of the bees of this island mainly based on material collected during the Bonaire Estafette Expeditie in 2022-2023. At present 15 species belonging to 13 genera and 5 families are known to occur on Bonaire. None of these are endemic to the island but three of them seem to be restricted to the Guajira-Barranquilla ecoregion. An analysis is presented of the biogeography and floral host plants. It is expected that fieldwork in other parts of the year will result in the discovery of additional species.

INTRODUCTION

Bonaire is an understudied oceanic island regarding bee diversity and pollination systems. It is part of the tropical dry forest and xeric shrubland ecoregion, well known for its characteristic columnar cacti that dominate the landscape. The island is part of the smallest of the Neotropical semi-arid ecoregions. Other similar ecoregions like the Caatinga and the Chaco are over 3000 km away. This ecoregion stretches across the coastal regions of Venezuela, Colombia and covers the ABC islands (Aruba, Bonaire and Curaçao), sometimes it is called the Guajira-Barranquilla ecoregion (WWF 2014). Bonaire is located on the Caribbean-South America plate, only about 87 km from the coast of Venezuela. The island is separated from South America (Bonaire Trench) and Curaçao by 1300 to 1700 m deep seas (Stoffers 1956) and is a typical oceanic island with a low species richness of pollinators (Martén-Rodríguez et al. 2009, Olesen et al. 2002, Traveset et al. 2016).

The pollinator species or flower visitors that were known from Bonaire: two resident hummingbirds (Wells et al. 2017), two species of nectivorous bats (Genoways & Williams 1979, Simal et al. 2015), 32 species of butterflies (Miller et al. 2003), one or two bee species (Ascher & Pickering 2020,

Figure 1. Feral honey bee workers Apis *mellifera* gathering around the nest entrance. The nests are built inside trunks of *Guaiacum officinale*. All photos by Jelle Devalez, unless mentioned otherwise.

Dutchcaribbeanspecies.org) and an unknown number of flower-visiting moths, wasps, flies and beetles (e.g. Colijn et al. 2020). These groups play a specific role in their respective pollination systems (e.g. Albuquerque-Lima et al. 2023, Bauder et al. 2015, Domingos-Melo et al. 2023, Flórez-Gómez et al. 2020, Las-Casas et al. 2012). These pollination systems and the plant-pollinator interactions have not been studied on Bonaire.

In the Neotropical xeric regions, flowers with attributes related to pollination by bees can represent around 60-65 % of the diversity. The butterflies, moths, bats and birds represent the only other major pollinator group with 20-25 % of the pollination syndromes encountered (Cortés-Flores et al. 2017, Quirino & Machado 2014). Both woody and herbaceous species are mainly pollinated by bees and they are the dominant diurnal pollinators (Frankie et al. 2004, Quirino & Machado 2014). Floral resources are available throughout the seasons, but the flowering plant community changes between the long dry season and the shorter rainy season (Cortés-Flores et al. 2017). The keystone species are crucial to provide floral resources and preserve interactions. They are of high conservation concern (Burkle et al. 2013, Garibaldi et al. 2013).

This paper endeavours to compile a checklist of bee species across diverse habitats in Bonaire, based on new field studies. In addition, plant-bee interactions are documented for the first time and keystone species are highlighted. This is a preliminary study, as the dry season remains largely unstudied and some bee genera need further study. Finally, the depauperate bee fauna of Bonaire makes it also possible to associate the females and males of little-known species, detect introduced species and associate cuckoo bees. The new knowledge obtained during this study will be crucial for conservation efforts and future research.

MATERIAL & METHODS

The checklist was created based on data from specimens and observations. The primary source of occurrences was obtained from specimens collected during the Bonaire Estafette Expeditie (BEE) (Kalkman et al. 2025). The specimens were obtained using three passive trapping methods (pan traps, malaise traps and lightsheets) and active collecting with an insect net. Only the use of an insect net, pan traps and malaise traps resulted in the capture of wild bee specimens. In this paper only the bees collected by netting are investigated. The results of the passive trapping methods will be published in a forthcoming paper. Collecting trips have been made in all accessible parts of the island to cover as many localities and habitats as possible. Most occurrences have been recorded and reviewed using the citizen science platform Observation.org. In addition, occurrence records on the citizen science platform iNaturalist.org have been reviewed. All records up to December 2023 have been critically evaluated. All records based on images or voucher specimens have been verified or identified by the first author (Devalez 2024). Any doubts about the locality, date, flower species visited and other data have been checked with the contributor and corrected if needed.

The bee genera are diagnosed based on the following keys: Michener (1954, 2007) and Silveira et al. (2002).

The majority of specimens will be accessible in the collection of Naturalis Biodiversity Center (RMNH), Leiden (the Netherlands). A synoptic collection is retained at the Zoological Collections in Tartu, Estonia (TUZ). The full occurrence data is available as a flat file conform Darwin Core: doi.org/10.5281/zenodo.14569227

The nomenclature and taxonomy of genus group and species group names follow Ascher & Pickering (2020). The family group names follow the most recent systematics as summarised in Engel et al. (2020). The plant taxonomy and nomenclature follows POWO (2023).

RESULTS

The records obtained from iNaturalist.org and Observation.org resulted in 629 bee records, including 357 flower visitation records. The conspicuous *Centris niveofasciata* was the only wild bee species known from Bonaire (Ascher & Pickering 2020). Honey bees *Apis mellifera* were introduced to the ABC islands in the early 20th century (Van Buurt & Debrot 2011). Most of the individuals have been recorded between September 2022 and February 2023 during the BEE. So far, 15 species are recorded belonging to 5 New World bee families (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae).

All described species known from Bonaire are here presented in a checklist, organised by family, subfamily, tribe and genus. For ease of use by non-taxonomists, the families, subfamilies, tribes and species (or genera) are listed alphabetically.

The following information is provided for each species: type locality, distribution in the Neotropics, remarks on the taxonomy, literature for identifications and the verified floral host genera recorded in Bonaire. The floral host genera are listed based on the verified archived records at: Zenodo.14569227.

Family Andrenidae
Subfamily Panurginae
Tribus Calliopsini

Only the genus *Acamptopoeum* occurs in this ecoregion (Ascher & Pickering 2020, Michener 2007, Moure & Melo 2022a). One species of *Acamptopoeum* is currently known from Bonaire.

Acamptopoeum colombiense Shinn, 1965

Type locality Colombia: Caribbean region, Magdalena, Ciénaga.
Neotropical distribution Colombia: Caribbean Region of Colombia (Ascher & Pickering 2020, Gonzalez et al. 2012, Moure & Melo 2022a, Shinn 1965).
Plant genera visited *Heliotropium* Tourn. ex L. and *Stylosanthes* Sw.
Taxonomy There are 11 species of *Acamptopoeum* (Ascher & Pickering 2020, Shinn 1965). All species are confined to the Neotropics (Ruz 1991). *Acamptopoeum colombiense* is a smaller species closely related to *A. vagans* (Cockerell, 1926). *Acamptopoeum colombiense* has a dark integument without metallic blue or green reflections and can be separated from related species by the entirely yellow front and middle tibia (Shinn 1965).
Remarks The species appears to be mesolectic, collecting pollen from Fabaceae and Boraginaceae. Other genera in the tribus Calliopsini are also specialised on Fabaceae. This has been well studied in the sibling genus Calliopsis (Michener 2007).

Family Apidae
Subfamily Apinae
Tribus Apini

Only the genus *Apis* occurs in this ecoregion (Ascher & Pickering 2020, Michener 2007, Moure 2023). This is also the single genus in the tribe (Michener 2007). One species, the introduced *Apis mellifera* is known from Bonaire.

Apis mellifera Linnaeus, 1758

Type locality Europe.
Neotropical distribution The entire Neotropical region. It is a well-known cosmopolitan species (Ascher & Pickering 2020, Moure 2023).
Plant genera visited *Antigonon*, *Caesalpinia*, *Guaiacum*, *Indigofera*, *Lantana*, *Melochia*, *Passiflora*, *Prosopis*, *Sesuvium* are recorded, but possibly over 50 plant genera are visited.
Taxonomy It is the only extant corbiculate bee on Bonaire and can easily be identified with existing keys to the bee genera of the region (Michener 1954, 2007, Silveira et al. 2002). The subspecies of *Apis mellifera* are difficult to delimit. The Africanised honey bee is a hybrid between European subspecies of *Apis mellifera* and the African subspecies *Apis mellifera scutellata* Lepeletier, 1836

(Calfee et al. 2020). The African subspecies was imported to Brazil over 50 years ago and crossbred with European honey bees. Some queens escaped shortly after the introduction. The hybrid swarms dispersed and within 30 years resulted in the Africanisation of honey bees in the Neotropics (Calfee et al. 2020, Ruttner 1988). It remains to be seen if the genetic makeup of the Bonaire population is influenced by the presence of the Africanised honey bee in adjacent regions.
Remarks Feral honey bee colonies are common in Bonaire (fig. 1). Pollen is collected from plant families with various morphology and structural complexity (Michener 1962, 2007). At recommended stocking rates there is no evidence that Apis mellifera has an impact on the native bee fauna of tropical dry forests (Frankie et al. 2000, 2002). There have been several long-term studies on the impact of honey bees on native bee species and the spread of the Africanised honey bees (Roubik et al. 1986, Roubik 2009, Roubik & Villanueva-Gutierrez 2009). In general, there is a lack of evidence for competition with other bee species in the Neotropics, but the high abundances and the regular dominance of *Apis mellifera* in pollinator communities has shown a negative effect on the abundance of wild bee species (Garibaldi et al. 2021, Guzman-Novoa et al. 2020). In turn, high abundances can compensate for a low pollination efficiency in pollinating the native flora. So, generalist species of the native flora can benefit from these non-native flower visitors (Neves & Viana 2011, Osorio-Beristain et al. 1997).

Tribus Centridini

Only the genus *Centris* occurs in this ecoregion (Ascher & Pickering 2020, Michener 2007, Moure & Melo 2023a). One species of *Centris* is currently known from Bonaire.

Centris niveofasciata Friese, 1900

Type locality Venezuela, 'St. Parime'.
Neotropical distribution Colombia, Guyana, northern Brazil and Venezuela (Ascher & Pickering 2020, Friese 1900, Moure & Melo 2023a).
Plant genera visited *Byrsonima* Rich. ex Kunth, *Indigofera* L., *Melochia* L., *Prosopis* L., *Senna* Mill. (incl. *Cassia* L.) and *Solanum* L.
Taxonomy The species has a unique colour pattern (fig. 2-3) and is unlikely to be confused with any described species (Friese 1900, Moure 1969, Vivallo 2020).
Remarks The females in Centridini are particular in two ways. They are specialised in collecting floral oils and sonicate flowers with poricidal anthers (buzz pollination). This results in a strong preference for the families Malpighiaceae, Solanaceae and Fabaceae (Flórez-Gómez et al. 2020). The pollen of these families form a major part of the pollen diet. They do visit other plant families during the long flight season and are considered polylectic (Flórez-Gómez et al. 2020, Lima et al 2017, Santos et al. 2013). To collect pollen from Solanaceae, the females vibrate the anthers with a loud characteristic buzz to release the pollen. Buzz pollination is necessary to collect pollen from and pollinate *Solanum* L. (Solanaceae) and can only be performed by certain bee genera like the genus *Centris* (Michener 1962, Pacheco Filho et al. 2015, Vallejo-Marin & Russel 2023, Wille 1963). The main buzz pollinator of *Solanum* L. on Bonaire is likely *Centris niveofasciata*. The oil-producing flowers of the genus *Byrsonima* Rich. ex Kunth (Malpighiaceae) are crucial to feed the larvae and protect it from moisture and fungi, as the mother bee applies the floral oils to the inner nest cell wall (Torretta et al. 2022, Vinson et al. 1996, 1997, Vogel 1974). On Bonaire, *Centris niveofasciata* would be the sole pollinator of the native *Byrsonima crassifolia* (L.) Kunth and other native and non-native Malpighiaceae, as no other pollinators are known to visit this family. The bee genus *Centris* and the plant genus *Byrsonima* share a long coevolutionary history in the Neotropics (Torretta et al. 2022, Vinson et al. 1996, 1997, Vogel 1974). However, the relationship is not a species specific one. This is confirmed by the attractiveness of *Byrsonima lucida* (Mill.) DC., a non-native

Figure 2. *Centris niveofasciata* ♀, one of many, that was foraging on the large yellow flowers of *Senna* in an urban area.

Figure 3. *Centris niveofasciata* ♂.

species on Bonaire, for *Centris niveofasciata. Byrsonima lucida* (Mill.) DC. is endemic to the Caribbean region but does not occur naturally on the ABC islands (POWO 2023).

Tribus Meliponini

The genera *Melipona, Trigona* (s.l.) and *Trigonisca* occur in this ecoregion (Ascher & Pickering 2020, Camargo et al. 2023, Engel et al. 2019, Michener 2007). An unidentified species of *Trigona* s.l. was historically recorded from Bonaire.

***Trigona* spec. (s.l.)**

Neotropical distribution From Mexico south to Argentina (Ascher & Pickering 2020, Camargo et al. 2023).

Taxonomy The delimitation of this genus has changed historically and is often difficult to recognise (Schwarz 1932, 1948, Roubik 1992). This is not surprising considering that it is one of the most species rich endemic genera of Neotropical Meliponini. Other genera are also difficult to recognise and have fluid delimitations (Marconi et al. 2023, Michener 2007, Rasmussen and Camargo 2008). So, it is not certain to which currently recognised genus the historic record belongs. It is more likely to belong to either *Melipona* or *Trigonisca,* considering the latest knowledge on distribution, ecology and taxonomy (Engel et al. 2019, Nates-Parra & Roubik 1990, Roubik 1992). The genus *Melipona* has been reported from nearby Curaçao (Van Buurt & Debrot 2011).

Remarks One species was collected on the island of Klein Bonaire (GBIF 2023), deposited and studied in 1999 at the Snow Entomological Museum Collection (SEMC). It is well possible that one or more species of stingless bees (Meliponini) were historically present on Bonaire and Klein Bonaire. Stingless bees were not found in recent years and are possibly regionally extinct. Several species are known to nest in trees and columnar cacti in the nearby xeric shrubland and tropical dry forest of Venezuela and Colombia. The only species known to occur in the xeric La Guajira region are *Melipona favosa* (Fabricius, 1798) and *Trigonisca mepecheu* Engel & Gonzalez, 2019 (Engel et al. 2019). Other species and genera like *Cephalotrigona, Geotrigona, Nannotrigona* and *Trigona* prefer the wetter adjacent ecoregions in Colombia and Venezuela (Ascher & Pickering 2020, Salt 1929, Vit et al. 2013). Stingless bees are generalists and species in Venezuela and Colombia have been recorded visiting flowers of common plant species also widespread on Bonaire, like *Tribulus cistoides* L., *Haematoxylum brasiletto* H. Karst., *Antigonon leptopus* Hook. & Arn., *Terminalia* spec., *Hibiscus* spec. and also various other Fabaceae and Malvaceae (Salt 1929, Vit & Ricciardelli D'Albore 1994,

Figure 4-5. *Diadasia* cf. *tropicalis,* 4. ♂, 5. ♀.

Figure 6-7. *Florilegus* cf. *flavohirtus*, 6. ♂, 7. ♀.

Vit & Tomás-Barberán 1998, Vit et al. 2013). Some species of stingless bees are known to have dispersed to similar isolated islands in the Neotropical region (Camargo et al. 1988, Roubik & Camargo 2011).

Subfamily Eucerinae
Tribus Emphorini

The genera *Ancyloscelis*, *Diadasia*, *Melitoma* and *Melitomella* occur in this ecoregion (Ascher & Pickering 2020, Michener 2007, Moure & Melo 2023b). One species of *Diadasia* is currently known from Bonaire.

Diadasia cf. *tropicalis* (Cockerell, 1918)

Type locality Mexico, Veracruz, Pueblo Viejo.
Neotropical distribution Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico and Venezuela (Ascher & Pickering 2020, Gonzalez et al. 2012, Moure & Melo 2023b, Snelling 1994).
Plant genera visited *Abutilon* Mill. (syn. *Bastardia* Kunth), *Malvastrum* A.Gray and *Sida* L. The males also visit *Indigofera* L. and probably other flowers.
Taxonomy The species has a similar habitus to the co-occurring *Florilegus* cf. *flavohirtus* (fig. 4-5). The population of Bonaire is likely closely related to populations of Venezuela studied by Snelling (1994). Both sexes have been studied and they differ in the punctuation of the head and mesosoma,

being weaker and shallower, similar to *D. ochracea* (Cockerell, 1903). The density of the punctuation is more like typical *D. tropicalis*. The Neotropical species of the subgenus *Dasiapis* are in need of a modern revision (Snelling 1994).
Remarks The species belonging to the tribe Malveae are an important pollen source. All species of the subgenus *Dasiapis* appear to be specialised on this group of Malvaceae (Adlakha 1969, Linsley & MacSwain 1958, Snelling 1994).

Tribus Eucerini

The genera *Florilegus*, *Gaesischia*, *Melissodes*, *Melissoptila*, *Peponapis* and *Thygater* occur in this ecoregion (Michener 2007, Urban et al. 2023). One species of *Florilegus* and one species of *Melissodes* are currently known from Bonaire.

Florilegus cf. *flavohirtus* Urban, 1970

Type locality Colombia: Caribbean region, Bolívar, Cartagena.
Neotropical distribution Colombia: Caribbean Region of Colombia (Ascher & Pickering 2020, Gonzalez et al. 2012, Urban et al. 2023).
Plant genera visited *Melochia* L., *Sida* L. and *Varronia* P.Browne.
Taxonomy The species is rather unique. The thorax and abdomen are almost entirely covered with dense yellow pilosity in both males and females (fig. 6-7). In males the ventral surface of the posterior femur is entirely hairy and the shape of the seventh sternum is characteristic. The females have a yellow labrum and largely yellow clypeus. However, only a few specimens have been studied and there is intraspecific variation in the colour of the integument. Also during the revision of the genus in the 1960s only few specimens from the population in Colombia were studied (Urban 1970).
Remarks Possibly polylectic like the closely related and well-studied *Florilegus condignus* (Ducke 1910, LaBerge & Ribble 1966). It has been observed visiting Boraginaceae and Malvaceae on Bonaire.

Figure 8. During overcast weather and the night *Melissodes* cf. *rufodentatus* ♂ gather together to rest. Photo Jan-Joost Mekkes.

Melissodes cf. *rufodentatus* Smith, 1854

Type locality Lesser Antilles, Saint Vincent.
Neotropical distribution Brazil, Colombia, Dominica, French Guiana, Grenada, Saint Vincent and the Grenadines, Suriname, Trinidad and Tobago and Venezuela (Ascher & Pickering 2020, Gonzalez et al. 2012, LaBerge 1956, Urban 1973, Urban et al. 2023).
Plant genera visited *Alternanthera* Forssk., *Antigonon* Endl., *Gossypium* L., *Haematoxylum* L., *Indigofera* L., *Ipomoea* L., *Jatropha* L., *Lantana* L., *Melochia* L. *Metastelma* R.Br., *Prosopis* L., *Rhynchosia* Lour., *Sida* L. and *Tribulus* L.
Taxonomy This species is currently the only known species in the subgenus *Melissodes* that occurs throughout the Antilles southwards to northern Brazil, also on isolated islands in the Caribbean. It is similar to related Nearctic species (fig. 9-10). However, it is a polymorphic species and needs a modern revision (LaBerge 1956, Urban 1973). Its unusual biogeography might also indicate underlying problems with the species delimitation. The subgenus *Melissodes* mainly diverged in western North America with currently a total of 24 species in the New World. It is one of two lineages that colonised Central America and parts of South America (Wright 2018).
Nomenclature The name *Melissodes* is considered masculine (ICZN 1999: art. 30.1.2 and 30.1.4.4),

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Figure 9-10. *Melissodes* cf. *rufodentatus*, 9. ♂. 10. ♀.

although in the literature *Melissodes* has historically been treated as feminine (LaBerge 1956, Urban 1973). The erroneous treatment as feminine was already noted by Steyskal (1982).
Remarks The species mainly visits Asteraceae, Fabaceae and Malvaceae just as in related species, e.g. M. tepaneca Cresson (LaBerge 1956, Mitchell 1962, Wright 2018). The males often rest or sleep together (fig. 8).

Subfamily Xylocopinae
Tribus Ceratinini

Only the genus *Ceratina* occurs in this ecoregion (Ascher & Pickering 2020, Michener 2007, Moure & Melo 2023c). One species of *Ceratina* is currently known from Bonaire.

Ceratina spec.

Neotropical distribution The genus is widely distributed in the Neotropics and the species shows affinity with the equally widely distributed subgenus *Ceratinula* (Ascher & Pickering 2020, Moure & Melo 2023c).
Plant genera visited *Sesuvium* L. (GloBI Community 2023).
Taxonomy The taxonomic study of this genus is ongoing in the region (Michener 1954, De Oliveira et al. 2020, Flórez-Gómez & Griswold 2020, Flórez-Gómez et al. 2022). The species likely belongs to the subgenus *Ceratinula.*
Remarks Recent photographs posted on iNaturalist.org show a male and a female (GBIF 2023) visiting flowers of *Sesuvium portulacastrum* (L.) L. There is also an indication of successful nesting on the island. This would confirm the establishment of this unidentified species in the area of Kralendijk. These records and interactions are archived by GloBI (Poelen et al. 2014). This is the only recorded locality, despite extensive surveys of flower visitors of *Sesuvium portulacastrum* (L.) L. in multiple localities around the island. The only species listed for the Caribbean region of Colombia is *Ceratina* (*Ceratinula*) *tricolor* Michener, 1954 (Gonzalez et al. 2012).

Tribus Xylocopini

Only the genus *Xylocopa* occurs in this ecoregion (Michener 2007, Moure & Melo 2023c). One species of *Xylocopa* is currently known from Bonaire.

Xylocopa muscaria (Fabricius, 1775)

Type locality Neotropics (Rio de Janeiro?, Guyana Shield region?).
Neotropical distribution Bolivia, Brazil, Colom-

Figure 11. *Xylocopa muscaria* ♂.

bia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Honduras, Mexico, Panama, Paraguay, Peru, Trinidad and Tobago and Venezuela (Ascher & Pickering 2020, Hurd 1978, Gonzalez et al. 2012, Moure & Melo 2023c).
Plant genera visited *Indigofera* L., *Melochia* L., *Senna* Mill. (incl. *Cassia* L.) and *Solanum* L.
Taxonomy The genus and subgenus are well defined (Hurd 1956, Lucia et al. 2015). This blue metallic species (fig. 11-12) is unique within the subgenus and is unlikely to be confused with other species in the region (Mawdsley 2018, Villamizar et al. 2020).
Remarks Polylectic, visiting various plant families, a known buzz pollinator (Villamizar et al. 2020, Wille 1963).

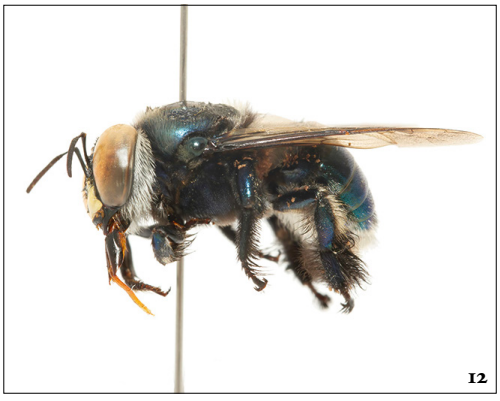

Figure 12. *Xylocopa muscaria* ♂.

Family Colletidae
Subfamily Hylaeinae
Tribus Hylaeini

Only the genus *Hylaeus* occurs in this ecoregion (Ascher & Pickering 2020, Michener 2007, Urban & Moure 2022). One species of *Hylaeus* is currently known from Bonaire.

Hylaeus cf. *preposterosus* Snelling, 1982

Type locality Bolivia, Beni.
Neotropical distribution Bolivia (Ascher & Pickering 2020, Urban & Moure 2022).
Plant genera visited Unknown.
Taxonomy The subgenus *Gongyloprosopis* Snelling includes currently three described species (Snelling 1982). Very little is known about the species belonging to this subgenus.

Family Halictidae
Subfamily Halictinae
Tribus Halictini

The genera *Agapostemon*, *Habralictus*, *Halictus*, *Lasioglossum* (s.l.) and *Sphecodes* occur in this ecoregion (Michener 2007, Moure & Melo 2022b). It is yet unknown how many species are found on Bonaire, but the estimate is that at least two or three species occur on the island.

Lasioglossum (Dialictus) spec.

Neotropical distribution The subgenus *Dialictus* is widely distributed in the Neotropics (Ascher & Pickering 2020, Moure & Melo 2022b).
Plant genera visited *Antigonon* Endl. *Capraria* L., *Corchorus* L., *Cyanthillium* Blume, *Desmanthus* Willd., *Euphorbia* L., *Heliotropium* Tourn. ex L., *Indigofera* L. *Jatropha* L., *Launaea* Cass., *Leucophyllum* Bonpl., *Melochia* L., *Metastelma* R.Br., *Phyla* Lour., *Prosopis* L., *Portulaca* L., *Rhynchosia* Lour., *Rivina* Plum. ex L., *Sesuvium* L., *Sida* L., *Strumpfia* Jacq., *Stylosanthes* Sw., *Trianthema* L., *Tribulus* L., *Tridax* L. and *Waltheria* L.

Figure 13-16. *Lasioglossum* (*Dialictus*) spec., a subgenus in need of revision in the region, 13. ♂, 14. ♀, 15. ♂, 16. ♀.

Taxonomy Species related to *L. gundlachii* (Baker, 1906) and *L. umbripenne* (Ellis, 1913), possibly over 10 described and undescribed species are part of this diverse group in this ecoregion. This group is characterised by its green metallic head and thorax, as in sibling species occurring throughout the distribution range of the subgenus (fig. 13-16). The inner hind tibial spur of females is pectinate with a few large teeth. Currently, this group of species cannot be confidently identified (Ellis 1914, Landaverde et al. 2023).

Family Megachilidae
Subfamily Megachilinae
Tribus Megachilini

The genera *Coelioxys* and *Megachile* occur in this ecoregion (Ascher & Pickering 2020, Michener 2007, Moure & Melo 2021). One species of *Coelioxys* and two species of *Megachile* are currently known from Bonaire.

Coelioxys abdominalis Guérin-Méneville, 1845

Type locality U.S. Virgin Islands, Saint Thomas? The type from Cuba must be mislabeled.
Neotropical distribution Barbados, Colombia, Dominica, Ecuador, Grenada, Montserrat, Panama, Puerto Rico, Saint Vincent and the Grenadines, U.S. Virgin Islands and Venezuela (Ascher & Pickering 2020, Gonzalez et al. 2012, Michener 1954, Moure & Melo 2021).
Plant genera visited *Melochia* L. and *Prosopis* L.
Taxonomy The species belongs to the well-defined subgenus *Neocoelioxys* (Mitchell 1973, Moure 1951, Rocha-Filho & Packer 2017) and the species

description can be used to diagnose the species (Friese 1921). The integument of the abdomen and legs is almost completely red. The pattern of tomentose hair on the thorax also seems characteristic, with two large tomentose hair spots on the scutellum, small white hair patches adjacent to the tegulae on the scutum and tomentose hair covering the pronotum and mesepisternum. The abdomen has fine apical hair bands on T1-5 (fig. 17-18).

Remarks The host of this species on Bonaire is almost certainly *Megachile furcata*. The closely related species within the subgenus *Pseudocentron* systematically co-occur with *C. abdominalis* throughout its Caribbean range. The only potential host on Bonaire is *M. furcata.* The other *Megachile* species found on Bonaire, *M. concinna*, was introduced to the Caribbean and is associated with the cuckoo bees in the subgenus *Allocoelioxys*. On Martinique a female was collected flying near a nest of *Megachile* (*Pseudocentron*) *luctifera* Spinola in the chalky wall of a chapel (Meurgey & Dumbardon-Martial 2019).

Megachile concinna Smith, 1879

Type locality Dominican Republic, Santo Domingo.

Neotropical distribution Barbados, Cuba, Dominica, Dominican Republic, Haiti, Jamaica and Puerto Rico (Alvarez et al. 2012, Ascher & Pickering 2020, Genaro 1994, Moure & Melo 2021, Rasmussen 2012, Soltani et al. 2017).

Plant genera visited *Haematoxylum* L., *Heliotropium* Tourn. ex L., *Indigofera* L., *Jatropha* L., *Launaea* Cass., *Prosopis* L., *Rhynchosia* Lour. and *Stylosanthes* Sw.

Taxonomy The species belongs to the subgenus *Eutricharaea.* This is the most diverse subgenus of *Megachile*. The approximately 240 species in the subgenus are all Old World species (Michener 2007). All species occurring in the New World are introduced. Only recently two species are recognised as being introduced to the Neotropics (Soltani et al. 2017). Both *Megachile pusilla* Pérez, 1888 and *M. concinna* Smith, 1879 belong to the *concinna* complex within the *leachella*-group (Praz 2017, Soltani et al. 2017). The *concinna*-complex is well defined (Mitchell 1933, 1943, Rebmann 1968, Praz 2017, Soltani et al. 2017). There are no reliable diagnostic characters to distinguish the males of both species. The females of *M. concinna* have white spots of appressed hairs on T6 that are clearly visible and the white scale-like hairs are abundant throughout the mesonotum (fig. 19-20). Furthermore, the punctation on the disc of T4 is usually denser. Females of *M. concinna* have a body length of around 8-9 mm (Soltani et al. 2017).

Remarks *Megachile concinna* was accidentally introduced from Africa to the Caribbean, possibly

Figure 17-18. *Coelioxus abdominalis*, 17. ♂, 18. ♀.

Figure 19-20. *Megachile concinna*, 19. ♂, 20. ♀.

over 200 years ago during the slave trade (Genaro 1994, Mitchell 1962, Raw 1985, Smith 1879). The species became the most widespread introduced wild bee species of the ABC islands, but all identifications need to be verified. Both *Megachile pusilla* Pérez and *M. concinna* are probably becoming widespread in the New World (Álvarez et al. 2012, Rasmussen 2012, Soltani et al. 2017). Further study is needed in countries where both species currently could co-occur and expand their range in the coming decades. The species mainly visits Fabaceae, but is also often seen visiting Asteraceae, Lamiaceae and other plant families (Mitchell 1962).

Megachile furcata Vachal, 1909

Type locality Mexico, Chihuahua.
Neotropical distribution From Mexico south to Colombia and Venezuela (Ascher & Pickering 2020, Gonzalez et al. 2012, Michener 1954, Moure & Melo 2021).
Plant genera visited *Abutilon* Mill. (syn. *Bastardia* Kunth), *Indigofera* L., *Leucaena* Benth., *Prosopis* L. and *Rhynchosia* Lour.
Taxonomy The subgenus *Pseudocentron* Mitchell, 1934 is one of the largest groups of Neotropical *Megachile* and is in need of revision. *Megachile furcata* is illustrated on plates X-XIII in Mitchell (1930). The species is closely related to the North American species *Megachile pruina* Smith, 1853. This is also the type of the subgenus *Pseudocentron* (Durante & Díaz 2002). The shape of the front tarsi and T6 is characteristic in the males. The size of both females and males is distinctly larger than the co-occurring *Megachile concinna* on Bonaire (fig. 21-23). The females have a white scopa and T6 is largely covered in white appressed hairs (Friese 1911, Mitchell 1930, 1933, 1937, 1943, Vachal 1909). The females of *Megachile furcata* were described from Colombia (Mitchell 1930).
Remarks The species in the subgenus *Pseudocentron* nest in cavities in the ground or above ground (Landry et al. 2014, Marinho et al. 2018). *Megachile furcata* has been seen nesting in cavities above ground on Bonaire. The species cuts and uses leaf fragments in the construction of nest

Figure 21. *Megachile furcata* ♀ visiting flowers of *Rhynchosia minima*.

Figure 22-23. *Megachile furcata*, 22. ♂, 23. ♀.

cells, just as other sibling species (Marinho et al. 2018). The species seems to have a preference for Fabaceae, as in many other Megachilini (Marinho et al. 2018, Michener 2007).

SPECIES RICHNESS

The current estimate is that 15 bee species occur on Bonaire, that is about one fifth of the species that occur in the same ecoregion and altitude range in Colombia (table 1).

FLORAL HOSTS AND KEYSTONE SPECIES

In 2022 the following plant families and keystone species were recorded:
Malvaceae *Melochia tomentosa* L. is a keystone species in the wet season during the months of November and December. It belongs to the subfamily Byttnerioideae. *Melochia tomentosa* is known to be an important pollen source and keystone species in the other xeric ecoregions, like the Caatinga (Aguiar 2003, Machado & Sazima 2008). Another subfamily of the family Malvaceae, subfamily Malvoideae, also includes important keystone species on Bonaire, like the genera *Sida*, *Abutilon* and *Malvastrum*. The bee species of the subfamily Eucerinae are regularly found on Malvaceae, with at least *Diadasia tropicalis* known to be a specialist of Malveae (Snelling 1994).

Fabaceae *Prosopis juliflora* (Sw.) DC. and *Haematoxylum brasiletto* H.Karst. are keystone species in February and March. Both species have been recorded as an important pollen source in the Caribbean region of Colombia (Flórez-Gómez et al. 2020). Other weedy Fabaceae, like *Rhynchosia minima* and *Stylosanthes hamata* are also important pollen sources. Fabaceae are diverse and flower both in the wet and dry season. For example, *Prosopis juliflora* is a preferred floral resource late into the wet season, while *Haematoxylum brasiletto* is a preferred pollen and nectar source well into the dry season (Flórez-Gómez et al. 2020). The Fabaceae are especially important for the Calliopsini, Eucerini and Megachilini and are regularly visited for pollen (Michener 2007, Raw 2007).

Boraginaceae *Heliotropium angiospermum* Murray and other *Heliotropium* species are also keystone species in the wet season, as in other similar ecoregions (Viana et al. 1997). The Boraginaceae are important for the Calliopsini and Halictini, who regularly visit the flowers and it is possibly one of the preferred pollen sources.

Aizoaceae *Sesuvium portulacastrum* is a keystone species in saline and alkaline coastal wetland habitats, as it is often the only halophyte flowering in these habitats. It is mainly visited by Halictini and an unknown *Ceratina*.

Table 1. Bee genera and species richness comparison between Bonaire and coastal semi-arid areas in the Caribbean region of Colombia. Genera are listed alphabetically.

Genus	Bonaire	Caribbean region	References
Acamptopoeum	1	2	Gonzalez et al. 2012
Agapostemon	0	1	Gonzalez et al. 2012
Ancyloscelis	0	1	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Anthidium	0	1	Gonzalez et al. 2012
Apis	1	1	Gonzalez et al. 2012
Augochlora	0	1	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Augochlorella (s.l.)	0	1	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Bombus	0	1?	Gonzalez et al. 2012
Centris	1	7	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Ceratina	1	5	Flórez-Gómez & Griswold, 2020, Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Coelioxys	1	1	Gonzalez et al. 2012
Colletes	0	1	Gonzalez et al. 2012
Diadasia	1	2	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Eulaema	0	1?	Gonzalez et al. 2012
Exomalopsis	0	1	Gonzalez et al. 2012
Florilegus	1	2	Gonzalez et al. 2012
Frieseomelitta	0	1	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Gaesischia	0	1?	Gonzalez et al. 2012
Geotrigona	0	1	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Halictus	0	2	Gonzalez et al. 2012
Heriades	0	1	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Hylaeus	1	1	Discoverlife.org/mp/20m?kind=amnh_bees
Lasioglossum (s.l.)	2?	3?	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Leioproctus (s.l.)	0	1	Gonzalez et al. 2012
Megachile	2	11	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Melipona	0	2	Engel et al. 2019, Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Melissodes	1	1	Gonzalez et al. 2012
Melitoma	0	1	Discoverlife.org/mp/20m?kind=amnh_bees
Melitomella	0	1	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Mesocheira	0	1	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Mesoplia	0	1	Discoverlife.org/mp/20m?kind=amnh_bees
Stelis	0	1	Gonzalez et al. 2012
Tapinotaspoides	0	1	Gonzalez et al. 2012
Thygater	0	1	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Trigona (s.l.)	1?	1?	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Trigonisca	0	1	Engel et al. 2019
Xylocopa	1	4	Flórez-Gómez et al. 2020, Gonzalez et al. 2012
Total	**15?**	**69?**	

Other families known to be important pollen hosts for Neotropical bee communities, like Asteraceae, Convolvulaceae and Cactaceae have very few or no recorded bee interactions. This is in contrast with the importance of Asteraceae in the wider biogeographic region, especially for Eucerini and Megachilini (Pacheco Filho et al. 2015, Schlindwein 1998). The families Convolvulaceae and Cactaceae are usually visited by a specialised community, including pollen specialists of the tribe Emphorini (Pacheco Filho et al. 2015, Schlindwein & Wittmann 1997, Tenorio-Escandón et al. 2022). Other important floral host families are mainly visited by a rich community of social

bees of the tribes Halictini and Meliponini (Flórez-Gómez et al. 2020), and consequently many of these bee-plant interactions probably don't exist in the species-poor community of Bonaire.

DISCUSSION

The bee fauna is mainly South American in origin as can be expected from studies on other terrestrial fauna groups (Crews et al. 2019, Crews & Esposito 2020, Miller et al. 2003, Wagenaar Hummelinck 1940). The range-restricted bee species are endemic to the Guajira-Barranquilla ecoregion covering the ABC islands and the coastal region of Colombia and Venezuela. This distribution pattern can also be seen in better known species, like the bird species Bare-eyed Pigeon *Patagioenas corensis* and Yellow-shouldered Amazon *Amazona barbadensis*. Species and genera that reach the edge of their distribution range in adjacent regions of Colombia or Venezuela and have their core distribution in the Nearctic or Greater Antilles are absent from Bonaire, e.g. *Heriades* and *Stelis*. Also xeric species with their core distribution in the Caatinga and other more southern semi-arid ecoregions are absent, e.g. *Leioproctus* and *Tapinotaspoides.*

Currently there are three species known to be range-restricted: *Acamptopoeum colombiense, Centris niveofasciata and Florilegus flavohirtus*. The other taxa are widespread native or introduced species. The species *Coelioxys abdominalis*, *Diadasia tropicalis, Megachile furcata*, *Melissodes rufodentatus* and *Xylocopa muscaria* probably all naturally colonised Bonaire. *Apis mellifera* and *Megachile concinna* are without doubt introduced. We currently know very little about the *Ceratina*, *Hylaeus, Lasioglossum* and Meliponini (*Melipona* and *Trigona*?) species of the region.

A large part of the BEE surveys were conducted in an extended rainy season. The beginning of the dry season should be surveyed to record the peak and full diversity of bees present in this climate zone (Michener 1954, Flórez-Gómez et al. 2020).

It is clear that the Malvaceae and Fabaceae sustain a major part of the bee diversity found during the wet season on the island of Bonaire. The plant families Solanaceae and Malpighiaceae provide pollen to *Centris niveofasciata* on Bonaire. Most other plant families are usually only visited by *Lasioglossum* (*Dialictus*) spec. and *Apis mellifera*, as is the case in similar ecoregions (Pacheco Filho et al. 2015). Both can be considered the most generalist or broadly polylectic species of Bonaire.

Only a small proportion of the native and exotic flowering plants was surveyed for flower visitors, considering that over 350 species are known from Bonaire (Janssen et al. 2022). However, almost exclusively the Magnoliopsida (dicots) of Bonaire have attributes related to pollination by animals. The diversity of plants depending on bee pollination systems or mixed pollination systems (60-65 %) could be over 200 native species. Many of these might be important floral hosts for the native bees. The dominant higher vegetation of dense scrubland needs further study on 'canopy dwelling' bees and other pollinators (Dorey et al. 2024, Pacheco Filho et al. 2015).

Island ecosystems are particularly sensitive to negative changes caused by anthropogenic disturbances (Nogué et al. 2021). The landscape of Bonaire has changed dramatically and is degraded mainly due to deforestation and the introduction of grazing animals that took place over the past three centuries (De Freitas et al. 2005, 2008). In recent decades urban development has expanded as did the distribution range of invasive species (Van Buurt & Debrot 2011). A strong decline in both species richness and abundance of wild bees has been found in a long-term study of tropical dry forest in Costa Rica. The main cause of this decline is suggested to be habitat destruction through urbanisation, rapid changes in land use and the introduction of invasive species (Frankie et al. 1997, Vinson et al. 1993). The invasive species are better adapted and have co-evolved

with herbivores, anthropogenic disturbances and competitors. Only in recent history the native island flora and fauna have been exposed to these herbivores, disturbances and competitors and are not well adapted (D'Antonio & Dudley 1995, Paulay 1994).

The threat of introduced pollinators, like *Apis mellifera* is more complex and both positive and negative effects have been found on the native fauna and flora of tropical ecosystems after introduction events (Neves and Viana 2011, Osorio-Beristain et al. 1997, Roubik 2000, 2009). More studies are needed on beehive stocking densities and their effect on the pollinator community. High stocking densities of *Apis mellifera* can have a negative impact on pollinator communities (Garibaldi et al. 2021, Guzman-Novoa et al. 2020). Abrupt shifts and disruptions in pollination networks are major threats to conserving bee diversity. A healthy ecosystem of lowland tropical dry forest and xeric shrubland can harbour a unique bee fauna in this biogeographic region (Gonzalez et al. 2012).

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SAMENVATTING

Geannoteerde naamlijst van de bijen van Bonaire en hun waardplanten (Anthophila)
Bonaire is een geïsoleerd oceanisch eiland aan de rand van de Guajira-Barranquilla ecoregio, gedomineerd door tropische droge bossen met een unieke bijenfauna. Sinds 2022 zijn de inventarisaties van de terrestrische fauna van Bonaire ook gericht op bijen, waardoor er steeds meer exemplaren en waarnemingen beschikbaar komen voor onderzoek. Hier wordt een voorlopige lijst van 15 soorten in 13 genera en vijf families gerapporteerd van het eiland en de naburige eilandjes. Slechts twee soorten, *Centris niveofasciata* en *Apis mellifera*, werden eerder gemeld van het eiland. Geen van de bijensoorten wordt momenteel als endemisch beschouwd, maar drie soorten zijn waarschijnlijk endemisch in de Guajira-Barranquilla ecoregio. De biogeografie, bestuivingssystemen en gastheerassociaties worden geanalyseerd. Er zijn aanvullende onderzoeken gepland en in combinatie met de benodigde taxonomische revisies zal de checklist blijven veranderen en groeien. Deze studie vormt de basis voor een beter begrip van de bijenfauna en toekomstige natuurbeschermingsacties.

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