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# The importance of wild pollinators for indigenous crop pollination: The case of *Cyclopia* (honeybush)

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ABSTRACT

Pollination is an important ecosystem service. Animal-mediated pollination (mostly insects) increases the production of 35% of global crops. Honey bees (*Apis mellifera*) are considered important crop pollinators globally, but are under pressure and therefore the value of wild pollinators for crop production is receiving more attention. The importance of pollinators (including non-*Apis*) has been extensively studied in the agricultural sector of South Africa, however little research is available on the pollination of indigenous crops. With the considerable value of the indigenous honeybush (*Cyclopia* Vent.) in the tea industry, it is important to determine the pollinators since *Cyclopia* is widespread across the fynbos biome and the pollinators are largely unknown. Here we ask whether carpenter bees (xylocopid bees) are the only pollinators of commercially important *Cyclopia* species, or if honey bees contribute to pollination. Floral observations and camera trapping confirmed that six species of xylocopid bees were the only pollinators of four commercially important *Cyclopia* species. Honey bees were observed to be ineffective pollinators of *Cyclopia* owing to their inability to trip *Cyclopia* flowers and gain access to the floral reproductive parts. Similarly, an additional seven species including Diptera, Apidae and *Lema* sp. were unable to gain access to *Cyclopia* flowers, although were observed visiting. Nectar measurements revealed the highest nectar volume in *C. genistoides,* while *C. intermedia* had the highest nectar sugar concentration (above 35% for all species). The value of native non-*Apis* insects for crop pollination in a changing world is highlighted in *Cyclopia,* an indigenous legume gaining traction in the global tea market and therefore in cultivation.



## 1. Introduction

Pollination is a valuable ecosystem service, essential for crop productivity (Garibaldi *et al.,* 2020) and ecosystem functioning (Genung *et al.,* 2017). Approximately 80% of the 250 000 global angiosperms rely on animal-mediated pollination for sexual reproduction (Rodger *et al.,* 2021). Animal-mediated pollination (mainly insects) increases the production of approximately 35% of global crops in volume (Klein *et al.,* 2007), illustrating the exceedingly dependent relationship of humans on insect pollinators (Potts *et al.,* 2016). Honey bees (*Apis mellifera*) are considered economically important pollinators owing to their widespread distribution and generalist foraging behaviour (Hung *et al.,* 2018). The drastic population declines of honey bees in North America (Stokstad, 2007; Watanabe, 1994; Pettis & Delaplane, 2010) and Europe (Potts *et al.,* 2010; Biesmeijer *et al.,* 2006) have urged the question of whether wild pollinators may fulfil the role of honey bees in terms of crop pollination (Winfree *et al.,* 2007; Garibaldi *et al.,* 2013).

There are a handful of studies confirming the importance of pollinator species richness for some commercially important crops in South Africa (reviewed by Melin *et al.,* 2014), but little is known about the pollination of indigenous crops (but see Melin *et al.,* 2014). In South Africa, there are numerous indigenous plant species used in cultivation, viz buchu (*Agathosma* spp.) (Moolla & Viljoen, 2008; Van Wyk, 2008), and *Aloe* L. (Cousins & Witkowski, 2012; Cowling *et al.,* 1996). Many of these indigenous species, e.g., the leguminous rooibos tea (*Aspalathus linearis*) have floral traits adapted to pollination by non-*Apis* pollinators, including Megachilinae, Masarinae and Xylocopinae (Gess & Gess, 2014). The pollinators of many potentially economically important plants in South Africa are however unknown. For successful conservation, it is necessary to determine the identity and availability of pollinators of these commercially valuable indigenous plant species.

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Honeybush (*Cyclopia* Vent.) is a model genus for such a pollination study as it is widespread across the fynbos biome (Schutte, 1997), a number of species are cultivated, and it has considerable value in the tea industry of South Africa (McKay & Blumberg, 2006; Koen *et al.*, 2019). Smith (1966) claimed that the earliest indication of *Cyclopia genistoides* being used as tea, is implied by the vernacular name "Honigtee" [honey tea] that was recorded by Carl Thunberg in the 1770′s, during his botanical explorations in the Cape (Smith, 1966). However, the name Honigtee does not appear in his travel journal, but the possibility exists that the name was recorded on the reverse of some of the herbarium specimens of the species that he collected. The first explicit record of *Cyclopia* species being used for tea (actually as medicinal tea) was that of Bowie in 1830 (Van Wyk & Gorelik, 2017). There are six *Cyclopia* species recognised for their value in the tea industry; *Cyclopia genistoides* (L.) R. Br, *C. intermedia* E. Mey, *C. maculata* (Andrews) Kies, *C. subternata* Vogel, *C. sessiliflora* Eckl. & Zeyh., and more recently *C. longifolia* Vogel (Joubert *et al.*, 2011), but the pollinators of *Cyclopia* species still remain largely unknown.

The calyx in the *Cyclopia* genus is characterized by having two fused upper lobes and three lower lobes with varied appearance of size and shape between species (Fig. 4) (Schutte, 1997). All species have a bright yellow, continually structured corolla (with the exception of the duller *C. sessiliflora*) with sweetly-scented, rigid flowers (Schutte, 1997). The moveable lateral and ventral petals require active handling by pollinators in order to reveal the reproductive parts of the plant and perform successful pollination (Córdoba & Cocucci, 2011). This mechanism is referred to as “tripping” (Córdoba & Cocucci, 2011), and large bees, such as carpenter bees (Xylocopinae) have the ability to trip leguminous papilionoids (Westerkamp, 1992; Etcheverry *et al.*, 2008; Grobler & Campbell, 2020). *Bombus* sp., another genus of great stature and likely ability to trip legumes are not pollinators of *Cyclopia* as they are not present in South Africa.

Based on research conducted on other leguminous papilionoids, it is likely that carpenter bees are the primary pollinators of *Cyclopia*. However, the lack of research conducted on pollination of *Cyclopia* provides little validation (but see Schutte (1997) and Grobler & Campbell (2020)). Therefore, this study aims to investigate what pollinators are responsible for pollination of wild and cultivated populations of four commercially important *Cyclopia* species. Specifically, we asked (1) are carpenter bees the only pollinators of commercially important *Cyclopia* species, and (2) can honey bees contribute to pollination of *Cyclopia*?

## 2. Methods

### 2.1. Study area, site selection and study species

The study was conducted in the fynbos biome of the Western and Eastern Cape provinces in South Africa (Fig. 1 A). Sites were chosen according to the availability of both cultivated and wild-growing *Cyclopia*. At these sites, harvesting of cultivated plants was postponed (since flowers were needed for the pollination aspect of the study), whilst no wild harvesting is conducted. Four of the six commercialized *Cyclopia* species were selected according to their importance in the honeybush tea industry of South Africa (Joubert *et al.*, 2011). These species were chosen according to cultivated patches in near proximity to wild *Cyclopia* with an overlap in flowering time between the wild and cultivated plants (which formed another aspect of the broader study, however not included in this publication). Additionally, with the use of paired plots for the study (requiring wild and cultivated plants in close proximity), not all commercialized *Cyclopia* species were studied.

Two commercial honeybush farms were identified as suitable study sites based on proximity of planted *Cyclopia* to wild populations (Fig. 1). The first was located at Pearly Beach in the Overberg Municipality (34°41’43.1”S 19°36’15.5”E), Western Cape (Fig. 1 B). This study site was dominated by Overberg sandstone fynbos vegetation. This vegetation type has a mean annual precipitation of 450 – 830 mm (with most rainfall in July and August), mean daily temperatures ranging between 6.3°C and 25.6°C, and a low frost incidence of 2-3 days is experienced in this region per year (Mucina & Rutherford, 2011). This farm consisted of 1.7 ha of cultivated *Cyclopia genistoides*, with a few *C. subternata* plants under cultivation, and a patch of wild growing *C. genistoides*. *Cyclopia genistoides* “kustee” or coastal tea, flowers between September and November (Motsa *et al.*, 2017; Slabbert *et al.*, 2019) and *C. subternata* “vleitee” or marshland tea, flowers between September and October (Motsa *et al.*, 2017).

The second site was located at Twee Riviere (33°52’08.6”S 23°54’54.2”E) just outside of Joubertina, in the Eastern Cape (Fig. 1 C). This study site was dominated by Tsitsikamma sandstone vegetation, with a mean annual precipitation of 575 mm throughout the year (Cape Farm Mapper 2.6.15). The mean annual temperature is 15.7°C (Cape Farm Mapper 2.6.15), with 2-10 days of frost incidence per year (Mucina & Rutherford, 2011). The cultivated species on this farm included *Cyclopia subternata* and *C. maculata*, with wild-growing *C. subternata* along the riverbanks, as well as wild *C. intermedia* higher up in the surrounding mountains within 1 km from the cultivated site. *Cyclopia maculata* “needle-leaf honeybush” and *C. intermedia* “bergtee” or mountain tea flowers between September and November (Slabbert *et al.*, 2019; Barnado, 2013).

### 2.2. Pollinator observations

Floral observations were conducted to determine whether carpenter bees are the primary pollinators of commercially important *Cyclopia* species. Observations took place during warm and sunny conditions, with inclement weather avoided, from September to October 2021. A total of ~46 hours of observations were conducted at the Twee Riviere study site, and ~19 hours of observations were conducted at the Pearly Beach study site (Table 1). Insect identifications were conducted in field using a *Xylocopa* key where possible (Eardley, 1983). If identification was not possible, a description of the visitor was recorded in the place of the species name on observation logs, for later identification purposes. Representatives of the flower visitors observed accessing the *Cyclopia* flowers were collected for more accurate identification purposes where gender was also identified. These specimens were pinned and accessioned into the Iziko South African Museum (Appendix 1A).

*Cyclopia* plants were observed over a period of time, noting the number of flowers visible to the observer, the number of flower visits made by each flower visitor and the type of interaction observed (pollination, robbing or thieving). Plants, specifically in the wild study sites were observed more than once, as there were a limited number of plants available to observe in comparison to the cultivated study sites. The number of flowers observed changed according to the availability of flowers, as well as the species (e.g., *C. intermedia* had fewer flowers than some of the *C. subternata* plants).Visitation rates were standardized by flower count even though some sites were recorded more often. All observations were made on days with weather suitable for pollinator activities. To avoid the use of ambiguous terminology regarding floral larceny, the definitions outlined by Inouye (1980) were used. Primary nectar robbing is defined as: “a hole is made and used to obtain nectar, bypassing the opening used by pollinators” and secondary nectar robbing occurs when visitors make use of holes created by primary nectar robbers (Inouye, 1980). Nectar thieving is defined as: “no hole is made in the flower, the thief uses the opening of the flower which is used by pollinators however due to a mismatch in morphologies pollination is precluded” (Inouye, 1980).

Floral visitors were scored as potential pollinators when observed tripping the flowers and gaining access to the anthers and stigma (Fig. 2). If insect visitors did not trip flowers and failed to gain access

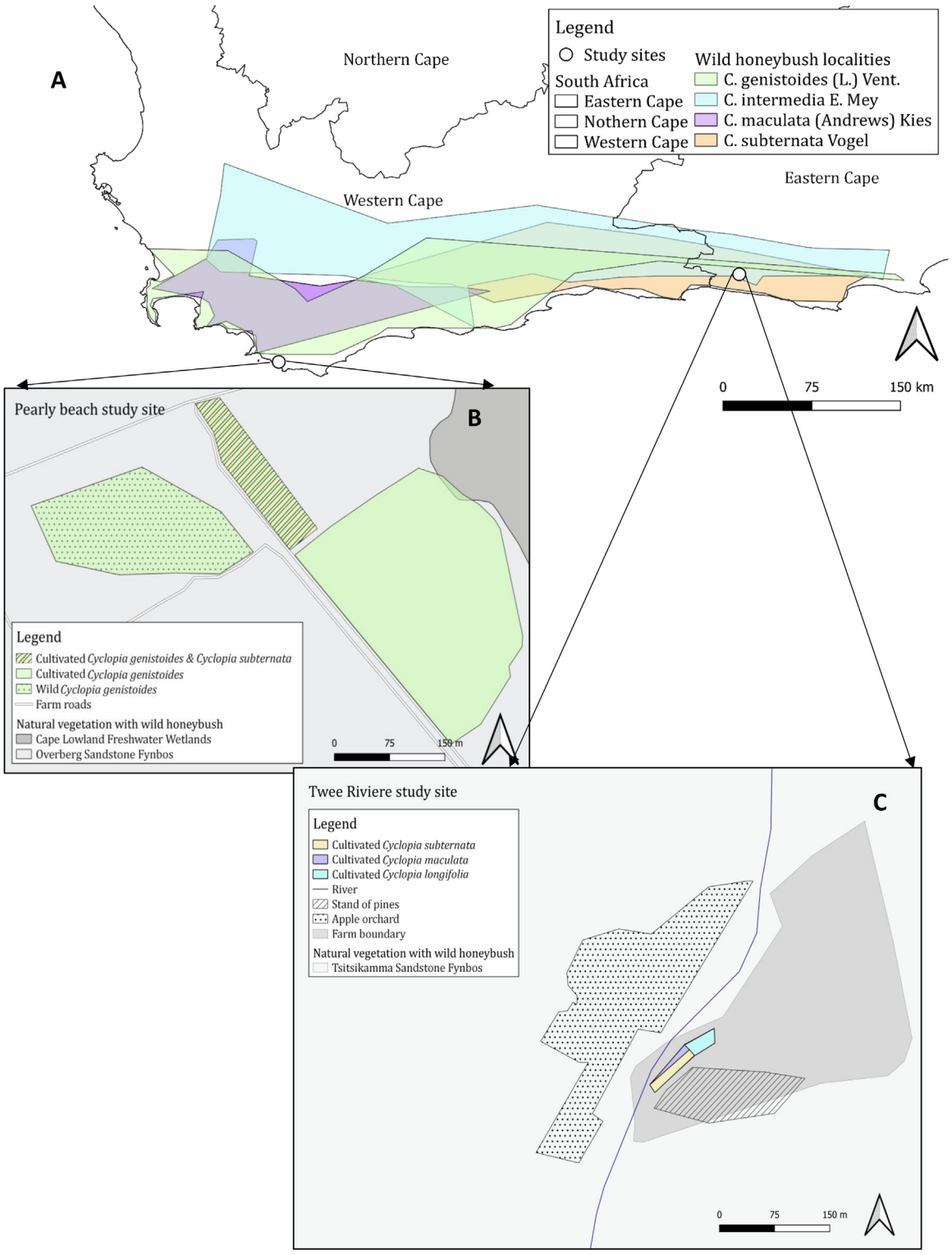


**Fig. 1.** (A) Location of the two study sites in the Western and Eastern Cape provinces of South Africa, (B) the wild and cultivated *Cyclopia* population localities at the Pearly Beach study site and (C) the natural vegetation areas abundant with native *Cyclopia*, and the cultivated *Cyclopia* at the Twee Riviere study site.

to the reproductive floral parts, the visit was deemed ineffective. These visitors were recorded as floral robbers or thieves.

Observations were supported with the use of camera traps (Bushnell Trophy Cam HD Max trail camera and Bushnell Core Low Glow trail camera) taking photographs when triggered by floral visitors, placed at a distance approximately 30-50 cm away from flowers. Similarly to the floral observations, the number of plants in the wild study sites were observed more than once and the number of flowers observed varied according to availability for camera trap observations. Camera traps were tested at the start of the field season to assess the settings required for sound pollinator observations. Visitors the size of carpenter bees and larger were able to trigger the camera traps, however smaller visitors such as honey bees were not observed in camera trap footage, likely due to their small size that is

**Table 1**
Observed visitation rate by Xylocopa species (visits/flower/hour) to *Cyclopia*, including the number of hours of observations per species in both the wild and cultivated study sites. On average, 370 flowers were observed in the wild site per observation period.

| | Wild | | | Cultivated | | |
|---|---|---|---|---|---|---|
| | *C. subternata* | *C. genistoides* | *C. intermedia* | *C. subternata* | *C. genistoides* | *C. maculata* |
| **Time (hrs)** | 6.03 | 1.8 | 10.22 | 18.55 | 17.58 | 11.05 |
| ***X. capitata*** | 1.5e-2 | 3.3e-3 | - | 4.4e-3 | 7.5e-4 | 1.0e-2 |
| ***X. flavorufa*** | 1.2e-3 | - | - | 1.3e-4 | - | 7.0e-6 |
| ***X. caffra*** | - | 4.9e-2 | 3.2e-3 | 7.3e-5 | 4.4e-3 | 4.5e-5 |
| ***X. rufitarsis*** | 8.5e-4 | - | 1.8e-3 | 4.4e-5 | 1.5e-4 | 2.7e-4 |
| ***X. scioensis*** | 1.1e-4 | - | - | - | 2.8e-3 | 4.9e-4 |
| ***X. sicheli*** | - | 2.0e-3 | - | - | - | 1.3e-3 |
| **Total** | **1.7e-2** or **0.016832** | **5.5e-2** or **0.054798** | **5.0e-3** or **0.004973** | **4.6e-3** **0.004596** | **8.157e-3** or **0.008157** | **1.2e-2** or **0.012356** |

**Table 2**
Visitation rate by Xylocopa species (visits/flower/hour) during diurnal hours to *Cyclopia* calculated from camera trap data, including the number of hours of observation time per species in both the wild and cultivated study sites. On average, 400 flowers were observed in the cultivated site per observation period.

| | Wild | | | Cultivated | |
|---|---|---|---|---|---|
| | *C. subternata* | *C. genistoides* | *C. intermedia* | *C. subternata* | *C. maculata* |
| **Time (hrs)** | 110.67 | 1544.41 | 178.17 | 20.16 | 130.58 |
| ***X. capitata*** | 3.8e-3 | - | 4.7e-3 | 9.9e-3 | 3.3e-3 |
| ***X. caffra*** | - | - | - | - | 9.1e-6 |
| ***X. rufitarsis*** | - | 1.3e-5 | 3.1e-4 | - | - |
| **Total** | **3.8e-3** or **0.0037857** | **1.3e-5** or **0.0000129** | **5.0e-3** or **0.0049849** | **9.9e-3** or **0.0099206** | **3.3e-3** or **0.0032820** |

unable to trigger the motion-sensitive camera traps. The camera traps were set to trigger during the day and at night to identify whether nocturnal pollination was occurring (Somanathan *et al.*, 2019).

A camera trap picture demonstrating noticeable tripping by a floral visitor was recorded as one visit to one flower. There were visitors that triggered the camera trap multiple times within a short (30 second) timeframe while visiting a single flower. In this case, all of the pictures that were captured within a 30 second range were recorded as one visit (unless movement to a new flower was clearly visible). This was to ensure that a single visit was not counted more than once.

Camera traps were placed in the wild and cultivated study sites between September and November 2021. On average, 400 flowers from one plant were observed per camera per observation period. Since camera traps were used in supplementation to direct floral observations, priority was given to *Cyclopia* species that were not as frequently observed. This was to ensure that all *Cyclopia* species received adequate pollinator observation. Therefore, *Cyclopia genistoides* had the highest number of hours of camera trap observation and *C. subternata* had the least (Table 2).

### 2.3. Nectar properties

In order to determine nectar volume and concentration, *Cyclopia* flowers were collected from inflorescences in secured mesh bags which were placed over branches for 24 hr period prior to exclude pollinators. All collected flowers were in the same phenological phase (a fully opened flower just after the bud maturation phase; Motsa *et al.*, 2017). The volume of nectar for each species was measured using micro-capillary tubes, and nectar sugar concentration was measured using a 0-55% handheld refractometer (Bellingham and Stanley, UK). Flowers were collected from each *Cyclopia* study species for measurement (cultivated *C. subternata* $n$ = 30, cultivated *C. maculata* $n$ = 39, cultivated *C. genistoides* $n$ = 48, wild *C. subternata* $n$ = 7, wild *C. intermedia* $n$ = 32).

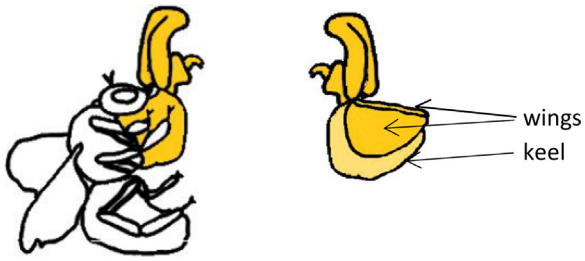


**Fig. 2.** A *Xylocopa capitata* tripping (actively handling the lateral "wing" and ventral "keel" petals) a *Cyclopia* flower to gain access to floral rewards.

### 2.4. Data analyses

The visitation rate of pollinators to each *Cyclopia* species in both the cultivated and wild study sites was calculated as visits/flower/hour. Camera trap visitation rate was calculated by determining the number of visitors recorded by each camera trap, approximating the number of flowers visible on the camera trap images and finding the sum of hours each camera trap was set up for. The visitation rate calculated from the camera trap data was adjusted to exclude night time hours as there were no nocturnal visitors recorded.

The visitation rates for each pollinator to each *Cyclopia* species was calculated separately using the floral observation data and the camera trap data. The daily mean visitation rate was used in all data analyses to avoid bias toward *Cyclopia* species with a higher number of observation hours. These visitation rates were then used to construct pollination networks visualizing pollinator sharing among *Cyclopia* species using the "bipartite" package (v2.16; Dormann *et al.*, 2009) in R (R Core Team, 2021). Thereafter, the mean visitation rate between the floral observations and camera traps was calculated for each pollinator to each *Cyclopia* species under study, and additional pollination networks were constructed using the "bipartite" package (v2.16; Dormann *et al.*, 2009) in R (R Core Team, 2021). No difference

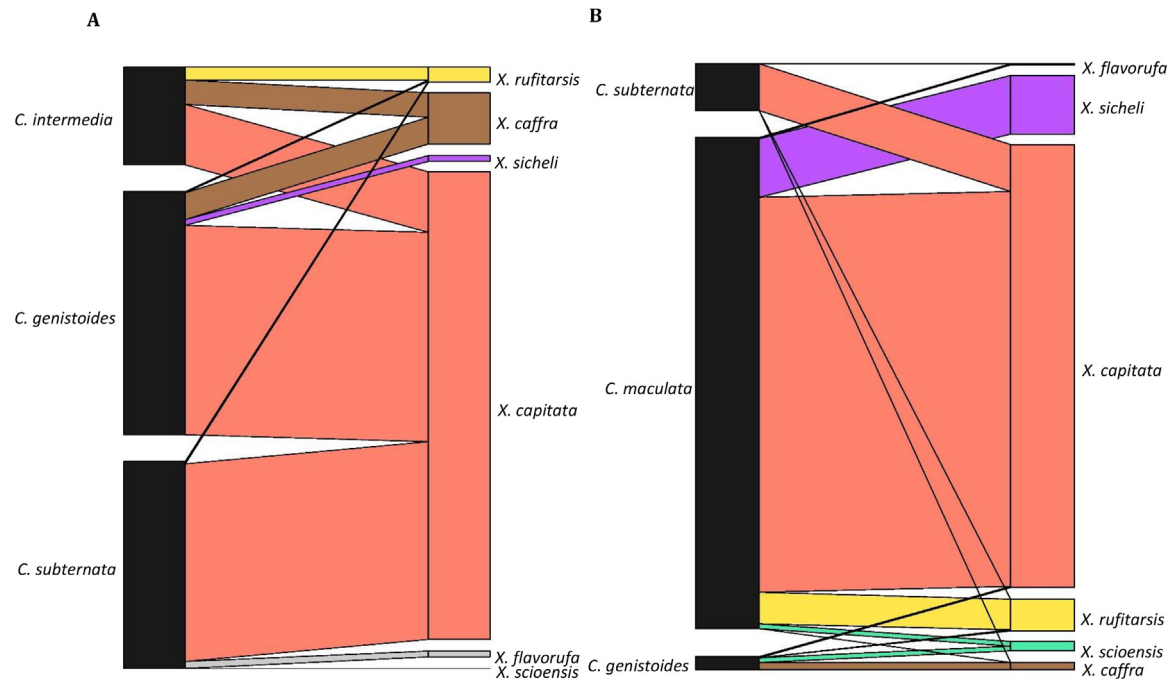


**Fig. 3.** Pollination networks visualizing pollinator sharing among *Cyclopia* species from (A) the wild and (B) cultivated study site. The visitor species are on the right side of the networks, each with unique colour (Yellow: *Xylocopa rufitarsis*, Brown: *X. caffra*, Purple: *X. sicheli*, Red: *X. capitata*, Grey: *X. flavorufa*, Turquoise: *X. scioensis*). The *Cyclopia* study species are on the left of the networks. The visitation rate of each visitor is indicated by the width of each rectangle alongside the species name. The link between each visitor species and plant study species indicates visitation interaction, the visitation rate indicated by the width of the lines between the pair (plant – pollinator). Visitation rate was calculated from both direct observation and camera trapping.

was observed between these two methods, but combined they paint a more complete picture (Fig. 3, Appendix 1B & C). Network metrics (links per species and connectance) were calculated in R (R Core Team, 2021) to aid data interpretation. Links are the number of unique interactions between plants and pollinators. Connectance is defined as the realized proportion of possible links (Dunne *et al.*, 2002), by taking into consideration the total number of links and network size (Jordano, 1987).

The difference in nectar volume and sugar concentration between *Cyclopia* species were not normally distributed and was therefore analysed using a Kruskal-Wallis test. Statistical pairwise comparisons of nectar volume and concentration between *Cyclopia* species were calculated using a Dunn Test (Dunn, 1964) computed in R (R Core Team, 2021).

## 3. Results

### 3.1. Pollinator observations

A total of 65.23 hours of direct observation revealed six different carpenter bee species visiting wild and cultivated *Cyclopia* plants, these included; *Xylocopa capitata* Smith, *X. flavorufa* De Geer, *X. rufitarsis* Lepeletier, *X. caffra* Linnaeus, *X. scioensis* Gribodo and *X. sicheli* Vachal (Table 1; Appendix 1B & C). *Xylocopa capitata* was the most frequent visitor in the wild and cultivated sites (Fig. 3 A, Table 1; Fig. 4 A, B & C). *Xylocopa caffra* had the second highest visitation rate to wild *C. genistoides* and wild *C. intermedia,* while the remaining visitors maintained comparatively low visitation frequencies (Fig. 3 A & Table 1). Wild *Cyclopia genistoides* and wild *Cyclopia subternata* was visited by four pollinator species (Fig. 3 A & Table 1). Wild *Cyclopia intermedia* had only three recorded pollinator species with similar visitation rates, *X. caffra, X. rufitarsis* and *X. capitata* (Fig. 3 A). There were overall fewer visits in the cultivated site (Fig. 3 B), with *C. genistoides* rarely receiving visitation (Fig. 3 B).

No night time pollination was observed in camera trap pictures; pollination triggers occurred only between 08:30 and 17:45. Three pollinator species were recorded by the camera traps; *Xylocopa capitata* visiting *Cyclopia subternata, C. intermedia* and *C. maculata, X. caffra* visiting *C. maculata,* and *X. rufitarsis* visiting *C. genistoides* and *C. intermedia* (Table 2). The camera trap recorded little visitation to wild *C. genistoides,* with only one pollinator species, *X. rufitarsis,* observed interacting with wild *C. genistoides* (Table 2). Wild *Cyclopia genistoides* had the lowest visitation rate, with only four individual *X. rufitarsis* captured in over 1544 hours of observation time (Table 2). The camera trap data revealed only two pollinator species, *X. capitata* and *X. caffra,* visiting the cultivated *Cyclopia,* with *X. capitata* making up the vast majority of visitation (Appendix 1C). Cultivated *Cyclopia subternata* had the highest camera trap visitation rate from only one species, *X. capitata,* in just over 20 hours of observation time (Table 2). Cultivated *C. maculata* was visited primarily by *X. capitata* with some *X. caffra* camera trap observations (Appendix 1C).

#### 3.1.1. Network metrics

The links per species in the wild site was lower than the cultivated site (1.2 and 1.5 links, respectively). Fewer links indicate a higher degree of specialization. The cultivated site had a slightly higher connectance value than the wild site (0.778 and 0.6111, respectively; Fig. 3). Although, with no basis for comparison, we cannot authoritatively say that this indicates a site with higher connectance or specialization.

#### 3.1.2. Other floral visitors

Other species were observed visiting the *Cyclopia* flowers, attempting to gain access to floral rewards, including rodents (Fig. 4 D) and honey bees (*Apis mellifera* Linnaeus) (Fig. 4 E & Table 3). The camera trap captured five individual striped field mice (*Rhabdomys* sp.) visiting (likely consuming) *C. genistoides* flowers (Fig. 4 D). During floral observations a total of 69 honey bees (*Apis mellifera*) were observed attempting to gain access to *Cyclopia* floral rewards (63 observed on cultivated *C. subternata,* three observed on wild *C. subternata* and three on wild *C. intermedia*) without contributing to pollination (Table 3). Other visitors, i.e., Diptera, Apidae and

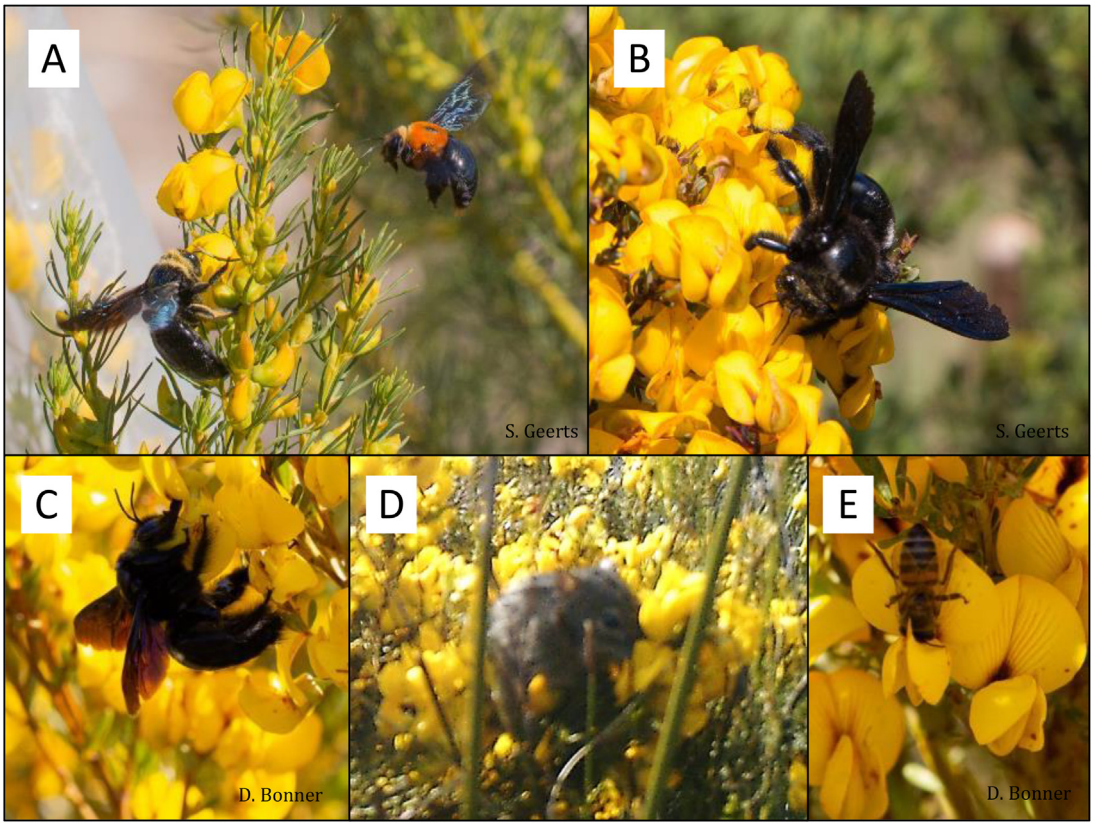


**Fig. 4.** (A) *Xylocopa capitata* individual visiting a *Cyclopia maculata* flower (left) and a *X. flavorufa* individual approaching the same *C. maculata* plant (right), (B) *Xylocopa capitata* visiting a *Cyclopia subternata* flower, (C) *Xylocopa capitata* successfully tripping and gaining access to a *Cyclopia* flower (*C. subternata*), (D) a striped field mouse caught by a camera trap foraging on *C. genistoides*, (E) honey bee (*Apis mellifera*) unsuccessfully attempting to access a *Cyclopia* flower.

**Table 3**
Visitation rate (visits/flower/hour) calculated from direct floral observation plots (not camera traps) by non-pollinator visitors

| | | Wild | | Cultivated | | |
|---|---|---|---|---|---|---|
| Order/Family | Visitor | C. subternata | C. intermedia | C. maculata | C. subternata | Interaction |
| Diptera | sp. 1 | - | - | - | 1.9e-5 | Thieving tripped flowers |
| Diptera | sp. 2 | - | - | - | 1.5e-5 | Thieving tripped flowers |
| Apidae | sp. 1 | 1.7e-4 | - | - | 2.9e-5 | Attempted access |
| Apidae | Apis mellifera | - | 9.4e-5 | - | 2.8e-4 | Attempted access/thieving |
| Apidae | sp. 2 | 1.7e-4 | - | - | 6.8e-5 | Thieving tripped flowers |
| Diptera | sp. 3 | 3.4e-4 | - | - | - | Attempted access |
| Apidae | sp. 3 | - | 3.1e-5 | - | - | Thieving tripped flowers |
| Chrysomelidae | Lema sp. 1 | - | - | 7e-6 | - | Attempted access |

Chrysomelidae, were also observed on *Cyclopia* flowers during floral observations (Table 3) however, none were able to successfully trip the flowers and perform pollination.

### 3.1.3. Nectar properties

The highest mean volume of nectar was extracted from cultivated *C. genistoides*, while the lowest mean volume was recorded in cultivated *C. subternata* (Fig. 5 A). There was a significant difference in nectar volume between the study species (Kruskal-Wallis $\chi 2 = 33.47$, df = 4, $P < 0.001$; Fig. 5 A). Cultivated *C. genistoides* flowers has significantly more nectar than the other study species besides from wild *C. subternata* (Fig. 5 A).

The mean nectar sugar concentration percentage remained above 35% for all species, with *C. intermedia* the highest at over 55% (Fig. 5 B). Nectar sugar concentration was significantly different between the study species (Kruskal-Wallis $\chi 2 = 40.15$, df = 4, $P < 0.001$; Fig. 5 B), with wild *C. intermedia* significantly higher (Fig. 5 B).

## 4. Discussion

Carpenter bees (*Xylocopa* Latreille) were the only pollinators observed to access the reproductive parts of *Cyclopia* flowers. *Xylocopa* have the ability to actively handle the moveable lateral and ventral petals donned by *Cyclopia* spp., much like their papilionoid fabaceous relatives (Westerkamp, 1992; Etcheverry *et al.*, 2008; Grobler & Campbell, 2020). The ability of carpenter bees to trigger the "tripping" mechanism can be associated with their body size and strength (Córdoba & Cocucci, 2011).

Generally, visitation rates were low, but slightly higher for all *Xylocopa* visitors, other than *X. scioensis*, in the wild versus the cultivated sites, despite cultivated and wild sites being in close proximity. There are many factors that influence the habitat preference of carpenter bees, including disturbance. Despite evidence of many pollinators being negatively affected by anthropogenic disturbance (Quintero *et al.*, 2009; Vanbergen, 2014; Geerts, 2011; Geerts & Pauw, 2011; Mnisi *et al.*, 2021), there are cases where species have

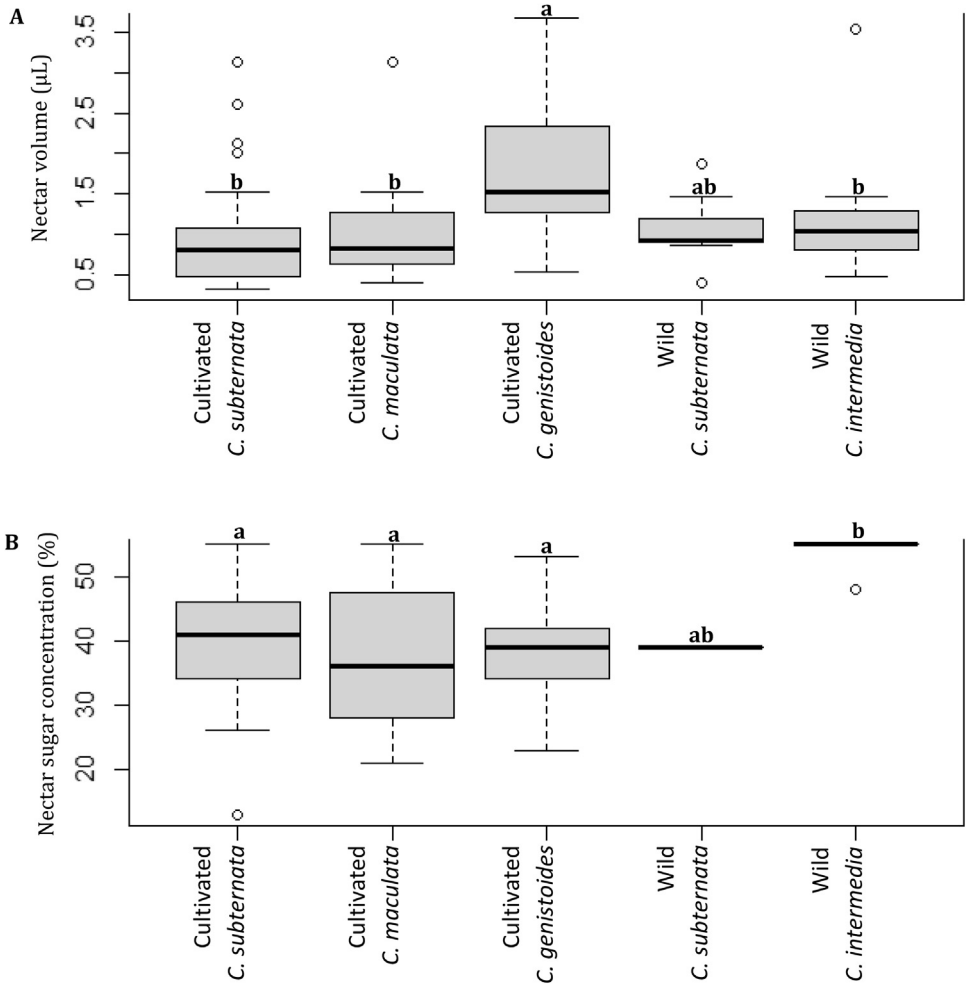


**Fig. 5.** (A) Nectar volume ($\mu$L) and (B) nectar sugar concentration (%) per flower for the *Cyclopia* spp. under study. Different letters indicate statistically significant differences. The thick line in each box represents the median, the box itself represents the interquartile range (IQR), and the whiskers extend the maximum and minimum values within 1.5 x IQR (white dots are the outliers).

thrived in altered landscapes such as *Xylocopa virginica* Linnaeus that nests in artificial wooden structures associated with human activity (Vickruck & Richards, 2017). The focus of pollination impacts of alien invasive tree species has been on resource competition (see for example Adedoja *et al.*, 2021), but impacts of alien invasive trees can also be unexpected, such as enhancing nesting sites for native pollinators in agricultural landscapes. In this study, the availability of nesting material (non-native *Pinus* spp.) may influence carpenter bee abundance. In addition, the abundance of forage in the cultivated site would be expected to attract more pollinators. However, we speculate that the higher floral visitation rate in the wild sites is because *Cyclopia* plants are more sparsely distributed, and a territorial *Xylocopa* male therefore defends fewer flowers, resulting in individual flowers receiving more visits by this male carpenter bee. Additionally, females are not territorial and therefore potentially disperse pollen more than males. Conversely, the abundance of plants and flowers in the territories defended in the cultivated sites will receive lower visitation if territories are similar in size since flower numbers are artificially high in plantations and with fewer flowers visited by defending males, who also limit other visitors, lower visitation may be the result. Therefore, the territorial behaviour displayed by males (Leys, 2000; Sugiura, 2008; Hefetz, 1983) may positively influence floral visitation in the wild study sites. As such, perhaps patterns of resource-use may be sex-specific in carpenter bees, like those recorded in hummingbirds (Maglianesi *et al.*, 2022), thus, resulting in lower visitation rates observed in the cultivated site in comparison to the wild site (Garibaldi *et al.*, 2011).

Plant-pollinator interactions, including flower visitation, may be affected by co-flowering plants through interspecific competition for pollinators, or at least plants which overlap in flowering phenology (Kehrberger & Holzschuh, 2019; Bergamo et al., 2020). Furthermore, the low overall visitation rates of most Fabaceae species could be accounted for by the abundance of floral resources (pea plants have many flowers), resulting in competition between flowers for pollinator visits, similar to those recorded in Bergamo et al. (2020) with under 1 visit per flower per hour on average. Grobler & Campbell (2020) studied the visitation rate of pollinators to *Cyclopia pubescens* at different distances from the roadside, and Córdoba & Cocucci (2017) obtained visitation rates for the pollinators of five papilionoid Fabaceae. Studies by Grobler & Campbell (2020) and Córdoba & Cocucci (2017) recorded low visitation rates, similar to those recorded in this study, which is likely a result of abundant floral resources common in Fabaceae. Additionally, large flowering displays typical in cultivated patches are highly attractive and may likely attract bees from farther away (such as observed in Pasquet *et al.*, 2008). Unfortunately, due to the change in carpenter bee community over time (Shaw-Bonner pers. obs. 2022), which results in the absence of certain species during different *Cyclopia* species flowering times, analysis of difference in carpenter bee visitation rates across species was limited. These patterns require further investigation (Appendix 1D).

It is proposed that the lack of honey bee (*Apis mellifera*) pollination, as well as other non-*Xylocopa* visitor pollination, in the genus *Cyclopia* (Table 3) is due to the floral morphology. The petals of

*Cyclopia* flowers are like those present in all papilionoid Fabaceae; a keel-wing unit that requires active handling to expose the reproductive parts of the flower (Córdoba & Cocucci, 2011; Córdoba & Cocucci, 2017). When visitors are unable to exert the force required to open papilionoid flowers, they generally rob the flowers in search of floral rewards (Córdoba & Cocucci, 2011). *Cyclopia* flowers are likely too rigid to be opened by honey bees (Shaw-Bonner pers. obs. 2021). While signs of robbing were noted on cultivated *Cyclopia* flowers, no robbing was observed during floral observations. Whether honey bees can collect pollen on older tripped flowers, and thus contribute to pollination, needs to be explored. It is unlikely since honey bee visitation was low, all honey bee visits were to untripped flowers, and no contact with reproductive parts of the flowers were observed.

The nectar volume of the *Cyclopia* flowers under study is low in comparison to other forage plants' flowers utilised by carpenter bees (Raju & Rao, 2006). Carpenter bees are generalist pollen and nectar foragers (Kaesar, 2010). However, carpenter bees (*X. micans*) have shown indifference to variability in nectar volume and sugar concentration in laboratory experiments (Perez & Waddington, 1996). The lower volume of nectar produced by *Cyclopia* flowers should have limited impact on carpenter bee foraging. The percentage sugar concentration of *Cyclopia* flowers is relatively similar to the 21 species reviewed by Raju & Rao (2006), further supporting the notion that *Cyclopia* flowers are adapted to carpenter bee pollination. Furthermore, the higher sucrose – hexose ratio of usually higher than 9:1 in *Cyclopia* flowers allows for a source of higher energy value as opposed to other legumes with more balanced sucrose – hexose ratios (see Van Wyk, 1993).

With relatively large bees as the only pollinators, game camera traps, which have been identified as effective tools for insect monitoring that is comparable with human observation, could be used (Naqvi *et al.,* 2022). However, the pollinator species richness observed from camera trapping was much lower than floral observations, with only *X. capitata, X. caffra* and *X. rufitarsis* observed gaining access to flowers. While *Xylocopa caffra* was identified as the most important pollinator for *Cyclopia intermedia* from floral observation visitation rates, only two *Xylocopa* species were observed visiting *C. intermedia* in a 10-hour observation period, none of which were *X. capitata* (the most important pollinator for *C. intermedia* according to visitation rates calculated from the camera trap data). This illustrates the importance of the blended approach in using both floral observations and camera traps to identify pollinators, as the observed interactions between the two methods were similar, however visitation rates were much lower using camera traps likely owing to low detectability. In addition, the combined pollination network (drawn using data collected from both floral observations and camera trapping) (Fig. 3 A) is comparable to the pollination network from floral observation in the wild study sites (Appendix 1B). This indicates that the camera trap data did not contribute any observable changes to the overall visitation rates, besides to *Xylocopa caffra* rates in the cultivated study site (cultivated *Cyclopia genistoides*), where camera traps picked up interactions which was not directly observed during floral observation. This could be due to the motion-sensing trap setting, which has been known to capture fewer insect visitors than scheduled camera trap settings (Naqvi *et al.*, 2022).

The cultivation of indigenous plants is gaining more attention among local farmers, and the native pollinators of these plants can provide substantial increase in seed and fruit quantity and quality (Winfree *et al.,* 2007; Garibaldi *et al.,* 2013). Such is the case of *Cyclopia*, an indigenous legume gaining traction in the global tea market (Joubert *et al*., 2011), which can only be effectively pollinated by one bee genus, *Xylocopa*. While autonomous selfing has previously produced fruit and seed set in *Cyclopia intermedia*, in the same study, seed set was not produced for *C. maculata* or *C. subternata* (Koen, 2020). In addition, self-sterility in the *Cyclopia* genus was revealed through pollinator exclusion experiments (de Lange, 2010). *Cyclopia* may have varying degrees of selfing capabilities, but this requires further research. The role of *Cyclopia* pollinators is potentially critical for many *Cyclopia* species, in particular since seeds harvested from wild populations is a limited source.

Kaesar (2010) reviewed the potential for commercialisation of large carpenter bees as agricultural pollinators, arguing that their range of forage, activity in high temperature, ill-illuminated conditions and length of seasonal activity makes them ideal candidates for agricultural pollination. Although carpenter bees may reduce fruit and seed set significantly through nectar robbing of certain crop species such as rabbiteye blueberry *Vaccinium ashei* (Dedej & Delaplane, 2004; Sampson *et al.,* 2004), they have also been identified as efficient pollinators in other important crops such as passionfruit (Corbet & Willmer, 1980; Junqueira *et al.,* 2012). Here we show the valuable contribution of carpenter bees for successful pollination of *Cyclopia*, thus the value of these native pollinators is crucial for the honeybush tea industry.

The cultivation of indigenous plants in their natural range can pose challenges for conservation. While cultivation can be beneficial for the prevention of overharvesting in the wild (Bester, 2013), conservationists may argue that extensive cultivation of indigenous plants may threaten biodiversity (Van Wyk & Prinsloo, 2018). When indigenous plants are moved across their natural range for cultivation, the threat of genetic contamination through pollen transfer is substantial (Ford-Lloyd *et al.*, 2006). This may be a concern for the *Cyclopia* genus, where different species are moved across the range, sometimes beyond their natural distribution, for cultivation. This study provides baseline information on the pollination of commercially important *Cyclopia* species, useful for the management of cultivated plants and conservation of those in the wild. Future work should investigate the distance that these pollinators can move and whether there is potential for movement between cultivated and wild sites.

## Declaration of Competing Interests

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

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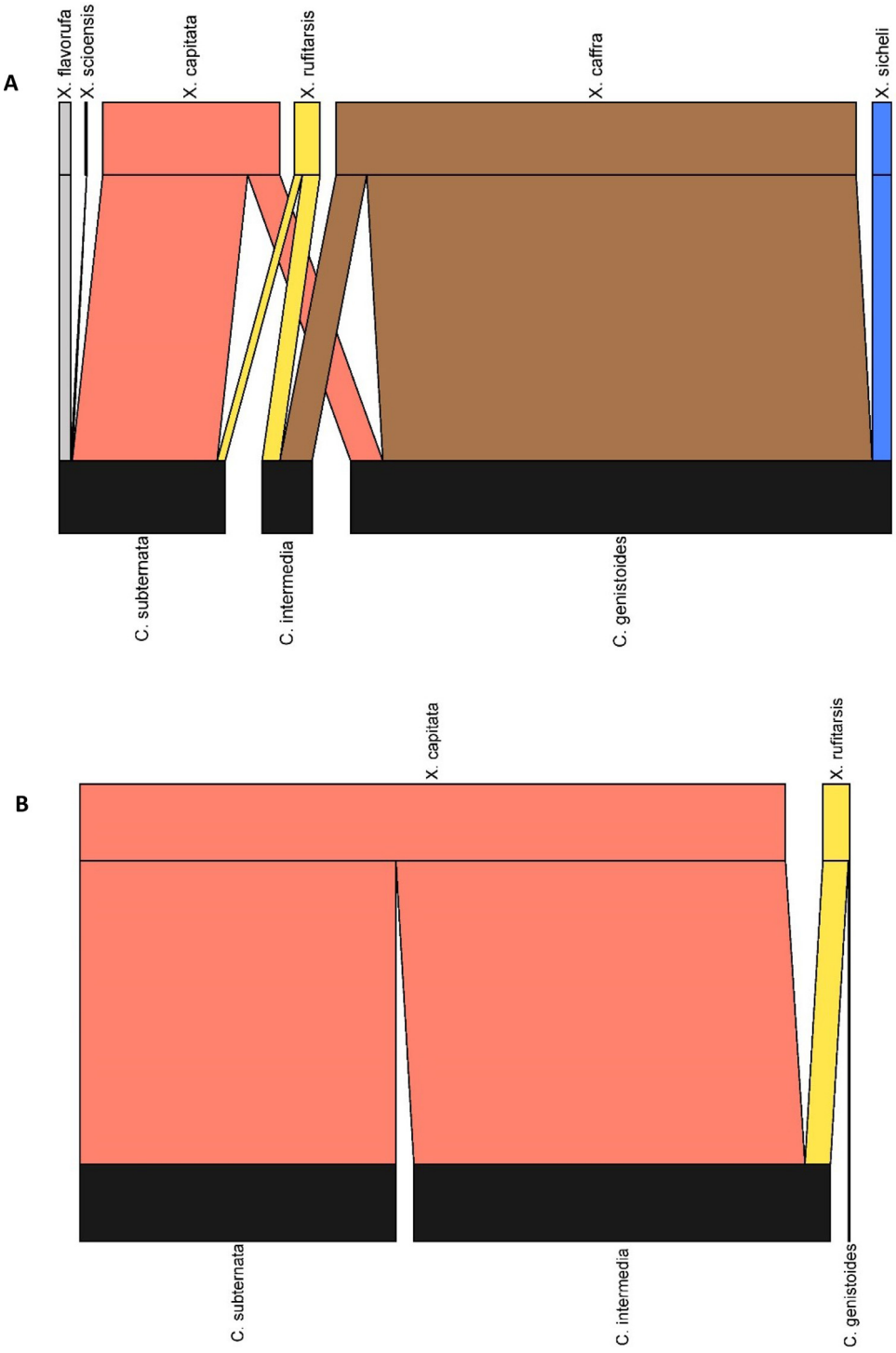
## Appendices

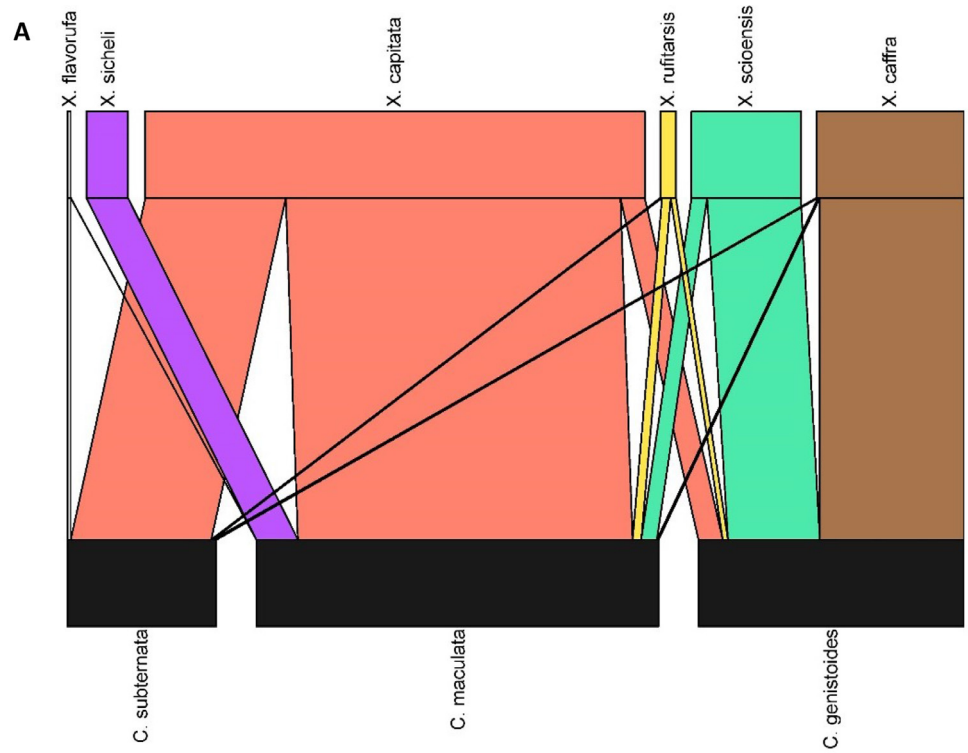
*Appendix 1A Accession numbers for specimen accessioned into the Iziko South Africa Museum. The specimen included representatives of flower visitors observed accessing* Cyclopia *flowers*

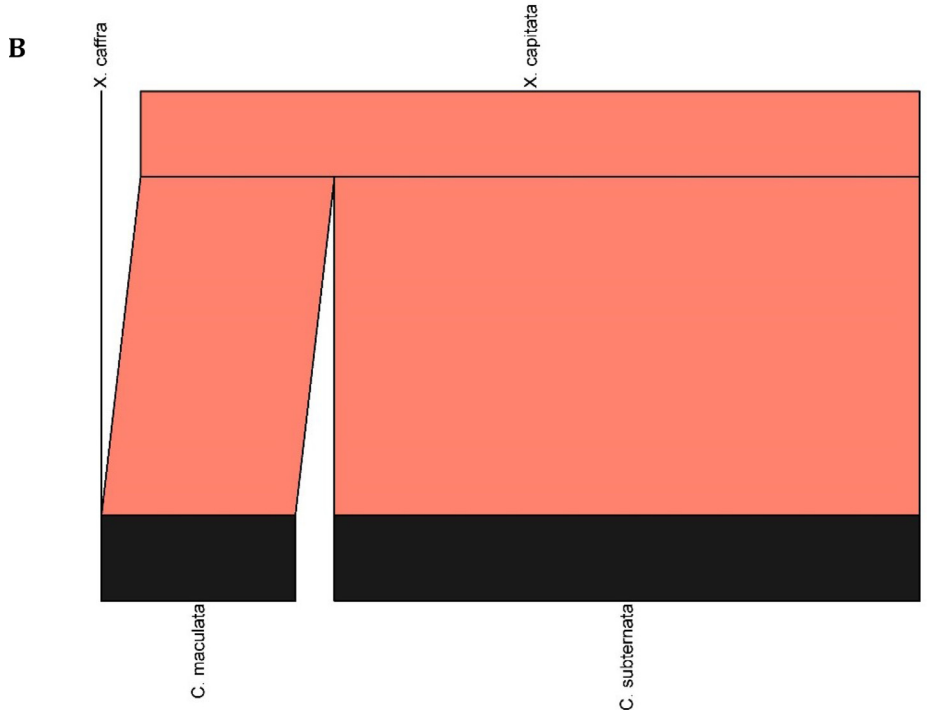
| Accession no. | Species |
|---|---|
| SAM-HYM-B027144 | *Xylocopa scioensis* |
| SAM-HYM-B027145 | *Xylocopa scioensis* |
| SAM-HYM-B027146 | *Xylocopa flavorufa* |
| SAM-HYM-B027213 | *Xylocopa caffra* |
| SAM-HYM-B027214 | *Xylocopa caffra* |
| SAM-HYM-B027215 | *Xylocopa rufitarsis* |
| SAM-HYM-B027216 | *Xylocopa sicheli* |
| SAM-HYM-B027217 | *Xylocopa capitata* |

*Appendix 1B. Pollination network for wild* Cyclopia *spp. from the visitation rates calculated from: (A) the floral observations data, (B) from the camera trap data*

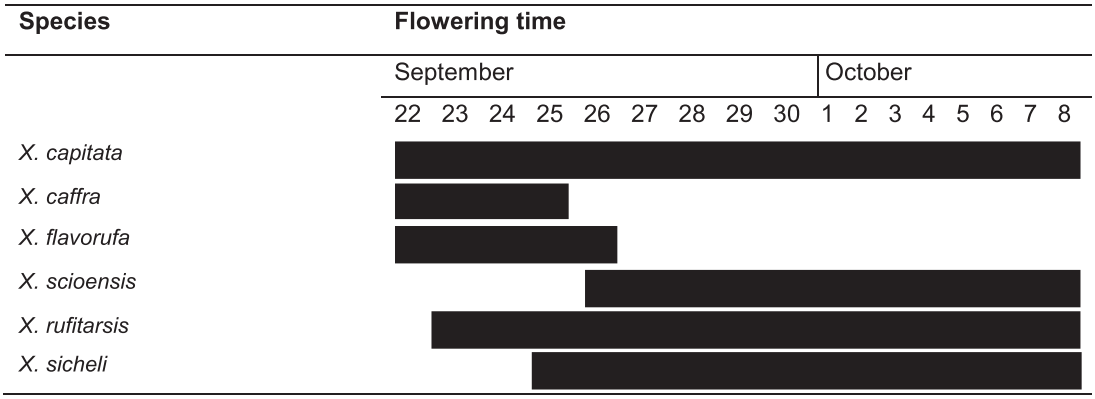


*Appendix 1C. Pollination network for cultivated* Cyclopia *spp. from the visitation rates calculated from: (A) the floral observations data, (B) from the camera trap data*



*Appendix 1D. Carpenter bee species observed over time during the 2021 and 2022* Cyclopia *floral observation period (Shaw-Bonner pers. obs. 2022). This graph represents a portion of the* Cyclopia *genus flowering period in its entirety, which spans over multiple months (Motsa* et al., *2017)*

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