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RESEARCH ARTICLE

Generalist southern African temperate forest canopy tree species have distinct pollinator communities partially predicted by floral traits

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Abstract

Forest canopies provide important resources for insect communities via flowers. Yet, pollination systems of tall forest trees are poorly studied, resulting from the difficulties in observing pollinator activity at the canopy level and great temporal variation in flower production. In temperate forest canopies of the southern hemisphere, small, whitish and generalist flowers seem to dominate. Here, we observed insect flower visitors, at the canopy level, to four southern Afrotemperate forest tree species bearing small, white to green flowers in a large, indigenous forest. Additionally, we quantified flower traits and collected pollen from representative insect visitors. A total of 105 insect species, from 48 families and 7 orders, were observed visiting flowers. In terms of total flower visits, the generalist Cape honey bee (*Apis mellifera capensis*) made up ca. 57% of all flower visits. A third of the total observation time covered crepuscular to nocturnal flower visits; yet only 12.68% of total visits took place during this time. Interestingly, despite both trees and insects being largely generalist in their interactions with one another (supported by the presence of conspecific and heterospecific pollen on most flower visitors), some insect species showed strong preferences for specific species of tree, driving dissimilar, interspecific assemblages of flower visitors. The pollinator community disparity may be explained through the unique and dissimilar floral traits for each tree species, both in flower size and in petal reflectance. We conclude that within generalist pollination systems, distinct and non-random mutualisms can develop between different species of plants and a diverse suite of pollinators, and that floral traits could partially predict such interactions.

KEYWORDS
Apis mellifera, generalist pollination, temperate forest canopy, tree pollination

INTRODUCTION

It is well established that forest canopies are hotspots of local biodiversity with diverse insect communities (Erwin, 1983; García-Robledo et al., 2020; Stork, 1988, 2018). There may also be numerous functional linkages between canopy insect species and the various resources provided by tree crowns in these elevated systems (Kirmse & Chaboo, 2020). Forest canopies can provide important resources for insect communities via the large numbers

of flowers, albeit with great temporal variation (Inari et al., 2012). Temporal variation in canopy flower production is not only driven by differential flower phenology between tree species, but also by differential flower phenology of individual trees or populations (Bendix et al., 2006). This leads to annual and supra-annual, spatiotemporal variation in canopy flower production.

Pollination systems of tall forest trees are poorly studied, due to the difficulties in observing pollinator activity at the canopy level. Methods used to study pollination at crown height include using baited traps over tree branches (Roubik, 1993), elevated pan traps (Urban-Mead et al., 2021), camera trapping (Houlihan et al., 2019), canopy cranes (Inari et al., 2012), and rope climbing techniques (Rosa et al., 2013). Only the latter two enable direct observations of floral visitors and, thus, more reliable information of pollination. Spatiotemporal variation and accessibility challenges have seen pollination studies in undisturbed forest canopies being unevenly distributed across the globe, mostly restricted to areas where canopy cranes are in place and often covering northern temperate or tropical forest systems (Nakamura et al., 2017). There are large regional gaps in knowledge, despite the importance of pollination in successful, long term tree recruitment.

Globally, including temperate forests of the southern hemisphere, small, white and generalist flowers seem to be a dominant pollination syndrome in canopies. For example, Australia's rainforest trees bear small, whitish flowers (Delmas et al., 2020). In New Zealand temperate rainforests, flowers are mostly pollinated by generalist insects (Castro & Robertson, 1997), as they are often small, greenish white to cream coloured (Godley, 1979). In a New Caledonian rainforest, the dominant flower type is also small and relatively simple, mostly pale, or white in colour, indicating unspecialized flowers (Carpenter et al., 2003). Flower morphology of Australian, New Zealand and New Caledonian forests seem to bear noticeable resemblance to those of South Africa, including forests along the Afromontane archipelago (Griffiths & Lawes, 2006; Swart et al., 2023). These pollination syndromes are in fact very diverse in their advertisement and reward strategies. Research has shown how, via scent chemicals produced by flowers, specialized interactions can develop between orchid species and assemblages of pollinating insects in southern Africa (Van der Niet et al., 2010). Importantly, southern Afrotemperate trees have a rich, but largely undescribed, diversity of chemical scents (Phillips, 1926; Venter, 2011). Moreover, nectar rewards differ widely between African forest tree species' flowers (Janeček et al., 2021), an important factor that can drive differential insect assemblages between species (Potts et al., 2004).

Thus, innate variation between species of tree in rewards and attractants such as nectar and scent, should reflect in insect visitors, even within assumed generalist flowering systems. For example, a functionally grouped subset of the available pollinators within a community, being attracted to and utilizing a single plant species, can be regarded as a specialized interaction (Fenster et al., 2004). These linkages between species of plant and pollinator functional groups (e.g., nectar-collecting bees, Fenster et al., 2004), is then driven by scent, colour, rewards and morphology. It is also important to note that a functional group can consist of many or one pollinator species, and a pollinator species can belong to more than one functional group (Fenster et al., 2004).

It has been suggested that a dominance of small, white, open flowers is indicative of a generalist pollination system (termed allophily - Bawa & Opler, 1975; Renner & Feil, 1993). Specialization can be classified based on the number of taxonomic partners or functional groups pollinating a plant species (e.g., short-tongued insects and long-tongued insects; Armbruster, 2017). However, classifying the specialization of pollination systems disguises the degree of specialization of the plant and pollinator

separately. Whereas a plant species can be highly specialized and only pollinated by one mutualist partner, this same partner can be generalist in its feeding behaviour and visit many other species of plant. For instance, this is demonstrated in the bulbous plant *Chasmanthe floribunda*, from the Cape Floristic Region, which is pollinated by the long-billed Malachite Sunbird (*Nectarinia famosa*) only, which, in turn, visits many other plant species during foraging (Geerts, 2016; Geerts & Pauw, 2009). Alternatively, generalist plants can be pollinated by many specialist and generalist pollinators (Ashworth et al., 2004). Thus, generalization or specialization of plants and their insect pollinators are not restricted to dichotomous categories and is rather expressed along a range, with immense complexity (see Armbruster, 2017; Brosi, 2016; Fenster et al., 2004).

Pollinator generalist tree species typically support a high richness of floral visitors and therefore have a high conservation value (Smith-Ramírez et al., 2005). In addition, with new evidence emerging that generalist pollination interactions can persist temporally in both inter and intra annual aspects (Resasco et al., 2021), and small subsets of species can consistently comprise the core of the interactions (Miele et al., 2020), generalist systems might be less opportunistic and more deterministic than initially assumed. For example, in generalist pollination systems, resource partitioning can allow for the occurrence of distinct pollinator assemblages between plant species (Fründ et al., 2010). This resource partitioning may result from morphological differences in flowers. For example, Namaqualand daisies (Cape, South Africa) have open flowers and are therefore accessible to a wide range of pollinators, yet there is some partitioning in their bee fly pollinators due to local flower colour preferences (Ellis et al., 2021). Similar results were shown for native bumblebee species in a broadleaved mixed forest in Japan (Ishii et al., 2008). Apart from advertisement (i.e., colour or scent preferences), pollinator partitioning can also result from differences in reward (pollen, nectar, oil, resin) and timing of flower opening (Armbruster, 2017; Rosas-Guerrero et al., 2014). In generalist systems, temporal resource partitioning could result from high pollinator sharing, where flowering overlap is decreased temporally to reduce interspecific competition (Cummings et al., 2014).

The South African flora is disproportionately rich in species, with highly specialized pollination systems (Johnson, 2010). This is largely due to two centres of high plant endemism, the Greater Cape Floristic Region, which incorporates the fynbos and succulent Karoo biomes, and the Drakensberg mountains (Johnson, 2010). It has been hypothesized that a driving force behind the present richness and floral diversification of the southern African flora is adaptation to pollinators (Johnson, 1996). African montane forest trees at first glance seems an exception to this floral diversification, being dominated by small, whitish and open flowers (Swart et al., 2023). Part of the broader Afromontane archipelago forests, southern African temperate forests are dominated by evergreen trees with little apparent flower morphological disparity. Previous work on pollination in this system was done by Phillips (1926), in which the general fruiting and flowering biology of prominent tree species were studied; however, insect taxonomical diversity in relation to flowers were not studied in detail. Occurring as natural fragments along the south coast of the African continent, it is regarded as the largest indigenous forest in southern Africa (Mucina et al., 2006). It is largely neighboured by mega-diverse fynbos; a shrubby, sclerophyllous vegetation type where flower morphology shows high interspecific variation and complexities in display (Allsopp et al., 2014). This is contrasted against a forest flora of mostly small, white flowers. At present, little is known about the flower visitors in the canopies of generalist pollinator forest trees.

Here, we observed insect flower visitors, at the canopy level, to four southern Afrotemperate forest tree species in a large, indigenous forest

and quantified flower traits. Due to the focal tree species' flowers being small, open and white to green, we hypothesize that (1) tree species are generalist in their interaction with pollinators, (2) insect pollinators are generalist in their interaction with trees, (3) there is substantial overlap in pollinator assemblage compositions between tree species and (4) floral traits between tree species are largely similar.

MATERIALS AND METHODS

Study area

This study was conducted in Groenkop indigenous forest, southern Cape, South Africa (−33.947° S, 22.552° E). This is a relatively large forest for the fynbos biome (1380 ha) towards the western limit of the largest indigenous forest complex in southern Africa (Figure 1). Natural forests are mostly surrounded by a mosaic landscape of indigenous fynbos, small holdings, forestry plantations and pasture lands. Rainfall occurs throughout the year, and mean annual rainfall is 850 mm per annum (Geldenhuys, 1998) and peaks during autumn (March) and early summer (October–November). Mean maximum temperature is 23.8°C in summer and 18.2°C in winter and mean minimum temperature is 19.7°C in summer and 8.9°C in winter (Schulze & Maharaj, 2004). Canopy height is ca. 21 m (Geldenhuys & van der Merwe, 1988).

The tree species composition and relative abundance at Groenkop is known due to long-term (since 1970) monitoring by South African National Parks (SANParks). Permanent research plots are laid out totalling 40 ha of the forest, in which every tree larger than 5 cm diameter at breast height (DBH) is identified to species level and measured every 10 years (SANParks, Garden Route National Park). On these permanent plots, the 10 flowering canopy tree species (DBH of >30 cm; conifers excluded, re: Podocarpaceae) with the highest relative abundance are *Olea capensis* subsp. *macrocarpa* (Oleaceae) (28.14%), *Pterocelastrus tricuspidatus* (Celastraceae) (14.31%), *Apodytes dimidiata* (Metteniusaceae) (12.38%), *Curtisia dentata* (Curtisiaceae) (9.16%), *Elaeodendron croceum* (Celastraceae) (4.66%), *Nuxia floribunda* (Stilbaceae) (4.34%),

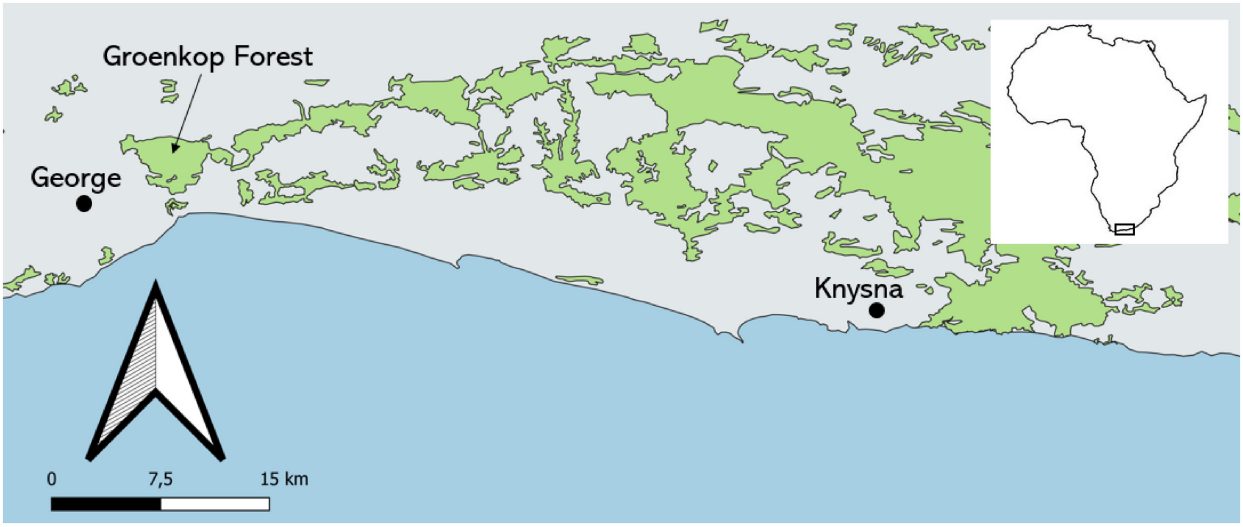

FIGURE 1 Distribution of the largest belt of southern Afrotemperate forests (green) in the southern Cape landscape, with Groenkop forest labelled. Map position relative to the African continent is shown on the top right.

Psydrax obovata (Rubiaceae) (3.22%), *Rapanea melanophloeos* (Primulaceae) (2.57%), *Ilex mitis* (Aquifoliaceae) (2.09%) and *Ocotea bullata* (Lauraceae) (0.96%).

Selection of tree species and individual trees

To test our hypotheses, we selected tree species from the 10 most abundant canopy tree species producing small, whitish flowers during the spring to summer months. During the study period (September 2021–January 2022), and of the 10 most abundant species on the permanent plots, three species did not flower (two winter flowering species, *N. floribunda* and *R. melanophloeos*, and one supra-annual mass flowering species, *O. c. macrocarpa*), one species reached the end of its flowering season (*P. tricuspidatus*), and two species saw only sporadic individuals flowering in very low numbers (*O. bullata* and *P. obovata*). Thus, of the top 10 abundant species, we ultimately selected three tree species that are known to have most individuals flower annually (*E. croceum, C. dentata, I. mitis*), and one species, *A. dimidiata*, which showcases a variable flowering season, producing flowers every second, third or fourth year, based on tree individual and site (Phillips, 1926; Table S1), but which were flowering abundantly during the study period. Focal trees had a DBH of over 30 cm and a spreading crown. To determine the flowering stage of tree individuals, from August 2021 until February 2022, crowns of focal tree species on the research plots were scanned with binoculars (Bushnell Powerview 10 × 50 mm), at least every 14 days, to note the emergence of flower buds and flowers.

Pollinator observations

When >20% of an individual trees' flower buds were considered open, its crown was accessed on the next rainless day by a single, trained researcher using a non-invasive, double rope technique, with a cambium saver to protect tree bark from damage. Six individual trees were accessed per species for diurnal observations, and of these six, a subset of three individual trees were accessed for crepuscular to nocturnal observations. Conspecific trees were at least 30 m apart (Figure S1). The three individual trees that were farthest from a conspecific tree were *A. dimidiata* 3 (1418.24 m), *I. mitis* 2 (223.81 m) and *C. dentata* 6 (180.08 m). Mean distance to nearest conspecific tree was 121.65 m for *I. mitis*, 82.23 m for *E. croceum*, 108.61 m for *C. dentata* and 320.34 m for *A. dimidiata*. The three conspecific pairs closest to each other were between *I. mitis* 1 and 4 (31.25 m), *C. dentata* 1 and 3 (49.76 m) and *E. croceum* 1 and 6 (50.38 m; Figure S1). For each tree species, flowering canopies were accessed a total of nine times, of which six visits were diurnal (continuous 4-h session between 8:20 and 15:00) and three visits were crepuscular to nocturnal (continuous 4-h session between 16:50 and 22:00). Diurnal visits were classified as either 'morning', if the 1-h sub session started on or before 11:30 (i.e., ends at 12:30), or 'afternoon', for sessions starting after 11:40. Sunrise shifted during the observational periods from 6:48 at the beginning of September 2021 to 5:22 at the end of January 2022. Sunset shifted from 18:12 to 19:38 at the end of January 2022. Diurnal observations started between 2 and 4 h after sunrise, and crepuscular to nocturnal observations started approx. 2 h before sunset, commencing until 2 h after sunset. In total, 144 observation hours were concluded, of which 96 h were diurnal observations (24 h per species) and 48 h crepuscular to nocturnal (12 h per species).

The observer was stationed within the flowering tree crown within 1–2 m of observed flowers. The number of flowers visible to the observer was quantified (i.e., not the whole tree). In the flowering crown, all insects that visited flowers were documented, including the number of visits per insect species, defined as the number of times an insect came into contact with the reproductive parts of an individual flower. The contribution of different visitors to pollination depends on many factors. We chose visits per insect species over number of individuals visiting, as (1) the observer's scope was limited to the immediate canopy zone wherein flowers were observed and (2) many insect visitors did short visits to flowers and we were not able to distinguish between different individual visitors over the full observational period with certainty. Distinguishing between different insect species was done with greater certainty, due to the close range of the observer. We use flower visits by species, then, as the main indicator of observed interaction. Where possible, a specimen of each new visiting insect species was sampled for later identification (re: if the species was not sampled once before) and pollen retrieval using a sweep net and placing the specimen in a plastic vial filled with 95% ethanol. For nocturnal observations, a red headlight (Petzl Tikka – brightness 2 lumens, distance 5 m) was used to prevent attracting insects towards the observer.

Pollen analyses

Sampled specimens were placed in ethanol for later pollen swabs in the laboratory. A few flowers per species were collected at random for pollen swabs. In the laboratory, insect specimens were placed on filter paper to allow the ethanol to evaporate. After 30 min, stained fuchsin gel was used to dab the entire body of the insect and then heated onto a microscope slide and covered with a cover slide (Kearns & Inouye, 1993). Additionally, using fuchsin gel, we dabbed the stamens of collected flowers (those in the bud stage), and made at least two slides per tree species to obtain a pollen morph reference for each of the four species. For each insect individual sampled, we determined the presence of conspecific pollen (to the tree species it was collected from) and heterospecific pollen using a light microscope at 40× magnification (Olympus CX21). Each individual insect visitor sampled was treated as an independent replicate for the specific species of tree from which it was sampled. We only noted the presence/absence of conspecific pollen, and presence/absence of heterospecific pollen types (which included the other three species of tree). This was determined in relation to the tree species from which insects were sampled; any pollen not from the focal tree species were considered heterospecific. Insects were identified to order or family level using a dichotomous key (Scholtz & Holm, 2003), and taxonomic experts (see Acknowledgements) identified bees, flies and moths to their lowest possible taxonomic classification.

Statistical analyses

Generalization and specialization

Here, we employ community level network metrices to a subset (re: four tree species only in the canopy layer) of the potential full network; as such, reported statistics should be viewed as being restricted to this subset. Reference to 'network' from here onwards then refers to this stated subset of four tree species. The flower to pollinator interaction networks and the graphical web was constructed using the *Bipartite* package (Dormann

et al., 2008). We used network level indices of weighted nested overlap and decreasing fill (NODF), Shannon diversity and modularity of the network to give an overall impression of the network (Dormann, 2011).

We also used Blüthgen's d' metric, which is the comparison of the distribution of the interactions maintained by each pollinator species to flowers of the four tree species (Blüthgen et al., 2006). This metric describes the degree of interaction specialization at the species level, and here, is essentially a measure of how specialized each pollinator is to the different plant species. If the pollinator is just visiting one plant species in the network (re: network subset, i.e., only one of the four tree species), then it is given a higher score (specialists) compared to those that visit multiple species in the network (generalists). We calculated the d' score for each pollinator species. To determine which tree species attracts more specialist pollinators, we summed the d' score for each pollinator species observed visiting the respective tree species. This showed us, between four tree species flowering in close proximity to one another in the canopy layer, which have more specialist flower visiting species relative to the other tree species in this same, elevated niche. We do not consider the larger, immediate floral community, such as flowering plant species in the understorey, in the canopy and subcanopy layer outside of the permanent plots, and in the neighbouring vegetation types (fynbos, invasive species), which can affect the statistics reported here. To determine the differences in the sum of d' per tree species, the distributions of models were checked using the *DHARMa* package (Hartig, 2017) and spatial autocorrelation was checked using correograms in the *ncf* package (Bjørnstad, 2020).

Pollinator assemblage composition

To analyse differences in species composition of pollinators that visit the flowers of each tree species, the *manyglm* function within the *mvabund* package (Wang et al., 2012) was used. All multivariate models were fitted using a negative binomial distribution, assuming quadratic mean–variance and based on the 'PIT-trap' resampling method with 999 permutations (Wang et al., 2012). Using the *manyglm* function, the response variable was visiting species assemblages, and predictor variables were tree species, month and session (morning, afternoon, crepuscular, nocturnal). Pairwise comparisons were also made between tree species, month and session. Results were visualized with multivariate abundance-based Bayesian models using the Markov Chain Monte Carlo estimation methods, with covariates and latent variables displayed with horizontal line plots in the *Boral* package (Hui, 2016).

Flower traits

From each individual tree (24 individuals from 4 species, at least 5 flowers per individual), flowers were collected to measure flower colour and leaves to measure background contrast in the laboratory with an Ocean Optics USB2000 spectrometer (Dunedin, FL). Data processing and analysis was conducted with the *pavo* 2.9.0 package (Maia et al., 2019). Firstly, overall petal similarity was assessed with raw reflectance values, making no assumptions about the receiver's perception. Reflectance values were standardized and binned into 21 nm intervals and a principal component analysis applied.

Secondly, distinctness and conspicuousness of the tree species' petal reflectance was assessed using visual modelling, which incorporates the

viewing conditions and perceiver's visual system. Spectra were smoothed (span = 0.2) and averaged for each tree species. Honey bee visual system was modelled using the receptor absorbance maxima of *Apis mellifera*, forest shade illumination, tree leaf as background and applying a von Kries colour correction. Species' flower distinguishability in honeybee visual space was calculated using the colour-hexagon model (Chittka, 1992), which quantifies colour distances in hexagon units and objects with >0.1 hexagon unit distances are distinguishable to bees (Dyer, 2006). We also determined whether hoverflies (the second most common flower visitors) could distinguish between the tree species' flower colours. Hoverfly visual system was modelled using the receptor absorbance maxima of *Eristalis tenax* (Lunau, 2014; Shrestha et al., 2016), forest shade illumination, tree leaf as background and applying a von Kries colour correction. Colour distances in fly visual space was determined using the colour-opponent coding model (Troje, 1993) with distances >0.096 Troje units (Tu) considered to be functionally discriminable and >0.206 Tu easily discriminable (Garcia et al., 2022).

Conspicuousness to bees was quantified as the chromatic contrast between petal and leaf reflectance in the honeybee visual system. Achromatic contrast could also be determined, which indicates the visibility of objects from a distance and under low light (Van der Kooi et al., 2019). The Receptor noise limited (RNL) model was used to calculate colour distances with the photoreceptor ratio of (1:1:1) and assuming Weber fractions of 0.13, 0.06 and 0.12 and that noise is proportional to the Weber fraction (Vorobyev & Osorio, 1998). This quantifies receptor noise-weighted Euclidean distances in the units Just Noticeable Differences (JND; Vorobyev & Osorio, 1998).

To quantify flower size, 12 individual flowers' petal length, petal width, pistil length (including ovary, style and stigma) and stamen length were measured from collected flowers at random and per species using a digital calliper under a compound microscope (Olympus SZ30). An analysis of variance (ANOVA) was performed on each of the four flower traits, between the respective tree species. Significant results were followed up by a TukeyHSD posthoc test to determine the pairwise differences. To visualize aforementioned flower traits per tree species, a principal component analysis was done using the package *ggord* in R (Beck, 2017). All analyses were performed in *R* (R Core Team, 2021).

RESULTS

Taxonomic overview

A total of 105 insect species, from 48 families and 7 orders, were observed visiting flowers. Species estimates were 119.22 ± 4.75 and 127.99 for Chao2 and Jacknife2 indices, respectively. The most speciose families were Syrphidae (14 species), Pyralidae and Vespidae (5 species each); Apidae, Chrysopidae, Scarabaeidae and Tachinidae (4 species each) and Cerambycidae, Geometridae, Muscidae, Tipulidae and Uraniidae (3 species each). The most speciose orders were Diptera (38 species), Lepidoptera (26 species – of which 3 species of butterfly), Hymenoptera (18 species) and Coleoptera (16 species). In terms of total flower visits, Hymenoptera was the highest-ranking order and Apidae the highest-ranking family (mainly owing to high numbers of *Apis mellifera capensis* - Table 1; Figure 2). Diptera (driven chiefly by Syrphidae), together with Hymenoptera, made up ca. 94% of flower visits, followed by Coleoptera (3.2%) and Lepidoptera (2.4%). For all four tree species, *A. m. capensis* was the most common visitor (Table 2). In terms of total flower visits of *A. m. capensis*, *I. mitis* had the

TABLE 1 Summary of the 10 most commonly observed insect species, placed in order and family, ranked according to number of flower visits to flowers (total = 7124) regardless of tree species in a southern Afrotemperate forest canopy.

Order	Flower visits	%	Family	Flower visits	%	Species	Flower visits	%
Hymenoptera	5031	70.62	Apidae	4276	60.02	*Apis mellifera capensis*	4057	56.95
						Allodapula sp.	209	2.93
			Vespidae	438	6.15	*Belonogaster* sp.	281	3.94
			Halictidae	296	4.15	*Lasioglossum* sp.	207	2.91
						Zonalictus sp.	89	1.25
Diptera	1660	23.30	Syrphidae	1236	17.35	*Asarkina* sp.	378	5.31
						Syritta angulata	250	3.51
						Allograpta fuscotibialis	227	3.19
						Mallota sp.	120	1.68
			Muscidae	132	1.85	*Phaonia* sp.	104	1.47
			Tipulidae	98	1.38			
Coleoptera	229	3.21	Cerambycidae	71	1			
			Mordellidae	57	0.8			
			Lycidae	54	0.76			
Lepidoptera	169	2.37	Pyralidae	36	0.51			
Neuroptera	30	0.42						
Psocoptera	3	0.04						
Blattodea	2	0.03						

highest number (2174), followed by *E. croceum* (1128), *A. dimidiata* (533) and *C. dentata* (222). Proportionately, *A. m. capensis* made up ca. 70% of flower visits to *I. mitis* and *E. croceum* compared to ca. 30% for *A. dimidiata* and *C. dentata* (Table 2). Proportionately, diurnal flower visits comprised 87.3% of total flower visits (66.7% of observation time) and crepuscular to nocturnal visitations comprised 12.7% of total flower visits (33.3% of observation time). Apart from three species of butterfly visiting flowers diurnally, *Belenois zochalia*, *Danaus chrysippus orientis* and *Amauris echeria echeria*, all Lepidopteran flower visits were by moths (23 species) during crepuscular to nocturnal observation periods. Despite a lower number of visits and less observational time spent relative to diurnal sessions, slightly more species visited flowers during crepuscular to nocturnal observations ($n = 70$) compared to diurnal observations ($n = 68$).

Generalist and specialist interactions

For insect flower visitors, the mean number of tree species links was 3.34, out of a possible 4, whereas tree species had a mean number of insect links of 41.37 (Figure 3). The overall network had a weighted NODF of 22.82, Shannon diversity of 3.04 and modularity of 0.27. Species strength was highest for *I. mitis* (31.43), followed by *A. dimidiata* (25.76), *E. croceum* (25.45) and *C. dentata* (25.36).

Apodytes dimidiata showed the highest Blüthgens d' (0.39) compared to the other tree species, *C. dentata* (0.31), *I. mitis* (0.3) and *E. croceum* (0.28; Table 2). *Apodytes dimidiata* and *C. dentata*, relative to *E. croceum* and *I. mitis*, had the most visits by specialist insect visitors (Figure 4). For *A. dimidiata*, this pattern was seemingly driven by three species of bee; *Lasioglossum* sp. 1 (exclusively visited *A. dimidiata* flowers, $n = 207$

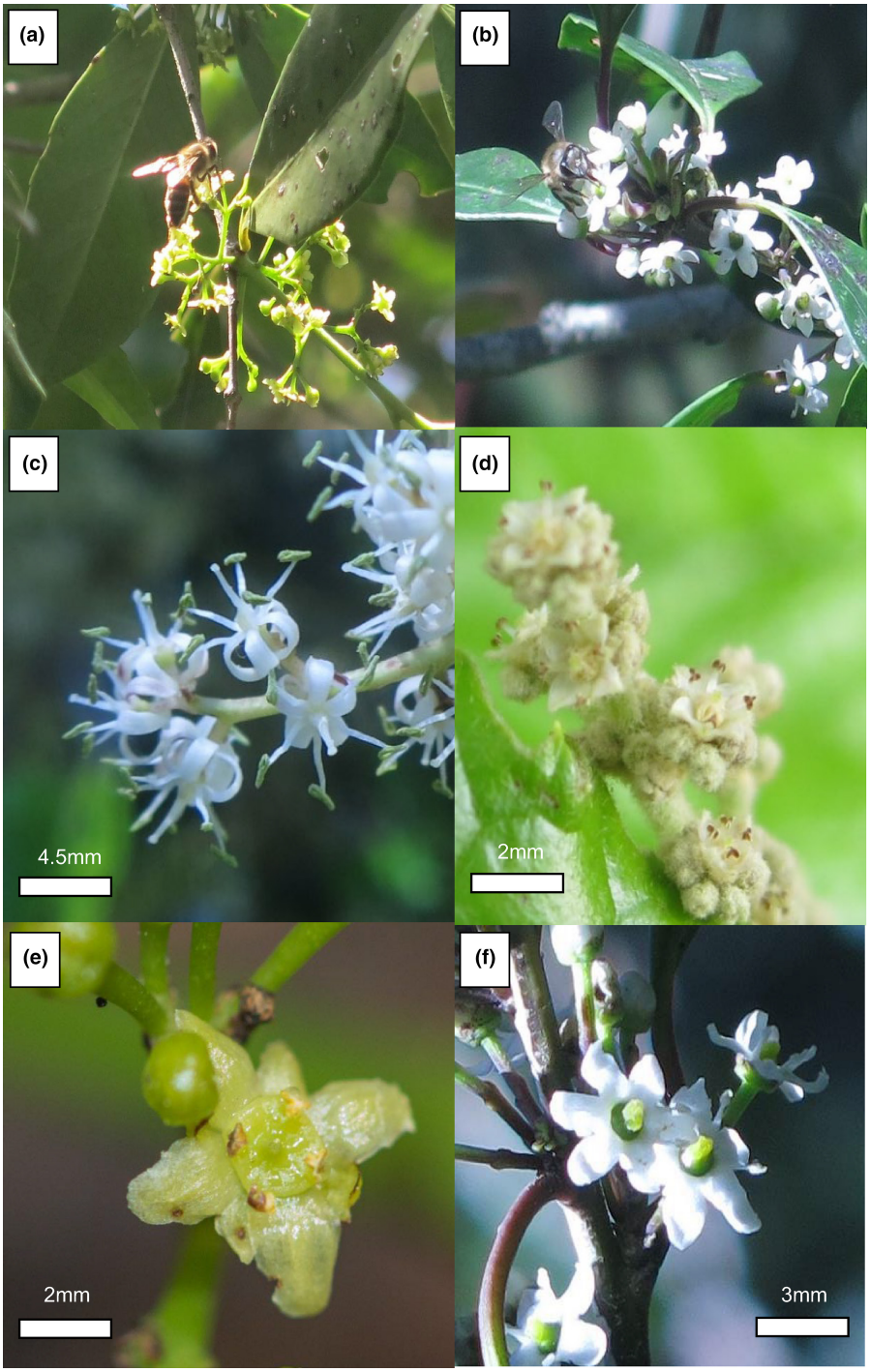

FIGURE 2 Flowers of focal tree species were all white to pale white in colour. Here are depicted *Elaeodendron croceum* (a) and *Ilex mitis* (female - b) with the most common flower visitor, *Apis mellifera capensis*, with scaled photos for *Apodytes dimidiata* (c), *Curtisia dentata* (d), *E. croceum* (e) and *I. mitis* (f). Flower size is greatest in *A. dimidiata* (c) and *I. mitis* (f), followed by *E. croceum* (e) and *C. dentata* (d). A rich, sweet fragrance is released by *A. dimidiata*, a slightly less rich, sweet scent is produced by *I. mitis*, with *E. croceum* having a very faint scent. No scent is recorded for *C. dentata*.

total flower visits, Blüthgens $d' = 0.39$), *Allodapula* sp. 1 (97% of visits to *A. dimidiata* flowers, n = 209 total flower visits, Blüthgens $d' = 0.35$) and *Zonalictus* sp. (96.6% of visits to *A. dimidiata* flowers, $n = 89$ total flower visits, Blüthgens $d' = 0.29$), and a species of hoverfly, *Syritta angulata* (83.6% of visits to *A. dimidiata* flowers, $n = 250$ total flower visits, Blüthgens $d' = 0.32$; Figure S2). When comparing the number of visits with the degree

TABLE 2 Summary of top five observed insect species visiting flowers of Afrotemperate forest tree species, including their number of flower visits, proportion and Blüthgen's *d′* value.

Tree species[a]	Blüthgen's *d'* (tree)	Family	Insect species	Flower visits	%	Blüthgen's *d'* (insect)
Apodytes dimidiata	0.39	Apidae	*Apis mellifera capensis*	533	29.97	0.12
		Syrphidae	*Syritta angulata*	209	11.75	0.32
		Halictidae	*Lasioglossum* sp	207	11.64	0.39
		Halictidae	*Allodapula* sp.	203	11.41	0.35
		Syrphidae	*Asarkina* sp.	157	8.83	0.1
Curtisia dentata	0.31	Apidae	*Apis mellifera capensis*	222	30.91	0.12
		Syrphidae	*Asarkina* sp.	62	8.63	0.1
		Syrphidae	*Mallota* sp.	58	8.07	0.21
		Syrphidae	*Syritta angulata*	40	5.57	0.32
		Pipunculidae	Pipunculidae sp.	35	4.87	0.43
Elaeodendron croceum	0.28	Apidae	*Apis mellifera capensis*	1128	73.87	0.12
		Syrphidae	*Allograpta fuscotibialis*	118	7.72	0.07
		Muscidae	*Phaonia* sp.	64	4.19	0.1
		Syrphidae	*Betasyrphus hirticeps*	30	1.96	0.28
		Agromyzidae	*Melanagromyza* sp.	22	1.44	0.27
Ilex mitis	0.3	Apidae	*Apis mellifera capensis*	2174	70.08	0.12
		Vespidae	*Belonogaster* sp.	236	7.6	0.14
		Syrphidae	*Asarkina* sp.	159	5.12	0.1
		Syrphidae	*Mallota* sp.	62	1.99	0.21
		Syrphidae	*Allograpta fuscotibialis*	60	1.93	0.07

[a]Six individual trees per species, each with one diurnal observation event (4 h), and a subset of three individuals with one crepuscular to nocturnal observation event (4 h). Total observation time per species is 36 h, of which 24 are diurnal and 12 are crepuscular to nocturnal.

of insect specialization, *A. dimidiata* was the only tree species which had high flower visits of more specialist insect species (Figure S2). *Curtisia dentata* had significantly more flower visits from specialist species compared to *E. croceum* and *I. mitis* (Figure 4), although this was largely driven by species with low flower visits (Figure S3). Pipunculidae sp. seemed an exception; it exclusively visited *C. dentata* flowers in relatively high numbers and is considered as a specialist in the studied network ($n = 35$ flower visits, Blüthgens $d' = 0.43$; Table 2; Figure S3). One species of hoverfly, *Betasyrphus hirticeps*, exclusively visited *E. croceum* flowers ($n = 30$ flower visits, Blüthgens $d' = 0.28$). Apart from *B. hirticeps*, *E. croceum* were visited by generalist insect species (Figure S4). Three species of wasp showed preferential interactions with *I. mitis*: *Polistes marginalis* (96.6% of visits to *I. mitis* flowers, $n = 37$ total flower visits, Blüthgens $d' = 0.11$), *Belonogaster* sp. (84% of visits to *I. mitis* flowers, $n = 281$ total flower visits Blüthgens $d' = 0.14$) and *Ropalidia* sp. (68.9% of visits to *I. mitis* flowers, $n = 87$ total flower visits, Blüthgens $d' = 0.06$; Figure S5). *Ilex mitis* had very few specialist species visiting its flowers in the studied network, and only in low numbers (Figure S5).

Pollinator assemblage composition

Tree species, month and session (morning, afternoon, crepuscular and nocturnal) significantly explained insect visitor composition (Table 3). Despite an interspecific dominance of *A. m. capensis*, the composition of insect visitors was dissimilar for each of the four tree species (Figure 5). Tree species significantly explained this pattern (residual df = 67, $p = 0.001$), while month

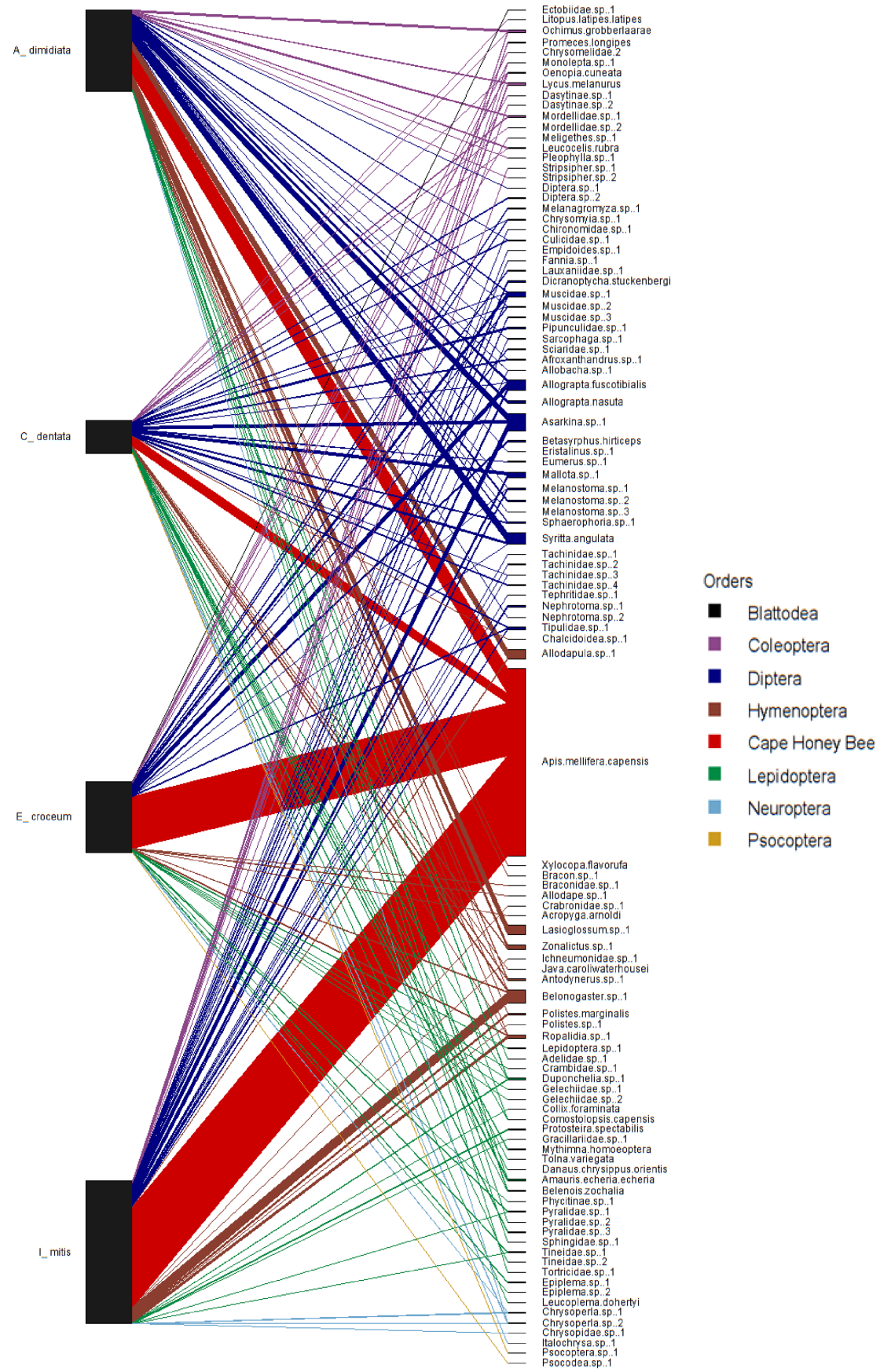

FIGURE 3 Insect pollinator visitation network showing the interactions between pollinator species (right-hand side) and tree species' flowers (left) that were visited. The width of the links represents the number of interactions (re: flower visits).

(residual df = 64, $p = 0.002$) and session (residual df = 61, $p = 0.001$) also had an effect. All pairwise comparisons between the composition of the pollinators to the tree species showed a significant difference (Table S2).

Pollen results

A total of 170 individual insects of 91 species (85.05% of total species count), were sampled for pollen presence/absence analysis (Table S3). *Curtisia dentata* had the highest percentage of insect visitors without any pollen (17.14%; six individuals); though 71.43% of its 35 sampled visitors (27 species) carried conspecific pollen (Table 4; Figure 6). All sampled visitors to *E. croceum* carried pollen (41 individuals from 30 species), and 97.56% of these carried conspecific, *E. croceum* pollen. *Apodytes dimidiata* also had high levels of conspecific pollen sampled from its visitors (90%; Table 4; Figure 6). All three species contrasted to *I. mitis*: only 47.73% of its visitors (44 individuals from 35 species) carried conspecific pollen (Figure 6). The highest proportion of heterospecific pollen was found for *I. mitis* (93.18%; Table 4; Figure 6). *Ilex mitis*, apart from having the lowest percentage of flower visitors carrying conspecific pollen relative to the other tree species, also had the lowest number of visitors exclusively carrying conspecific pollen compared to the other tree species (Figure 6).

Flower traits

Tree species separated based on measured flower traits, and none of the tree species studied had statistically similar means for the traits measured here (Table S4; Figure 7a). Petal, stamen and pistil length were greatest in *A. dimidiata* flowers, which had the largest flowers overall, followed by *I. mitis*, *E. croceum* and *C. dentata* in descending order (Table S4; Figure 2). Petal width was largest in *I. mitis* flowers. Raw petal reflectance data showed differentiation between species of tree, with the species *C. dentata* and *E. croceum* showing the highest clustering and *A. dimidiata* and *I. mitis* separating from the rest of the species (Figures 2 and 7b). All four tree species fell into the blue-green sector of hexagon colour space for bees and in the green sector for flies (Figure 8; Table S5). In bee vision, all species pairs were easily discriminable, except for *C. dentata* and *E. croceum* (greenish colours in human vision) and *A. dimidiata* and *I. mitis* (white flowers) under forest light conditions (>0.1 hexagon units) (Table S5). In the hoverfly vision, all the flowers were easily discriminable (>0.206 Tu; Figures 2 and 8; Figure S6). *Elaeodendron croceum* is less conspicuous to bees compared to the other three species which have similar chromatic contrasts (Table 5). *Ilex mitis*' flowers are the most conspicuous to honey bees, both in terms of chromatic and achromatic contrast to their leaf background, suggesting that they are most detectable to bees, especially from a distance and in low light conditions (Table 5).

DISCUSSION

The four studied southern Afrotemperate forest trees' flowers are visited predominantly by *A. m. capensis* (Cape honey bee), an endemic honey bee subspecies restricted to the fynbos biome of South Africa. We believe this is a natural phenomenon, and not resultant from beekeeping in the area. Nearly a century ago, with beekeeping much less extensive in the wider region than at present, Phillips (1926) noted that the main

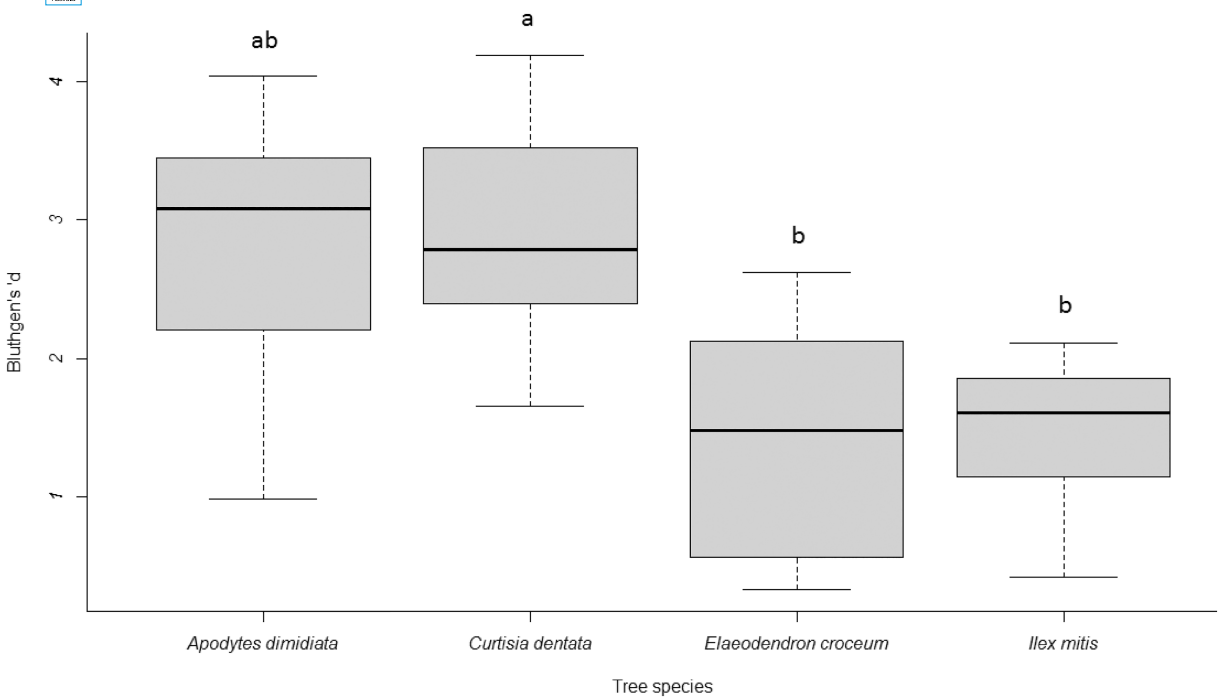

FIGURE 4 Distribution of the interactions maintained by pollinator species to flowers of the four tree species presented as Blüthgen's *d'*. The higher the value the more specialized the pollinator species are that visited those flowers. Different letters above bars indicates significantly different medians. Handles represent maximum and minimum values and boxes represent the interquartile range.

TABLE 3 Summary of the *manyglm* results comparing the response of insect visitor assemblages to tree species, month and session (morning, afternoon, crepuscular and nocturnal), including interactions among these factors.

Factor	Res. df	df. diff	Dev	*pr*(>dev)
(Intercept)	70			
Tree_Species	67	3	682.8	0.001***
Month	64	3	73.1	0.002**
Session	61	3	659	0.001***
Tree_Species × Month	60	1	0.0	0.91
Tree_Species × Session	51	9	156.9	0.001***
Month × Session	51	9	10.3	0.51

Note: Deviance and *p*-values were calculated using 999 resampling iterations.
*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

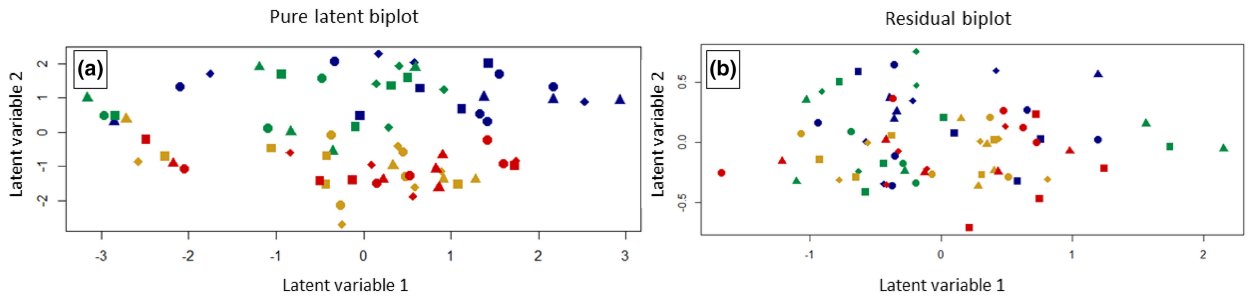

FIGURE 5 (a) Pollinator composition is driven by tree species; *Apodytes dimidiata* (blue), *Ilex mitis* (red), *Curtisia dentata* (green) and *Elaeodendron croceum* (yellow). Observation session is indicated by shape: morning (square), afternoon (circle), crepuscular (triangle) and nocturnal (diamond); (b) residual biplot once environmental variables are accounted for.

TABLE 4 Summary statistics of pollen (of any type) collected from 170 individual insects visiting flowers of four southern Afrotemperate tree species.

Tree species	Individual visitors sampled	Species sampled	Individuals with pollen (%)	Individuals without pollen (%)
Apodytes dimidiata	50	35	46 (92%)	4 (8%)
Curtisia dentata	35	27	29 (82.86%)	6 (17.14%)
Elaeodendron croceum	41	30	41 (100%)	0 (0%)
Ilex mitis	44	35	42 (95.45%)	2 (4.55%)

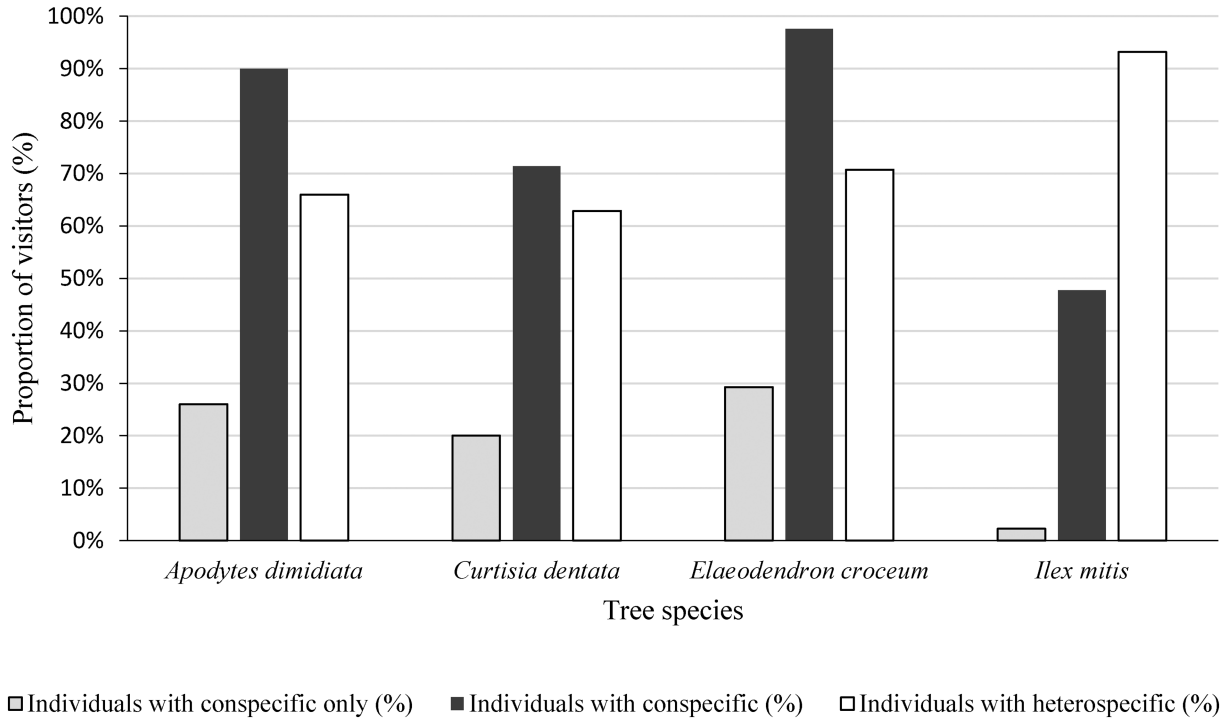

FIGURE 6 Proportion of total flower visitors per species sampled for pollen and categorized into individuals carrying conspecific pollen only (visitor exclusively carried conspecific pollen and no other pollen), individuals carrying conspecific pollen (visitor carried conspecific pollen only or both conspecific and heterospecific pollen) and individuals carrying heterospecific pollen (visitor carried heterospecific pollen or both heterospecific and conspecific pollen).

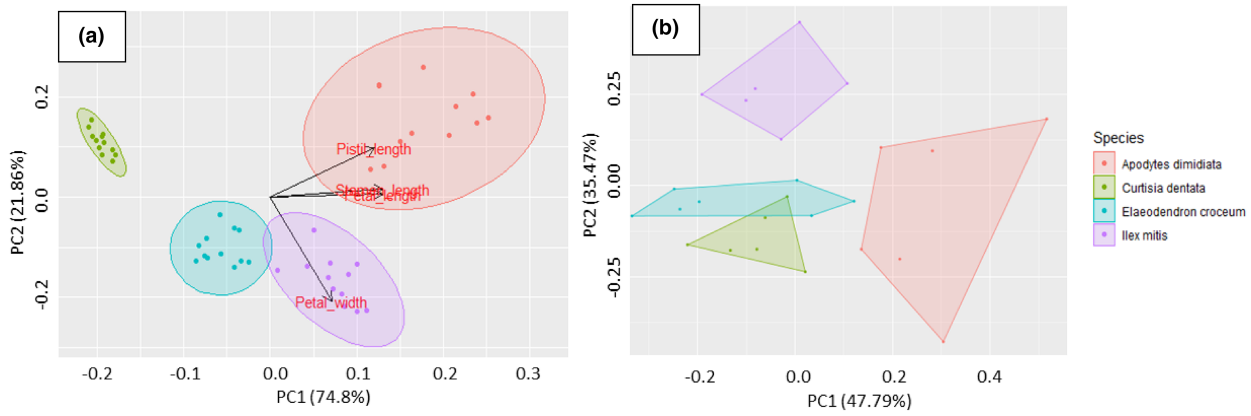

FIGURE 7 Principal component analysis (PCA) of (a) flower size traits and (b) raw reflectance of petals for southern Afrotemperate forest canopy tree species.

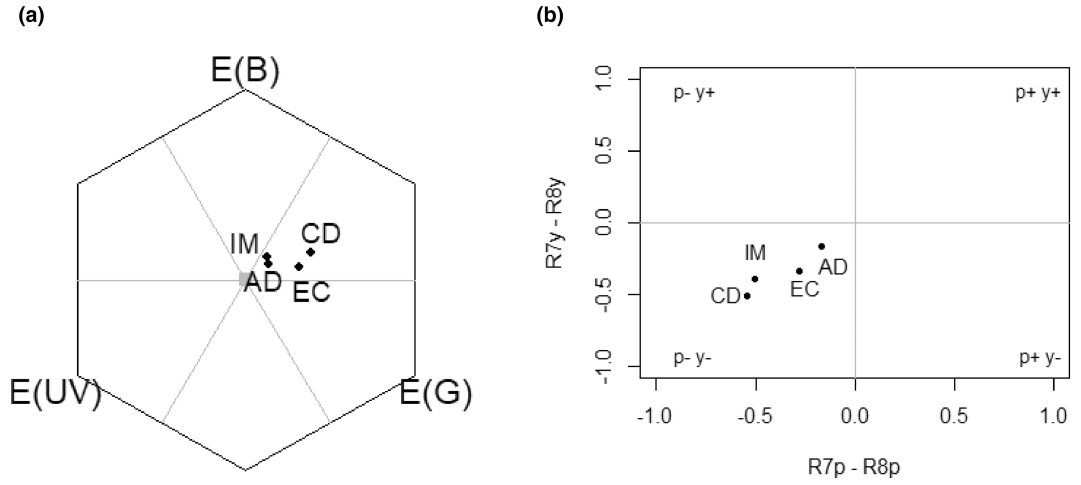

FIGURE 8 (a) Flower colour as depicted in honeybee visual space; the further points are from each other, the more likely the colours are to be distinguished from each other. The central point represents the tree leaf background, and the labelled corners represent maximum excitation of the three photoreceptors. (b) Flower colours depicted in fly visual space, with the quadrats representing excitation of the different photoreceptors, from top left clockwise: blue, UV, purple, and green. AD, *Apodytes dimidiata*; CD, *Curtisia dentata*; EC, *Elaeodendron croceum*; IM, *Ilex mitis*.

TABLE 5 Conspicuousness in honeybee vision quantified as chromatic contrast between a tree species' flowers and leaves.

Species	Chromatic contrast	Achromatic contrast
Apodytes dimidiata	10.32	13.88
Curtisia dentata	11.13	9.72
Eleaodendron croceum	5.83	6.55
Ilex mitis	11.63	16.49

Note: Achromatic contrast quantifies the 'brightness' contrast, with higher values being more conspicuous. Contrasts are receptor noise-weighted Euclidean distances.

pollinators of southern Afrotemperate forest trees are *A. m. capensis* and *Xylocopa caffra*, the latter a carpenter bee species relatively large in size. We only recorded 3 visits from carpenter bees, none of which were *X. caffra*, but the species *X. flavorufa*, and on *A. dimidiata* flowers only. Nearly one hundred years later, we confirm that *A. m. capensis* is a main pollinator of southern Afrotemperate forest trees, with a natural nest found in a tree in the study area. Apart from this single species (*A. m. mellifera*) dominance, a diverse suite of insect pollinators visited canopy flowers, a majority of which were generalist in their interactions with trees. However, some insect species showed strong preferences for specific tree species, driving dissimilar, interspecific assemblages of flower visitors. This is supported by the result that flower morphological traits differed significantly, and floral reflectance of most tree species pairs is distinguishable by the main insect visitors. For three of the four tree species (all except a dioecious species, *I. mitis*), the majority of flower visitors carried conspecific pollen, but in all species heterospecific pollen was also prevalent. This confirms the insects' role as pollinators as well as the generalist foraging behaviour in individual insects.

Evidently, *A. m. capensis* plays a key role in the pollination of several southern Afrotemperate forest tree species and this potentially has great implications for long-term recruitment. If this species' numbers decline past a threshold or get locally extirpated, it is possible that pollination services will not be maintained in the canopy at current levels, or at least for the four

species studied here. The interaction strength with *A. m. capensis* was not associated with the flowers' size, conspicuousness or visual similarity to each other. From the perspective of trees, the sharing of a single species could see heightened, interspecific competition or, beneficially, an increase in pollination facilitation. Ways in which plant species may reduce interspecific pollen transfer is through divergent pollen placement positions (De Jager et al., 2011; Muchhala & Potts, 2007; Pauw, 2006), floral constancy, wherein pollinators utilize plant species-specific cues to predominantly forage on one species (e.g., *Erica* species in the Cape Floristic Region; van der Niet & Cozien, 2022), or through decreasing flowering time overlap, i.e., asynchrony (Sargent & Ackerly, 2008), allowing for species co-existence despite pollinator sharing. Temporal niche partitioning, as predicted by several authors (Dante et al., 2013; Pleasants, 1980), is expected to increase in ecosystems or sites with high pollinator sharing (Jensen et al., 2019). Essentially, the same pollinator (re: *A. m. capensis*) used during different times can be viewed as pollination resource separation (Pauw, 2013). Observations on the temporal separation of flowering have been made in a cool, temperate New Zealand forest, where tree species shared a bat pollinator (Cummings et al., 2014). A limitation to our study is that observations were done over a single season, and our inferences do not include the possibility of interannual turnover of pollinator assemblages. Based on a recent study in a subalpine meadow, Colorado, USA, spanning over 5 years, in which the authors show how generalist plant-pollinator interactions persist across time and space, it is however plausible that the interactions reported here could hold similar, interannual persistence (Resasco et al., 2021). We provide a baseline for future studies on Afromontane tree pollination, and we suggest further work on the topic of temporal niche partitioning and interannual pollinator assemblage persistence in this warm temperate forest system.

We show that all four tree species attract a high richness of mostly generalist insect species (>35 insect spp. per tree species). Southern Afrotemperate forest trees can thus be considered generalist in their interactions with insect flower visitors. This potentially provides trees a degree of reproductive insurance in the case of mismatches in phenology of flowering and insect activity. Yet, differences were evident between tree species. The two tree species with the highest relative number of specialized insect species were *A. dimidiata* and *C. dentata*. The latter could be explained by a rich diversity of insect species that visited the flowers of *C. dentata*, but in very low numbers whereas many of the more specialized species had a high number of visits towards *A. dimidiata* rather. For *C. dentata*, most species had very few observations and might therefore not be specialists, but simply are species that occur in low abundances (Blüthgen, 2010).

We show that relative floral traits are predictors of the number of flower visits: *A. dimidiata* and *I. mitis*, the two species with the largest and brigthest flowers, attracted the most flower visits, and *C. dentata*, the smallest and least bright, attracted the least flower visits. Differences in rewards, such as pollen and nectar, can cause preferential foraging by bee species (Tan, 2008), but these need to be explored in this study system. Although we did not do scent analysis on our study tree species, it is expected to influence the reported visitation patterns. Drager et al. (2022) showed from an Afrotropical lowland forest how scent can drive different groups of visitors to flowering species, for example with sweet-scented flowers being more attractive to Hymenoptera and fermented flowers being more attractive to Diptera. Here, *A. dimidiata* forms large inflorescences and produces a sweet, rich odour unmatched by any of the tree species studied here (Phillips, 1926). *Elaeodendron croceum* produces a faintly sweet scent, and *I. mitis* produces a sweet scent, whereas *C. dentata* had no detectable

scent. Perhaps, scent could explain the relatively few flower visits of non-syrphid flies to the focal tree species, and the dominance in bees, wasps and hoverflies reported here. A lack of detectable scent could also explain the relatively low visitation rates to *C. dentata* specifically. Interestingly, *C. dentata* is also the only species not known to produce nectar (Phillips, 1926). Thus, although not experimentally tested in the current study, both scent and nectar could have significant effects on pollinator visitation differences between our study tree species, perhaps in conjunction with flower size and inflorescence density.

Weighted NODF becomes higher when networks become more nested, an indication of generalization. The weighted NODF reported here (22.82) is higher than late successional (19.53), early successional (17.5) and pristine (12.32) Renosterveld in the Cape Floristic region (Cowan & Anderson, 2019) and Mediterranean shrublands in Spain (16.05; Novella-Fernandez et al., 2019) and is also higher than an Australian rainforest canopy (13.82; Wardhaugh et al., 2015). In relation to non-forest temperate biomes and subtropical rainforest canopies, Afrotemperate forest tree-pollinator interactions are therefore more nested and less compartmentalized, and subsequently are considered more generalized (Wardhaugh et al., 2015). Plant species richness have been shown to be negatively correlated with nestedness (Petanidou et al., 2018), and Afrotemperate forests are significantly less species rich than Mediterranean shrublands at temperate latitudes, and subtropical rainforest canopies, perhaps explaining the reported result. Also, the mean specialization of insect visitors (0.17 ± 0.1) was low, when compared to Cederberg dry fynbos (0.55), another Mediterranean shrubland (Pauw & Stanway, 2015). Moreover, on a global scale, the specialization of insect visitors to flowers reported here is towards the lower spectrum (Pauw & Stanway, 2015; Schleuning et al., 2012), supporting our hypothesis that insect pollinators in our study system are largely generalist. This finding is consistent with our expectations, in that the dominance of small, white flowers leaves little space for truly specialized interactions to develop.

Interestingly, the only dioecious species, *I. mitis*, had the highest species interaction strength, with specific insect mutualists frequently interacting with the tree (Vázquez et al., 2012). Although *I. mitis* produces large quantities of nectar, perhaps explaining the recurring preference of numerous species, the nectar amount per flower is low (Chmel et al., 2021). Small reward amounts mean flower visitors need to visit many flowers to obtain sufficient nectar quantities, possibly increasing movements between flowers and trees and, thus, outcrossing. This strategy could enhance flower-to-flower movements of flower visiting insects, to ensure sufficient nectar quantities are obtained during foraging. From a tree's perspective, it increases the possibility of successful pollen movement between different individual trees (Brandenburg et al., 2009). It could be argued that, especially for dioecious species (compared to monoecious), between-tree movement is vital for successful pollen transfer. Contrastingly, the dioecious nature of *I. mitis* could explain the relatively low levels of conspecific pollen found on its visitors: many species could visit its flowers for the nectar reward, but few move between male and female trees successfully carrying out pollination.

Southern Afrotemperate tree species have great functional value, based on the associated insect species richness estimates (119–128 spp.) and the unique assemblages associated with each species of tree. Removing one tree species from this system will predictably have knock on effects on other species of tree (Kehoe et al., 2021). In a temperate rainforest in southern Chile, sharing plant lineages with South African and New Zealand temperate forests as Gondwanan relicts, one study reported 172

pollinator species, of which 168 were insects, when assessing pollinator diversity associated with 26 plant species (Smith-Ramírez et al., 2005). These figures are surprisingly close to species estimates reported here and supports previous findings showing similar canopy beetle richness between southern Chile and southern Afrotemperate forests (Swart et al., 2021). Not all these species are necessarily pollinators; here, many species visiting flowers did not carry conspecific pollen. Insects also visit flowers for egg deposition, mating sites, shelter, capturing prey and the development of young (Kirmse & Chaboo, 2020). We show that, although in low numbers, 23 species of moth visited canopy flowers (of which only a single interaction was a Sphingid moth) making it the second most species rich order after the flies (38 spp.). Moth pollination have been neglected compared to diurnal pollinators in the past, but new evidence suggests that 75 plant families globally are partially or exclusively moth pollinated (MacGregor et al., 2015). We also recorded crepuscular to nocturnal visits by lacewings, craneflies and mosquitoes. This is the first known report of nocturnal and crepuscular insect species visiting Afrotemperate forest tree flowers.

Many unanswered intricacies remain. For example, of the total southern Afrotemperate tree assemblage, only a few tree species flower during the cold and wet winter; how insect activity is affected by this remains uncertain. The extent to which pollinators in the canopy of southern Afrotemperate forests can utilize neighbouring, open habitats, could also shed light on this poorly studied system. Indeed, *A. m. capensis* is a wide-ranging species known to forage in the fynbos (Moodley et al., 2016), as well as some of the other insect species observed here. Thus, some insect species presented here as specialists might be utilizing non-forest flora in the wider landscape, a hypothesis that remains untested. We conclude that southern Afrotemperate forest trees and their flower visitors form a complex network of interactions and, despite being a generalist system with single-species dominance (*A. m. capensis*), distinct and non-random mutualists are prevalent in the canopy layer. Flower traits could partially explain pollinator preferences for certain tree species. Future work in this system should expand on floral rewards such as pollen and nectar, advertisement via scent, and flower phenology, and how effective insect flower visitors are in pollen transfer.

AUTHOR CONTRIBUTIONS

Rudi Crispin Swart: Conceptualization (lead); data curation (lead); formal analysis (equal); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (supporting); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (lead). **Sjirk Geerts:** Conceptualization (supporting); funding acquisition (supporting); project administration (supporting); resources (supporting); supervision (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **James Stephen Pryke:** Data curation (equal); formal analysis (equal); resources (equal); software (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Anina Coetzee:** Conceptualization (supporting); formal analysis (supporting); funding acquisition (equal); methodology (equal); resources (equal); supervision (lead); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

Full data available on request from the authors. The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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