Urban intensity and flower community structure drive monkey beetle assemblage in Cape Town

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Background: Urban landscapes present an important opportunity for pollinator conservation, but little is known about the status and distribution of pollinator populations in urban habitats in Africa. This represents a major gap in the development of a global understanding of urban pollinators – particularly from the rapidly urbanising context. This study uses a speciose clade of flower-visiting beetles (Coleoptera: Scarabaeidae: Hopliini) to explore patterns of pollinator distribution in a major metropolitan area in South Africa.

Objectives: We investigated community composition across gradients of urban intensity (defined according to the percentage of soil-sealing within 1 km² of each sampling location) and socio-economic status to determine pollinator responses to these urban landscape effects.

Methods: A selection of 142 sites were surveyed twice in the austral spring seasons of 2018 and 2019. Data were collected on habitat structure, flower diversity, and pollinator diversity.

Results: The study found that different feeding guilds of monkey beetles favoured different levels of urban intensity and that beetle richness significantly correlated with flower richness. It did not, however, correlate with diversity indicating that abundance is less impacted than the number of species present. Monkey beetles with moderate sensitivity to urban intensity benefitted from the presence of preferred species of flowers.

Conclusion: Overall, the findings demonstrate the importance of plant community assemblage in supporting urban monkey beetles. We recommend landscaping with preferred flower species in urban parks to support urban pollinators.

Keywords: Hopliini; Coleoptera; community assemblage; pollinators; urban ecology; South Africa.

Introduction

Urban environments are important for the conservation and stewardship of healthy pollinator populations (Hall et al. 2017). Globally, studies that investigated the response of pollinators to urban gradients found that certain guilds and taxa can take advantage of the resources and habitat conditions available in cities (Glaum et al. 2017; Theodorou 2020a; Wenzel et al. 2020). Others can do well when particular conditions are met, such as the provision of small scale floral patches or the introduction of preferred plants (Leveau 2013; Simao et al. 2018). Another group is negatively impacted by urban intensity (soil-sealing) and is intolerant of urban environments (Theodorou 2020b; Wenzel et al. 2020). A recent global systematic review found a taxonomic and geographic bias. Most studies conducted on urban pollinators reported findings for Hymenoptera, temperate regions, and the global north (n = 99, 117 and 120 studies, respectively). A smaller number reported findings from tropical

regions and the global south (n = 24 and 21, respectively) (Wenzel et al. 2020). There is still much to be learned about the responses of other pollinating taxa; cities in the global south; and in under-studied climatic regions, such as tropical, arid and Mediterranean ecosystems (Wenzel et al. 2020). Africa is the most poorly represented continent and offers an opportunity to add to the body of knowledge from a rapidly urbanising perspective (United Nations, Department of Economic and Social Affairs 2018).

Monkey beetles (Scarabaeidae: Hopliini) are diverse in southern Africa and therefore provide adequate richness to observe patterns of change in community compositions. South Africa is a centre of diversity for monkey beetles, where 65% of the world's species and 40% of the genera are concentrated (Colville et al. 2018). The greatest density of monkey beetle species is found in the winter-rainfall region of Namaqualand and the Cape Floristic Region (CFR), where they are important pollinators of several plant families (Bernhardt 2000; Goldblatt & Manning 2011; Mayer et al. 2006). This includes many of the popular flowers that attract local and international tourists during the austral spring season (Kruger et al. 2015). Monkey beetles are especially suitable for study in urban environments because there is existing evidence, which shows that they respond with shifts in feeding guild structure and host plant use in response to human-driven disturbance (Colville et al. 2002, 2018). Additionally, they are easy to collect due to their use of flowers as breeding platforms (Bernhardt 2000; Dafni et al. 1990).

Existing studies have established that biodiversity in urban landscapes is driven by urbanisation (measured by percentage of soil sealing in the surrounding landscape, where soil sealing is the amount of soil under buildings, roads and paving) (McDonnell & Hahs 2008), local habitat characteristics such as dominant land-use or local habitat structure (Theodorou et al. 2017; Theodorou et al. 2020b); and social factors such as socio-economic status and societal norms (Aronson et al. 2016; Lepczyk et al. 2017).

Cape Town is a rapidly urbanising city with a long history of spatially planned social segregation, and land dispossession (Cilliers & Siebert 2012; Lubbe et al. 2010; Rebelo et al. 2011). Until recently, tracts of land remained as natural islands due to their use as buffers between racially divided historical neighbourhoods under Apartheid urban planning (although many of these patches now face encroachment from both planned and unplanned urban expansion), in which neighbourhoods were spatially divided according to race and economic standing (Turok 2011). This legacy remains spatially entrenched.

Economic equality is typically measured by the Gini-coefficient. The closer it is to 1, the more unequal the society, the closer it is to 0, the smaller the difference between the individuals with the highest income and the lowest income. In 2016, Cape Town's Gini-coefficient was estimated at 0.62 (Western Cape Government 2020), slightly more equal than the national value of 0.63, which ranked the country as the most unequal society in the world (World Bank 2014). As such, Cape Town presents steep socio-economic gradients across the city. Cape Town is an important city in which to consider the social and spatial drivers of urban biodiversity because of the mega-diversity of the Cape Floristic Region (CFR) (Rebelo et al. 2011), rapid urbanisation (United Nations, Department of Economic and Social Affairs 2018), and socio-economic inequality.

This study investigates the community composition and distribution of monkey beetles across several environmental gradients in Cape Town, namely: income, urban intensity, and historical soil and vegetation. It compares these data with monkey beetle assemblage response to local habitat and flower community structure. It tests three hypotheses: 1. Monkey beetle feeding guilds will change along environmental gradients (urban-agricultural, urban-natural, and socio-economic gradients); 2. They will associate with specific flower communities (preferred flowers); 3. Beetle and flower diversity are linked.

Study area

Cape Town is the largest city in the Western Cape, South Africa, and has a population of ± 4.5 million citizens (Statistics South Africa 2011). It falls within the CFR, a global biodiversity hotspot with two centres of endemicity (Mittermeier et al. 1999; Rebelo et al. 2011). Within the city metropole, there are 19 vegetation ecosystems (Rebelo et al. 2011). Neighbourhood dwelling density varies from 1 dwelling unit per hectare (du/ha), to 160 du/ha in informal settlements (Mittermeier et al. 1999; Rebelo et al. 2011).

Methods

An environmental gradient is a change in environmental condition across space. Examples of commonly studied gradients include moisture and altitude. Studying environmental gradients help us to understand habitat requirements and species and community responses to changes in abiotic conditions. Urban intensity gradients have been used extensively to monitor the impacts and drivers of biodiversity in cities (Blair 1996; Dubois & Cheptou 2017; Hirzel & Le Lay 2008; Jongman et al. 2006; Lizée et al. 2011).

Sampling locations were thus selected across a range of conditions along an urban intensity gradient at ± 1 km intervals. The largest proportion of sites were
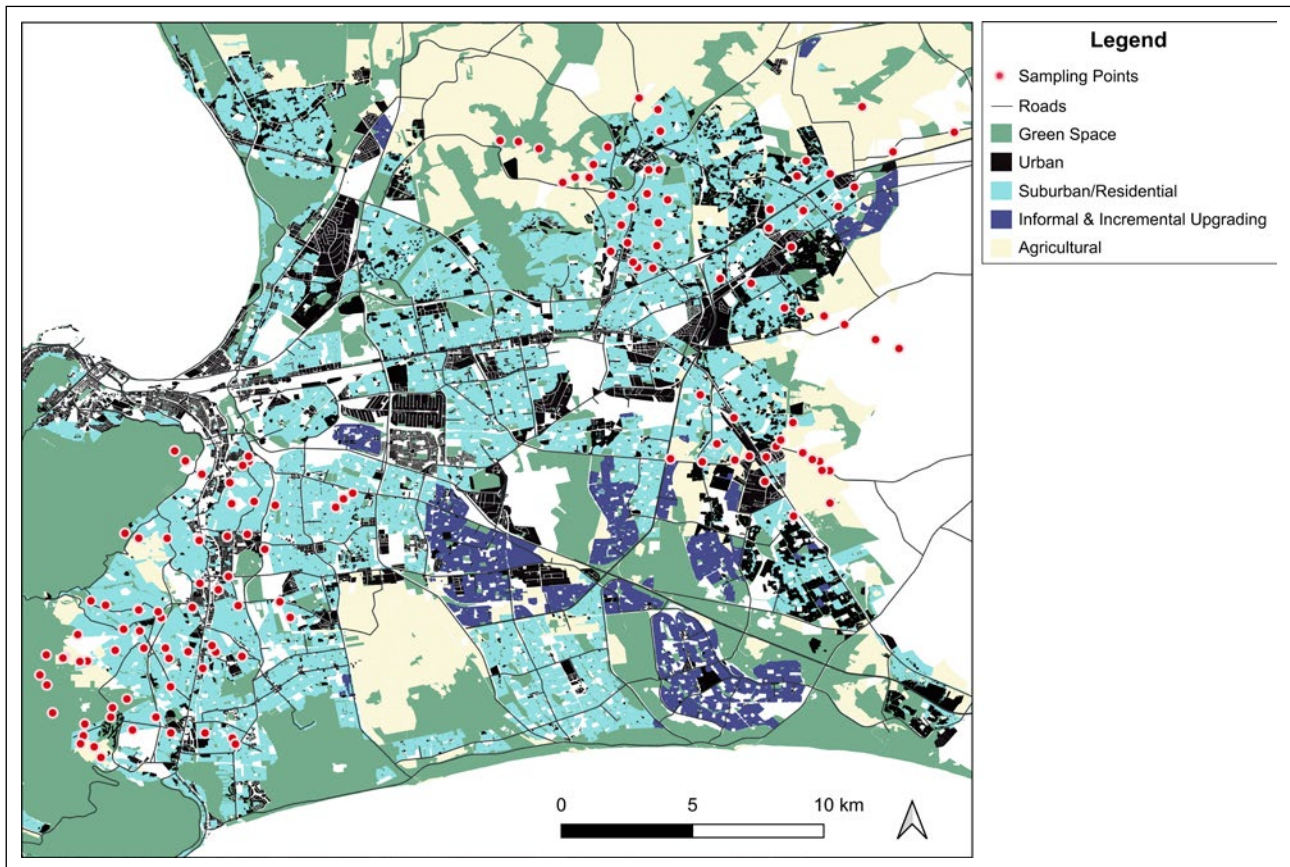
Figure 1. Monkey beetle sampling locations (n = 142) in Cape Town's city parks, vacant lots, farmland and islands of natural patches from which data were collected during the austral springs of 2018 and 2019.

community or district recreational parks, followed by vacant lots and road verges (Figure 1). Protected areas and cultivated farmland were included to represent unurbanised landscapes. To mitigate the effects of potentially conflicting environmental gradients and underlying heterogeneity, the sampling locations were stratified by historical vegetation type, income, and urban intensity in the second year of sampling. In 2018, 72 sites were visited. In 2019, the location of observation sites was adjusted to reduce the impact of variations in underlying vegetation and soil types across the city (a contextual adjustment that was required due to the underlying heterogeneity), resulting in 70 sites in 2019. The sites in the second year remained in similar locations to the first year. The second year's sampling had greater representative evenness across the urban intensity and economic gradients and corrected oversampling that had occurred in the suburban part of the gradients. In 2018, there were eight urbanisation gradients (five short gradients on the west of the city, two in the north and one to the east); in 2019, there were five gradients (two longer, rationalised gradients to the west, one in the east, one in northeast, one in the north of the city). Each blocked part of the gradient (urban, rural, natural, peri-urban, suburban) had at least six sampling locations within the corresponding block. Each block was sampled at least four times across the duration of the two years. Even though there were minor adjustments

to the locations, there were very similar conditions between the years and sites included in each blocked category. Counted without any statistical blocking, the total number of sites was 142. Each of these was independently visited at least twice during 2018–2019 (August–December).

Five sets of blue, yellow and white fluorescent-painted pan traps of 75 mm diameter × 40 mm depth were laid out at 1.5–3.0 m distance from each other in a linear or zig-zag pattern depending on the layout of the site. Pan trap colours were selected for Coleoptera in accordance with the findings of Shrestha et al. (2019) and Vrdoljak and Samways (2012). Each trap received ± 75 ml of 2:1 dilute propylene glycol. Because of permit conditions, traps placed at sites in the South African National Parks (SANParks) properties contained only soapy water. The traps were left in place for 48 hours, allowing at least one clear, warm, sunny day. On collection, the contents of like-coloured pan traps were pooled rendering one sample per trap colour (three samples) per sampling event at each site. Each pooled sample was labelled with the collection date, the location code and the pan trap colour.

Local habitat data were sampled in ten quadrats of 1 m² in a transect across each site at 2 m intervals (or in a randomised grid if the area of the site was too narrow for a

linear transect). Counts of open flowers were recorded within each quadrat. Capitulate flowers were counted as one to the first joint with the main stem. Notes were made of species that were uncommon but present outside of the sampled quadrats on the site. Flowers in the surrounding 30 m radius of the traps were searched for monkey beetles for 15 minutes. As far as possible, three pairs of each species in copula were collected to provide a reference for the identification of sexual dimorphism. The flowers from which the monkey beetles were collected were identified to genus or species level, to provide evidence of the preferences of monkey beetles for colours and for flower species.

Laboratory and desk-top processing

Monkey beetles were separated from the by-catch and were identified to morphospecies level. Representatives of each morphospecies at each site were pinned and an overall representative sample was pinned for cross-checking identification. Where possible, individuals were identified to species level and cross-checked using reference samples in the Iziko Museum of Natural History, Cape Town.

Soil-sealing is the quantity of ground that is covered with buildings and hard surfaces, thereby preventing infiltration and soil penetration by living organisms. The amount of soil-sealing in the surrounding area was used as a proxy for urban intensity. Landscape level patterns were quantified from aerial photographs. Photographs of 1 km^2 were extracted from the Google Earth Engine by loading the GPS co-ordinates of sampling locations into a semi-automated urban intensity scoring tool that runs on machine learning and was developed by Seress et al. (2014). The GPS points entered into the database were centralised to the position where pan traps were placed at each observation site. The semi-automated urban scoring tool requires a minimum of three training points per image (captured by the researchers). It quantifies the area under building, vegetation and roads; it next conducts Principal Components Analysis (PCA) to generate an urban index score. The output file contains data on vegetative cover, buildings, roads and a total PCA urbanisation score (Seress et al. 2014).

Historical vegetation information was extracted by importing the national vegetation map (Mucina & Rutherford 2006) into QGIS (version 3.6.1) and using the point-picker tool to select the data that correspond with the GPS co-ordinates at each sampling location. The shapefile used for this was the South African Vegmap (Mucina & Rutherford 2006) downloaded from the South African National Biodiversity Institute's (SANBI) biodiversity GIS web portal (www.bgis.sanbi. org). Site size was extracted in QGIS (version 3.6.1) from the Cape Town City Council's 2016 Integrated Zoning Map (City of Cape Town 2017). Sites were

post-coded to small (< 0.5 ha), medium (0.5–40 ha) and large (> 40 ha). Income data was sourced from the 2011 census (Statistics South Africa 2011), which reported mean household income by suburb. Values were post-classified into low = R0–R17 246, medium = R17 246–34 492, and high > R34 492, using the equal interval method.

Two separate data matrices consisting of counts of monkey beetle and flowers at each site were constructed. The matrix for the monkey beetles had 142 rows (sites) and 30 columns (Hopliini morphospecies) and the flowers contained 140 rows (sites) and 81 columns (flower species). Two sites had no flowers in bloom due to recent mowing. The elements of the matrices were square-root transformed and two dissimilarity matrices constructed using the Bray-Curtis index in Primer v 6.1.16 (Bray & Curtis 1957; Clarke & Gorley 2006). The one dissimilarity matrix contained dissimilarities between flower species (81 × 81), and the other one between beetle species (30 × 30). Hierarchical cluster analysis (group averages algorithm) were performed on both dissimilarity matrices (Kruskal 1964). Then non-metric multi-dimensional scaling (NMDS) was performed for both. The cluster analysis was overlain over the two-dimensional configuration generated by the NMDS (Everitt et al. 2011). Monkey beetle and flower species that were seen to be outliers in the NMDS and cluster analysis were mostly species which were seldom recorded (< 5 locations) and these rare species were removed from the dataset, so the dimensions of the dissimilarity matrices became smaller.

The NMDS and cluster analyses identified communities of co-occurring monkey beetles in the one matrix, and communities of co-occurring flowers in the other matrix. The groups generated by the hierarchical cluster analysis were added to the NMDS configuration as sets and subsets. Species-sets were grouped into a data vector (i.e., abundance was summed into one column) for each set and subset. Thus analysis was performed on groups of co-occurring monkey beetles and co-occurring flowers. Tests were run to determine what caused the beetle communities to cluster at different locations (i.e., was it the presence of specific flower communities or environmental factors?).

For economic and environmental factors, Kruskal-Wallis tests (Kruskal & Wallis 1952) were performed to test the null hypothesis that the species were randomly distributed across the categorical levels. Spearman's rank correlations (Glasser & Winter 1961) were calculated between the ranked sets and aggregated by each of the environmental factors to understand the direction of those relationships for which the null hypothesis could be rejected.

To examine the relationship between flowers and monkey beetles, the null hypothesis that monkey beetle

species would be randomly distributed across flower species was tested. A contingency table was generated for each monkey beetle species with cells containing the count of the number of sites at which each monkey beetle species was present or absent for each of the flower species. The chi-squared test of independence was performed on each table (Fisher 1922). If the test for a particular monkey beetle was significant, the frequency of co-occurrence with each flower species was ranked; this provided an indication of which flower species are associated with each monkey beetle. Because the data collection was done at the site level, there is a risk of producing misleading results in the context in which two flower species co-occur, but only one is attractive to monkey beetles. Hence, results were corroborated with field collections of monkey beetles collected off flowers and by examining the clustering of flower communities in the non-metric multi-dimensional scaling plots.

To investigate the relationship between the flower diversity and beetle diversity, two diversity indices (Shannon H-index, Inverse Simpson) (Hill 1973) were calculated at each of the 140 sites for both flowers and beetles, using the 'vegan' package (Oksanen et al. 2020) in R (RStudio version 3.6.0). Additionally, species richness (number of species) was calculated. Spearman's correlation was calculated for each diversity index and for species richness. In all statistical hypothesis testing, Bonferroni corrections were made if appropriate (Bonferroni 1936).

Results

A total of 19 387 individuals of monkey beetles were collected across 30 morpho-species. Non-metric multi-dimensional scaling and clustering produced two sets with 20% similarity (Set A and Set B) of commonly co-occurring monkey beetles (Figure 2). Set A included *Lepithrix ornatella* and *Heterochelus rufimanus*. The abundance of the species in Set A decreased with urban intensity and increased with site area. Set B incorporated eight species of monkey beetles. The abundance of individuals of each species in Set B increased with soil-sealing and decreased with site size, however when the subsets of Set B were assessed (40% similarity), only Subset 1 incorporating *Heterochelus* cf. *sexlineatus* and *Heterochelus hybridus* showed any relationship with soil-sealing. The underlying ecosystem, (soil and historical vegetation) was the main driver for the clustering of Subsets 2 and 3 (Table 1; Figure 3).

Flowers and beetles

Monkey beetle species composition was influenced by flower species assemblage at the local habitat scale for most species. The null hypothesis that beetles were randomly distributed across flower communities was rejected for all species except for *Lepithrix ornatella, Heterochelus gonager* and *Heterochelus rufimanus*. (Table 2). These species clustered in the NMDS results in Set A and were found in peri-urban areas and larger green areas, and indicate that the monkey beetle species *L. ornatella, H. gonager* and *H. rufimanus* have a generalist preference for flowers but require a greater percentage of green cover. For all other species, the flower species assemblage attracted specific monkey beetles to the site.

In the cluster analysis, the flower communities formed four co-occurring sets (10% similarity) and a further four subsets (20% similarity). Their clustering is attributable both to growth form and to location (Figure 4). For flowers, Set A consisted of ruderal species including
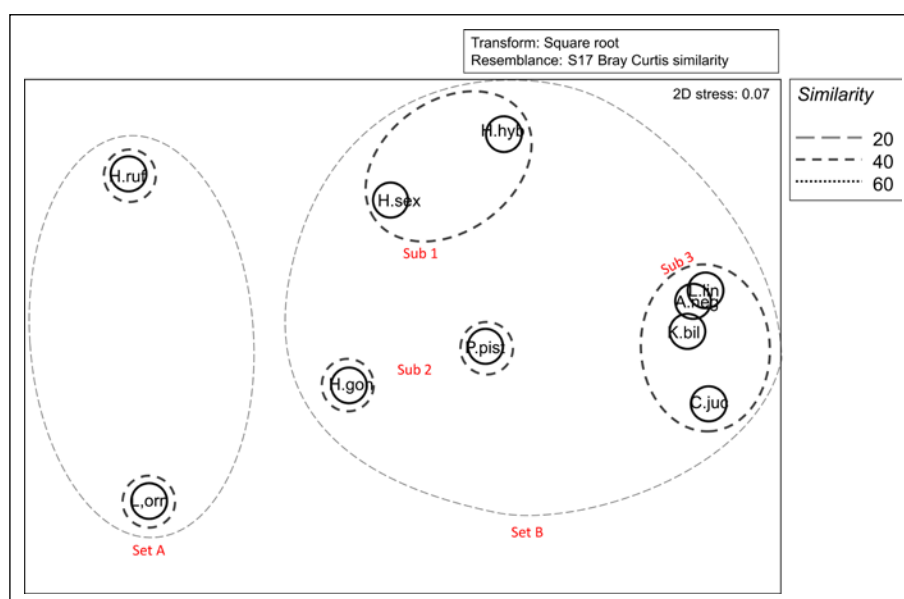
Figure 2. Non-metric multidimensional scaling with clustering overlaid showing the sets and subsets of monkey beetle communities in Cape Town. Set A (20% similarity): *Lepithrix ornatella* and *Heterochelus rufimanus*. Set B incorporated three subsets that were 40% similar, including: Subset 1: *Heterochelus* cf. *sexlineatus* and *Heterochelus hybridus*; Subset 2: *Heterochelus gonager* and *Peritrichia pistinaria*; Subset 3: *Khoina bilateralis, Chasme jucunda, Anisochelus neglectus* and *Lepithrix ornatella*.

Table 1. Summary of the tests for relationships between environmental variables and the species communities identified using NMDS and cluster analysis. The cluster analysis was 10% and 20% similarity between communities for sets, and 20% and 40% similarity for subsets of flowers and monkey beetles respectively. The p-values were determined using Kruskal-Wallis-tests against ranks of the abundance counts in each set and subset against four environmental factors. Soil-sealing is aggregated by the groups ex-urban (Ex), peri-urban (P), suburban (S) and urban (U). Site size is aggregated to small (S < 0.5 ha), medium (M = 0.5–40 ha) and large (L > 40 ha) and income is aggregated to low (Lo), medium (Me) and high (Hi). Historical vegetation type is assessed for Cape Flats Sand Fynbos (CFSF), Peninsula Granite Fynbos (PGF) and Swartland Shale Renosterveld (SSR). Bonferroni correction has been applied to the first level of significance (*=Bonferroni corrected significance threshold, ** = p<0.01, *** p <0.001)

Hopliini (monkey beetles)

	Soil Sealing					Site Size				Historical vegetation				Income			
	Ex	P	S	U	p-value	S	M	L	p-value	CFSF	PGF	SSR	p-value	Lo	Me	Hi	p-value
Set A	88.2	77.9	68.8	52.4	<0.001 ***	61.9	79.7	84.3	0.0030 **	58.0	86.7	67.6	<0.001 ***	57.7	61.5	83.8	<0.001 ***
Set B	52.3	58.2	85.8	87.9	<0.001 ***	85.7	58.4	53.5	<0.001 ***	83.7	36.4	36.5	<0.001 ***	96.9	78.0	54.8	<0.001 ***
Sub 1	49.1	54.0	90.3	90.6	<0.001 ***	90.8	51.4	49.5	<0.001 ***	83.0	32.8	42.5	<0.001 ***	96.5	79.0	54.0	<0.001 ***
Sub 2	72.3	72.2	70.8	70.8	0.990	70.3	73.1	72.5	0.9200	74.0	61.9	41.1	<0.001 ***	82.2	75.9	63.7	0.0390
Sub 3	69.0	67.0	76.0	73.0	0.600	73.1	65.5	74.3	0.4000	76.0	49.6	47.9	<0.001 ***	96.0	70.2	59.2	<0.001 ***

* Bonferroni adjusted significance threshold p-value = 0.01; ** p<0.005; *** p<0.001

Flowers

	Soil Sealing					Site Size				Historical vegetation				Income			
	Ex	P	S	U	p-value	S	M	L	p-value	CFSF	PGF	SSR	p-value	Lo	Me	Hi	p-value
Set A	56.0	62.3	78.8	95.1	<0.001 ***	86.7	62.2	56.5	<0.001 ***	72.5	42.4	77.4	0.001 **	81.1	78.0	67.8	0.6146
Set B	88.0	65.0	66.8	74.2	0.022	72.4	66.8	83.9	0.1114	68.8	70.2	63.8	0.723	72.5	75.8	73.1	0.2234
Set C	74.4	76.9	70.5	72.8	0.864	74.9	68.6	75.8	0.5615	72.3	52.7	69.1	0.019	76.3	84.3	67.6	0.9147
Set D	74.2	79.8	70.1	70.6	0.375	72.1	72.5	77.8	0.5619	71.0	60.3	66.2	0.149	69.7	77.6	73.8	0.0455
Sub 1	65.4	81.3	74.5	73.1	0.072	74.3	74.9	70.0	0.6233	65.0	69.4	75.1	0.138	67.3	70.6	77.8	0.0836
Sub 2	54.0	60.7	82.6	94.6	<0.001 ***	88.5	58.4	56.9	<0.001 ***	73.5	39.9	76.7	<0.001 ***	80.1	80.9	67.1	0.1581
Sub 3	88.3	68.4	68.0	69.6	0.010	71.1	66.6	86.9	0.0130	68.1	70.2	65.8	0.857	73.2	71.6	74.4	0.9045
Sub 4	73.0	74.7	70.3	76.2	0.842	75.9	70.8	71.3	0.6146	70.9	53.5	72.5	0.016	80.0	82.6	66.5	0.0114

* Bonferroni adjusted significance threshold = 0.00625; ** p<0.005; ***p<0.001

exotic and invasive weeds and the most common indigenous annuals. Set B was a combination of annuals and indigenous perennials. Apart from *Conicosia pugioniformis*, which is a disturbance tolerant species that resprouts from its taproot, Set C contained indigenous

annuals. Set D contained indigenous geophytes. Monkey beetle collections made from flowers provided insights into which of the flower species within subcommunities were most preferred by each of the monkey beetles species (Table 3).
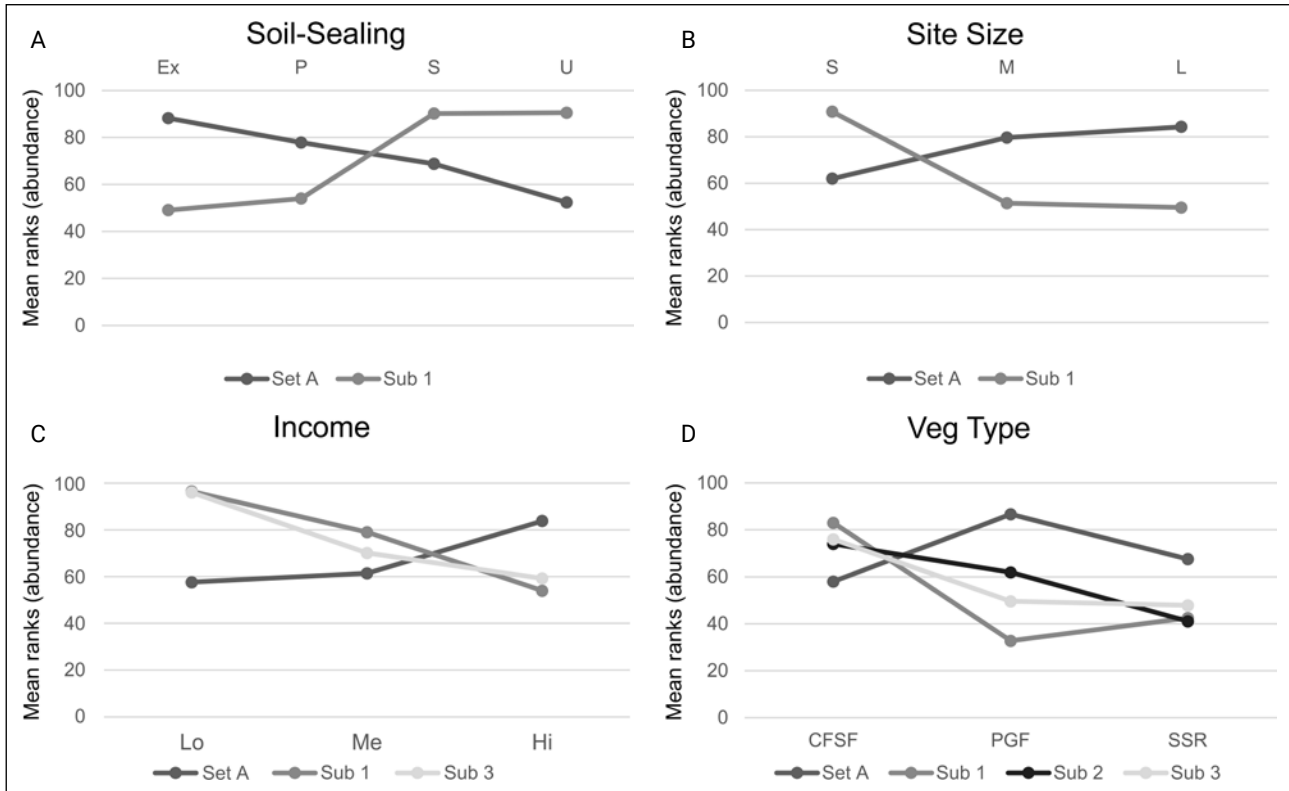

Figure 3. Plots of the means of ranked abundance of co-occurring monkey beetle species grouped by environmental gradients for which statistically significant relationships were observed. The plots are made to infer the direction of the relationships established in Table 1. Set A (20% similarity) contained *Lepithrix ornatella* and *Heterochelus rufimanus*. Set B incorporated three subsets that were at least 40% similar, including Subset 1: *Heterochelus* cf. *sexlineatus* and *Heterochelus hybridus*; Subset 2: *Heterochelus gonager* and *Peritrichia pistinaria*; Subset 3: *Khoina bilateralis*, *Chasme jucunda*, *Anisochelus neglectus* and *Lepithrix ornatella*. For the environmental factors, soil-sealing is aggregated by the groups: ex-urban (Ex), peri-urban (P), suburban (S) and urban (U). Site size is aggregated to small (S < 0.5 ha), medium (M = 0.5–40 ha) and large (L > 40 ha). Income is aggregated to low (Lo), medium (Me) and high (Hi) using the equal interval method from the 2011 national census data; and historical vegetation type is assessed for Cape Flats Sand Fynbos (CFSF), Peninsula Granite Fynbos (PGF) and Swartland Shale Renosterveld (SSR).

Table 2. Results of chi-squared tests on the contingency of Hopliini presence against flower presence. The null hypothesis was that each of 17 species of monkey beetle was distributed at random across 19 species of flowers. To counteract multiple hypothesis testing concerns, the Bonferroni correction was applied, so that the p-value for each individual test needs to be 0.05/17=0.0029 to achieve overall significance at the 5% level

	Chi-square	p-value		Chi-square	p-value
Lepithrix ornatella	21.02	0.0034	*Lepithrix lineata* (dark morph)	113.66	<0.0001
Heterochelus cf. *sexlineatus*	224.84	<0.0001	*Heterochelus gonager* (dark morph)	88.03	<0.0001
Heterochelus hybridus	42.12	<0.0001	*Heterochelus rufimanus*	24.74	0.0062
Khoina bilateralis	57.11	<0.0001	*Pachycnema crassipes*	90.38	<0.0001
Heterochelus gonager	22.70	0.0139	*Dicranocnemus* sp.	85.67	<0.0001
Anisochelus neglectus	52.94	<0.0001	*Heterochelus* sp. 1	72.09	<0.0001
Lepithrix lineata	64.52	<0.0001	*Heterochelus* sp. 2	79.29	<0.0001
Peritrichia pistinaria	49.98	<0.0001	*Chasme jucunda*	82.61	<0.0001
Dolichiomicroscelis gracilis	107.62	<0.0001			

Table 3. Number of monkey beetle morphospecies collected off each species of flower in Cape Town

Flower species	Flower guild	No. of monkey beetle species
Arctotheca calendula	Indigenous, annual	5
Cotula turbinate	Indigenous, annual	2
Dimorphotheca pluvialis	Indigenous, annual	3
Senacio sp.	Indigenous, annual	4
Ursinia nana	Indigenous, annual	3
Pauridia capensis	Indigenous, geophyte	1
Moraea miniate	Indigenous, geophyte	3
Heliophila sp.	Indigenous, annual	2
Echium sp.	Invasive, annual	1
Conicosia pugioniformis	Indigenous, perennial	4
Carpobrotus edulis	Indigenous, perennial	2
Pelargonium sp.	Indigenous, perennial	1

There was no relationship between overall floral diversity and beetle diversity ($p > 0.05$). Monkey beetle and flower species richness (number of species), however, showed a positive correlation ($rho = 0.31$, $p < 0.001$).

Discussion

This study revealed patterns in pollinator assemblage in response to urban landscape environmental gradients. It also identified species of flowers favoured by monkey beetles. Monkey beetle guilds, environmental gradients and flower preference are discussed below.

Divergent responses according to guilds

In response to urban intensity, the findings of this study were consistent with those done in other parts of the world for Hymenoptera. Some species exploit urban conditions, some species avoid them, and others depended on connected flower communities to move through the urban landscape (Wenzel et al. 2020). The divergence in bees is associated with differences in nesting requirements, body size and life histories (e.g., ground-nesting bees decline with an increase in urban intensity, and cavity nesters increase) (Brom et al. 2022; Cane et al. 2006; Merckx et al. 2018; Shwartz et al. 2014).

Not much is known about the life histories of monkey beetles, but some understanding of their behaviour and feeding differences is known (Colville et al. 2018; Karolyi et al. 2016; Mayer et al. 2006; Picker & Midgley 1996). Existing studies have demonstrated a shift in feeding guilds along disturbance gradients towards the embedding guild, which favours ruderal species (Colville et al. 2002). Monkey beetles utilise flowers as a breeding platform during the austral spring floral flush (Goldblatt & Manning 2011). The mechanism for pollination is the presence of hair-like setae on the backs and bodies of the beetles, which collect and deposit pollen loads during their movement across and between flowers (Bernhardt 2000; Mayer et al. 2006; Mayer & Pufal 2007). Three feeding and breeding guilds have been identified according to feeding and behaviour (Colville et al., 2002; Karolyi et al. 2016; Picker & Midgley 1996). Monkey beetle behaviour is classified either as embedding or non-embedding, where females in the embedding guild bury their heads into the centre of the flower while males compete over them to mate. Thus the males are predominantly responsible for the pollination because they fly between flowers looking for females (Bernhardt 2000). Embedding guilds eat pollen and nectar and are attracted to flowers with long-wave colours (red, orange and yellow). The non-embedding guilds are split into two groups, by colour attraction. One non-embedding guild is attracted to short-wave (blue, pink and violet) coloured flowers, and the other is attracted to long-wave colours (Colville et al. 2018; Picker & Midgley 1996). *Lepithrix*, *Anisonyx* and *Peritrichia* are recorded as feeding on pollen and do not embed themselves, whereas species in the genus *Heterochelus* tend to embed themselves (Picker & Midgley 1996). The non-embedding group are characterised by being hairy and mobile, moving around between flowers more frequently than their embedding counterparts. For this reason, they are considered to be more effective pollinators (Goldblatt & Manning 2011).
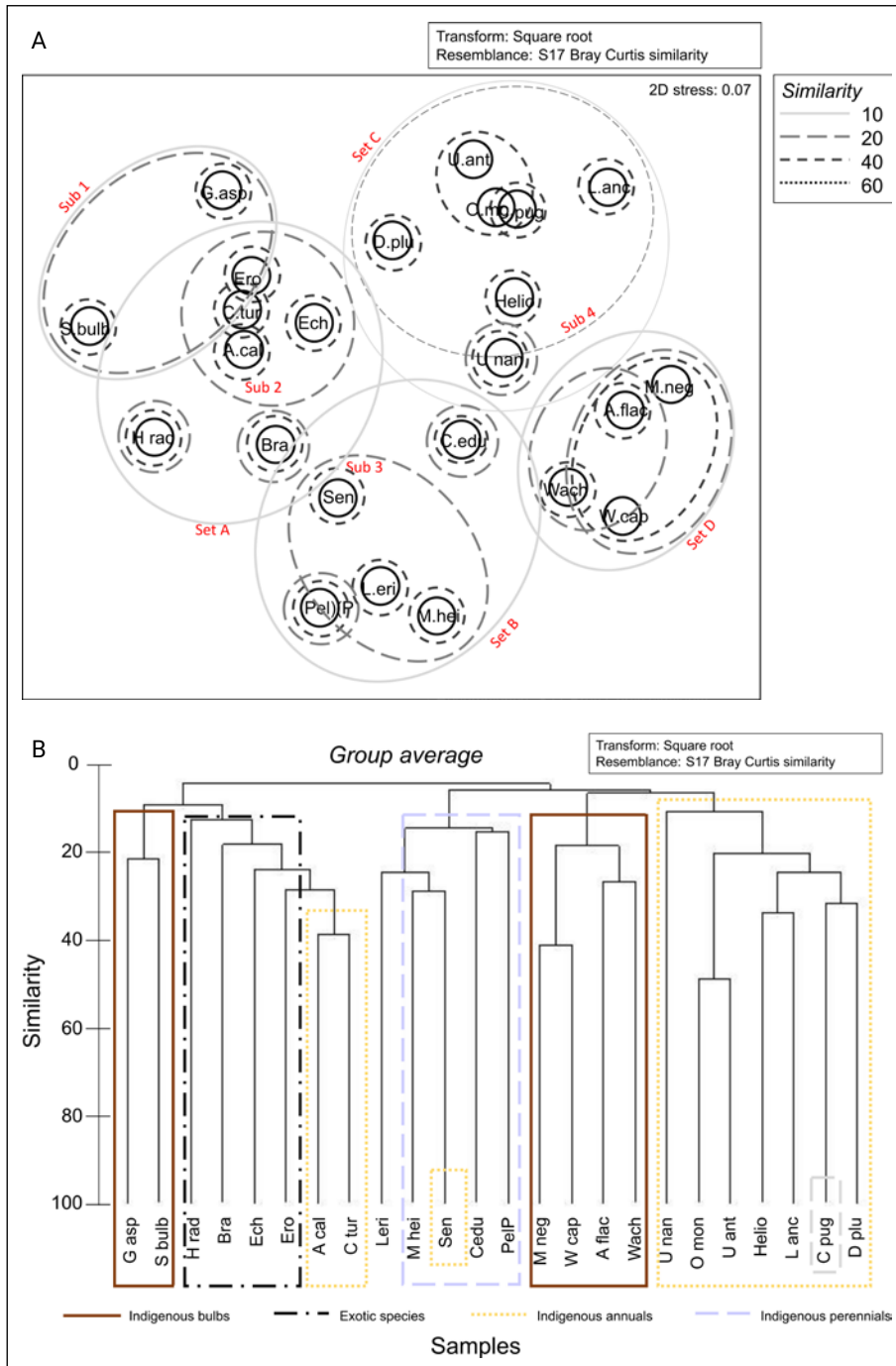
Figure 4. A, Clustering of flower abundance counts collected in Cape Town during spring season in 2018 and 2019; the plot represents the non-metric multi-dimensional scaling of the most commonly occurring species in the sample set including Set A: *Erodium* spp. *Cotula turbinata*, *Echium* spp. *Arctotheca calendula*, yellow Brassicaceae, *Hypochaeris radicata*; Set B: *Pelargonium* spp. (pink)., *Lobelia erinus*, *Senecio* spp., *Muraltia heisteria* and *Carpobrotus edulis*; Set C: *Ursinia anthemoides*, *Dimorphotheca pluvialis*, *Osteospermum monstrosum*, *Conicosia pugioniformis*, *Lapeirousia anceps*, *Heliophila* spp., *Ursinia nana*; and Set D: *Wachendorfia multiflora*, *Wahlenbergia capensis*, *Moraea neglecta*, *Albuca flaccida*; B, Group average clustering of flower species arranged according to growth form.

Response to urban environmental gradients

Comparisons between natural and agricultural landscapes revealed that monkey beetle species composition changes along gradients of disturbance where a 'shift away from perennial and bulb pollinator guilds towards those favouring weedy annuals' has been observed (Colville et al. 2002). The findings of this study were consistent with those earlier studies in that there was a shift towards species favouring ruderal annuals as soil-sealing (disturbance) increased. Specifically, the embedding *Heterochelus* cf. *sexlineatus* and

Heterochelus hybridis were associated with ephemeral plants, including ruderal asters and indigenous annuals, and were abundant in urban landscapes in suburbs and close to commercial centres. *Chasme jucunda*, *Khoina bilateralis*, *Anisochelus neglectus*, *Lepithrix liniata* and *Peritrichia pistinaria* are species of the 'non-embedding' guild (Picker & Midgley 1996). They are typically sensitive to disturbance, associate with somewhat established floral communities containing perennials and geophytes (Colville et al. 2002), and, in this study, were found in large (> 30 ha), relatively undisturbed islands in the city. These findings are consistent with earlier studies along disturbance gradients in agricultural landscapes (Colville et al. 2002).

The phenomenon of an increase in biodiversity with wealth is known as the 'luxury effect' (Wu et al. 2014) and has been demonstrated across several studies and taxonomic groups (Aronson et al. 2016; Lubbe et al. 2010; Ossola & Hopton 2018; Venter et al. 2020). This can be attributed to the fact that the number and size of community parks decreases as income decreases (Venter et al. 2020), but poverty is also associated with an increase in population density and urban cover, thereby representing a particularly dense form of urbanism (Turok 2011; Wilkinson 2000), particularly in areas of unplanned expansion and informality (Gómez-Baggethun et al. 2013). It is therefore unsurprising that the guilds of monkey beetles that respond negatively to urban densification, also respond negatively to a decrease in income, and vice-versa, and the correlation with income is not necessarily causative, but rather can be seen as a driver of other intervening processes (e.g., loss of green infrastructure). A study conducted on weedy species in okra cultivation in West Africa found, for example, that morphological plant traits were most affected by agricultural practices that were influenced by farmers' socio-economic background and market orientation (i.e., for sale vs for personal consumption), however more critical changes in functional guilds were observed due to a decrease in animal grazing along the rural to urban gradient: weed species reliant on animal dispersal were more present in rural and peri-urban study sites (Stenchly et al. 2017). In this study, parks in poorer communities were either benignly neglected or over-used, while those in wealthier neighbourhoods appeared to have larger, more frequently maintained lawns, unless there was an active strategic spring mowing suspension during the sampling period. Furthermore, the density of poorer neighbourhoods means that there is less available private green infrastructure in the form of gardens. Additional research on the effects of socio-economic status on factors such as actual maintenance frequency, foot traffic volumes and grass length during sampling would likely provide a more detailed and meaningful interpretation of the habitat dynamics driving plant and pollinator assemblages across the socio-economic gradient.

The role of flower preference

Monkey beetles are generalist pollinators and most species will visit at least two species of flowers (Mayer et al. 2006; Steiner 1998). Records of flower visitations by monkey beetles to date have peaked at a maximum of five monkey beetle species per flower species (Mayer et al. 2006). Determining the relative preference and attractiveness of different flowers to monkey beetles was outside of the scope and objectives of this study, however the results of collections from flowers and field observations provide preliminary indications of the ways in which flowers are being used by monkey beetles in urban habitats within Cape Town. Further research

investigating visitation rates is needed to confirm and clarify the relative importance of these species, however, when Table 3 and Supplementary Tables 1 and 2 are read together, co-occurrence data and the number of monkey beetle species collected off flower species point to the relative preferences for certain flowers. Of those observed, the most popular species were *Heliophila africana* and *Heliophila coronopifolia*, which were preferred by non-embedding monkey beetles who favour short-wave colours (visited by two species); *Conicosia pugioniformis* was preferred by the non-embedding guilds who favour long-wave colours (visited by four species); *Dimorphotheca pluvialis*, and *Ursinia nana* were visited by the embedding guild (three species); and *Arctotheca calendula* and *Senecio* sp., which are both mass-flowering spring annuals, and which can cover entire parks, were favoured by the embedding guild (three and four species respectively), but were also visited by the more sensitive non-embedding guild that were limited to peri-urban areas. These rates of 'most popular' are similar to other studies conducted in natural landscape settings (Mayer et al. 2006), indicating the viability of supporting monkey beetles through the introduction (or preservation) of targeted species of preferred flowers.

The occurrence of short-wave, non-embedding guilds was less common and associated with fewer flower species, which were relatively isolated across the city. Sites where floral communities included the most popularly visited species from all guilds, including *D. pluvialis, C. pugioniformis* and species of *Heliophila*, supported greater monkey beetle richness as reflected in the correlation between monkey beetle and flower species richness. It is therefore not only floral richness, but the presence of species preferred by the various guilds that drives monkey beetle richness.

Worth noting is that there was a relationship between richness but not abundance (diversity indices include calculations based on abundance), and that beetle species have preferred flowers; they are found where their preferred flowers occur. Some of the natural islands supported groups of flowers that were preferred by different species of beetles, but the abundance counts were hugely variable so we could not reject the null hypothesis that monkey beetle abundance was driven by flower abundance. One explanation could be based on temperatures. Weather in spring time is highly variable. Possibly, abundance was more directly affected by temperature on a given day.

Several studies conducted on urban pollinators have previously discussed the role of supplementary planting in urban landscapes and investigated the relative attractiveness of different species of plants in order to compile lists of recommended 'pollinator friendly' plants, or to assess the availability of foraging resources (Baldock et al. 2015; Garbuzov & Ratnieks 2014, 2015; Lowenstein et al. 2019; Martins et al. 2017; Michołap et al. 2018).

Garbuzov et al. (2017) tested if plants being advertised as 'pollinator friendly' by garden centres were accurately reflecting pollinator preferences and compared relative attractiveness of garden plants to generate a list of preferred species for their city (Garbuzov & Ratnieks 2014, 2015). Pauw and Louw (2012) considered the distribution of nectarivorous birds in Cape Town and suggested that the functional diversity of this bird guild could be restored across the city with strategic garden planting and the introduction of favoured plants. Introducing preferred species at regular intervals throughout the city can aid monkey beetle mobility and provide stepping stones between larger fragments. This could potentially be achieved by strategically identifying suitable pathways and implementing targeted landscaping along those routes (Cranmer et al. 2012; Simao et al. 2018). In addition to benefitting monkey beetles, other pollinators would be able to make use of the flower resources for foraging and as stepping stones (Brom et al. 2022). Collections from *Conicosia pugioniformis* consistently hosted the greatest number of monkey beetle species at any one site and was often found growing together with *Carpobrotus edulis*, a popular road verge plant for its hardiness, ease of propagation and brightly coloured flowers. *Conicosia pugioniformis* can easily be introduced as a co-plant to *C. edulis* along road verges and city parks. Further research is needed to determine the extent to which the introduction of favoured short-wave plants (e.g., *Heliophila* spp.), could restore the connectivity of landscapes for the non-embedding guild favouring blue and pink coloured flowers.

Conclusion

In this study, the distribution of monkey beetles was sampled in a metropolitan city in the Cape Floristic Region of southern Africa. It aimed to determine how monkey beetles were responding to urban environmental gradients and local habitat conditions. It found an established community of monkey beetles was responding in different ways to urban gradients. Embedding species were more tolerant of soil-sealing,

congregating on ephemeral species of Asteraceae and geophytes. Non-embedding species were associated with preferred flower species and reduced abundance was recorded as soil-sealing increased in the surrounding landscape. Non-embedding species demonstrated a need for a greater percentage of green space in the surrounding landscapes, but this sensitivity can be mitigated with the introduction of preferred species of flowers. *Conicosia pugioniformis* in particular, hosted the greatest richness of monkey beetles at within-site scale, but the sites containing combinations of *Heliophila africana*, *Dimorphotheca pluvialis*, *Ursinia nana* and *Senecio littoreus*, together as dominant species, provided the scaffolding for supporting healthy populations of monkey beetles. The findings suggest that widespread introduction of a community of beetle-preferred flowers, including *C. pugioniformis* as a cornerstone species, to provide stepping-stones through the urban matrix, will aid monkey beetle mobility.

This study found that there is an intact community of monkey beetles in the city, and that there is a reliance on particular plant communities for breeding and foraging. This finding is promising for the conservation of rare bulbs within the urban landscape, which rely on a healthy population of monkey beetles for pollination services (Barraclough & Slotow 2010; Goldblatt et al. 2013; Goldblatt & Manning 2006; Johnson & Steiner 2003; Steiner 1998).

Acknowledgements

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Supplementary Material

Supplementary Table 1. Sites at which flower species were present and the percentage of those where each species of monkey beetle co-occurred. Percentages in the column are the percentage of flower presence sites where the monkey beetle species co-occurs. The dark grey highlights are the three largest percentages in each column; the light grey highlights are the remaining two values in the top five of each column

	No. of sites where flower occurred	*Lepithrix ornatella*	*Heterochelus sexlineatus*	*Heterochelus hybridus*	*Khoina bilateralis*	*Heterochelus gonager*	*Anisochelus neglectus*	*Lepithrix lineata*	*Peritrichia pistinaria*	*Dolichomicroscelis gracilis*	*Lepithrix lineata* (dark morph)	*Heterochelus gonager* (dark morph)	*Heterochelus rufimanus*	*Pachycnema crassipes*	*Dicranocnemus*	*Heterochelus* sp. 3	*Heterochelus* sp. 2	*Chasme jucunda*	In Top 3	In Top 5	
Arctotheca calendula	71	30%	82%	38%	8%	30%	18%	14%	32%	6%	4%	8%	23%	11%	8%	11%	11%	10%	0	1	*
Carpobrotus edulis	16	31%	75%	38%	31%	31%	31%	25%	50%	19%	0%	13%	25%	19%	13%	31%	0%	38%	2	4	*
Conicosia pugioniformis	14	21%	93%	64%	50%	36%	71%	57%	93%	36%	29%	7%	0%	0%	29%	7%	7%	43%	11	11	*
Cotula turbinata	64	33%	69%	41%	14%	25%	16%	13%	30%	3%	6%	9%	30%	8%	9%	14%	9%	8%	0	0	*
Dimorphotheca pluvialis	19	32%	68%	63%	32%	32%	47%	32%	63%	16%	21%	5%	32%	5%	21%	11%	21%	37%	3	9	*
Echium sp.	47	34%	68%	40%	19%	32%	21%	19%	47%	6%	2%	9%	28%	9%	9%	13%	13%	13%	0	0	
Erodium sp.	51	22%	71%	31%	8%	16%	16%	12%	24%	4%	6%	8%	25%	10%	8%	10%	20%	8%	0	1	
Geissorhiza aspera	12	58%	33%	33%	8%	33%	0%	8%	8%	0%	0%	17%	25%	0%	17%	17%	25%	8%	2	4	
Heliophila sp.	9	11%	78%	78%	44%	56%	33%	33%	56%	33%	22%	0%	11%	0%	33%	22%	0%	56%	9	11	*
Lobelia erinus	9	44%	33%	11%	33%	11%	0%	11%	22%	0%	0%	22%	33%	0%	11%	11%	33%	11%	2	4	
Osteospermum monstrosum	10	30%	70%	60%	50%	60%	50%	40%	80%	30%	20%	0%	20%	10%	30%	10%	10%	50%	8	11	
Oxalis pes-caprae	21	19%	67%	52%	10%	24%	19%	5%	52%	10%	5%	0%	38%	14%	5%	5%	14%	14%	0	3	
Pelargonium sp. (pink)	14	50%	50%	29%	29%	29%	21%	14%	29%	14%	7%	14%	50%	0%	7%	14%	7%	14%	2	2	*
Romulea rosea	17	29%	82%	35%	6%	29%	6%	0%	41%	6%	0%	18%	24%	6%	18%	12%	0%	0%	0	3	
Senecio sp. (yellow)	25	36%	60%	56%	28%	24%	20%	12%	48%	4%	8%	12%	20%	12%	8%	8%	8%	16%	0	1	*
Trachyandra ciliata	10	10%	90%	80%	10%	10%	40%	30%	50%	0%	20%	0%	20%	0%	10%	10%	10%	0%	2	7	
Ursinia nana	14	21%	86%	50%	36%	36%	21%	21%	29%	14%	14%	7%	21%	7%	14%	21%	7%	29%	2	4	*
Vicia sp.	13	31%	38%	15%	15%	15%	8%	8%	23%	8%	0%	23%	38%	8%	0%	8%	0%	0%	2	2	
Brassicaceae spp. (yellow)	26	46%	62%	38%	23%	35%	15%	19%	42%	0%	0%	15%	35%	15%	8%	23%	4%	4%	2	5	*
Hypochaeris radicata	13	15%	69%	23%	8%	31%	15%	0%	23%	0%	0%	0%	15%	0%	0%	0%	8%	0%	0	0	
Lysimachia monelli	11	55%	9%	0%	18%	0%	0%	0%	36%	0%	0%	18%	64%	18%	0%	0%	27%	0%	5	5	

Supplementary Table 2. List of monkey beetle species collected from flowers across the City of Cape Town in 2018 and 2019

Hopliini	Flower	Flower colours
Non-embedding guild (short-wave colours)		
Dolichiomicroscelis gracilis	*Heliophila africana*	blue/violet
Peritrichia pistinaria	*Pelargonium, Heliophila africana, Echium* sp.	pink, blue/violet
Non-embedding guild (long-wave colours)		
Anisochelus neglectus	*Conicosia pugioniformis, Carpobrotus edulis*	yellow
Bizanus sp.	*Moraea miniata*	salmon-pink
Chasme jucunda	*Conicosia pugioniformis, Ursinia* sp.	yellow
Heterochelus rufimanus	*Bolusafra bituminosa, Arctotheca calendula*	yellow
Dicranocnemus	*Ursinia* sp.	yellow
Khoina bilateralis	*Conicosia pugioniformis*	yellow
Lepithrix lineata	*Arctotheca calendula, Conicosia pugioniformis, Senecio* sp.	yellow
Lepithrix ornatella	*Senecio* sp.	yellow
Pachycnema crassipes	*Carpobrotus edulis*	yellow
Platychelus lupinus	*Moraea miniata*	salmon-pink
Embedding guild (long-wave colours)		
Heterochelus sexlineatus sp.	*Arctotheca calendula, Cotula turbinata, Dimorphotheca pluvialis*	yellow, white
Heterochelus sp. 2	n/a	
Heterochelus gonager	*Dimorphotheca pluvialis, Senecio* sp., *Arctotheca calendula, Echium* sp.	white, yellow, blue/violet
Heterochelus hybridus	*Cotula turbinata, Arctotheca calendula, Ursinia nana, Dimorphotheca pluvialis, Pauridia capensis* (yellow), *Senacio* sp.	white, yellow
Ishnochelus sp.	*Hypochaeris radicata, Moraea miniata*	yellow, salmon-pink/yellow