The effects of urbanisation on bee and wasp communities in Cape Town, South Africa

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ABSTRACT

Bees and wasps provide essential regulatory ecosystem services by pollinating urban plants. However, there are massive global declines in many insect groups, and little is known about the impacts of urbanisation on pollinators in rapidly developing areas of Africa. South Africa is one of the most urbanised and biodiverse countries in Africa, and the Cape Floristic Region, one of the country's most important centres of biodiversity, is the only area in the world where bee and plant diversity hotspots coincide. Within the centre of this hotspot (Durbanville, Cape Town), I investigated the effects of urbanisation and availability of floral resources on bee and wasp (pollinator) diversity, community composition, and nesting guild distribution across an urban-rural/natural gradient. Using pan traps, specimens were collected from 18 sites in the austral spring of 2019 and 2020. A total of 433 bee and 45 wasp specimens, comprising of 45 bee and 27 wasp morphospecies respectively, were collected. Bees from the family Halictidae (particularly *Seladonia* and *Patellapis* species) were the most abundant. Except for *Apis mellifera*, all other bee species were solitary, and most (86.7%) collected pollen from flowers. A total of four different nesting guilds were identified, with the most common being ground-nesters (68.9%). Floral resources, rather than the degree of urbanisation, had a strong positive effect on pollinator diversity and community composition. The same trend was observed for nesting guilds at both the community and individual guild level. This study supports the development of several cost-effective and achievable conservation initiatives, such as adopting no-mow periods during austral spring and developing small-scale bee-friendly floral-rich patches, which can be undertaken by existing municipal structures and private landowners alike. Urban spaces in Cape Town have the potential to support important pollinator diversity, but more research is needed. Suggested future studies include investigating the ways pollinator diversity and community composition is influenced by 1) individual floral species and characteristics, 2) the size, shape, and location of habitat/floral patches, and 3) the effects of urban warming.

Key words: bees, wasps, urbanisation, flowering plants, South Africa

1. INTRODUCTION

Both wild and domesticated bees and wasps provide essential regulatory ecosystem services through plant pollination (WWF, 2018). Globally, 87.5% of wild flowering plant species depend on pollination by animals (Ollerton et al., 2011). Of these, 80% require pollination by insects for fruit and seed set (Potts et al., 2010). Similarly, in agricultural systems an estimated 70-75% of crops depend on insect pollination (Klein et al., 2007; Potts et al., 2010). Although determining the economic value of pollination services is challenging, Gallai et al. (2008) estimated that the global economic insect pollination value of the 100 most important crops used for human consumption is €153 billion per year, which is 9.5% of the total world agricultural production value. Whilst this percentage is small, their analysis showed that it can be as high as 94% depending on the crop produced and the region within which it is grown. A more recent report by the WWF (2018), stated that food producers benefit from a US$235-577 billion increase in the value of global crop production per year due to insect pollination services. In addition to this economic value, pollinators can increase the nutritional value of important food crops. For example, more than 90% of human-consumed vitamin C comes from animal pollinator dependent plants, and for many crops, insect pollination can increase crop yield by between 18-71% (Eilers et al., 2011; Bartomeus et al., 2014).

The species primarily responsible for pollination services within agricultural systems is the honeybee *Apis mellifera*, which alone has been shown to increase yield in 96% of animal-pollinated crops (Potts et al., 2010). However, the proportion of crops that are dependent on insect pollination is growing at a faster rate (>300% increase) than the supply of *A. mellifera* hives (ca. 45% increase) (Aizen & Harder, 2009). This leaves a deficit in managed pollination services, which makes the dependence of agriculture on a single pollinator species a serious threat to global food security. Additionally, there has been a global tendency towards agricultural expansion of only a few crop species, i.e. monocropping rather than agricultural diversification (Aizen et al., 2019). Whilst the high crop density in such areas can provide a vast amount of food for both *Apis* and non-*Apis* pollinators, this is often short-lived and the environmental degradation associated with monocropping can result in reduced insect-pollinator diversity and lower pollination rates (Rader et al., 2016; Aizen et al., 2019). As such, there is a global need for more diverse, pollinator-friendly practices to meet the growing need for pollination services (Aizen et al., 2019).

There is evidence that native wild bee populations can improve pollination efficiency and, under certain agricultural management practices (primarily organic farming), even meet the full pollination needs of crops with high pollination requirements (Kremen et al., 2002; Garibaldi et al. 2014a, b). However, relatively little is known about wild pollinator populations and communities (Potts et al., 2010). Moreover, several important wild pollinators are in decline, including many bumblebee species (*Bombus* spp.) found in Europe and North America (Goulson et al., 2008; Vanbergen et al., 2013; Cardoso et al., 2020). There is some evidence to suggest that pollinator groups with restricted or specialist diet and habitat requirements are declining at a greater rate than groups with more general requirements (Potts et al., 2010). However, there is still a need to study wild pollinators in order to better understand how to protect them and the essential ecosystem services they provide (Vanbergen et al., 2013; Garibaldi et al., 2014b).

1.1 Causes of pollinator declines

Human-mediated land-use changes are the biggest threats to global biodiversity and have also been attributed to the global declines in insect pollinators (Kremen et al., 2002; Potts et al., 2010; Vanbergen et al., 2013; WWF, 2018; Cardoso et al., 2020; Wenzel et al., 2020). One of the most destructive and pervasive ways that humans modify natural landscapes is urbanisation, which is growing globally at a rapid rate. Fifty percent of the global population currently live in urban areas, and it is predicted that by 2050 this will increase to almost 70%, with most of this shift predicted to occur in developing regions (Trzyna, 2014; United Nations, 2018; Wenzel et al., 2020). Despite this, relatively little is known about the effect of urbanisation on insect pollinators, and research that has been done has produced conflicting results, with urbanisation effects ranging from positive to negative (Wenzel et al., 2020). Furthermore, most research has focused on the global north rather than developing countries. A recent review found a significant lack of research on urban pollinators in Africa despite the fact that the continent is rapidly urbanising (Wenzel et al., 2020). Out of 141 global studies, they found only one study from an African country (Guenat et al., 2019), which accounts for 1 of the 21 studies conducted in developing countries. As such, Africa has been identified as a priority research area in this regard.

1.2 What is urbanisation, and how does it affect pollinators?

The term urbanisation can have multiple meanings depending on the field of research. Definitions range from quantifying the growth and development of human settlements over time (OECD et al., 2020a), as used in the urban planning literature, to a measurement of urban intensification or densification (Wenzel et al., 2020), as used in the urban ecology literature. In the latter research field, urban development is often categorised in two ways: urban sprawl, which is dominated by low-density residential housing, and urban densification, which is dominated by high-density development and a high proportion of sealed surfaces (Wenzel et al., 2020). In this study, I will be using the urban ecology definition of urbanisation, which in its simplest form can be quantified by calculating the proportion of impervious surfaces, such as buildings, paved surfaces (e.g. roads and car parks), and vegetation within a given area (McDonnell & Hahs, 2008; Seress et al., 2014; Geslin et al., 2016a; Wilson & Jamieson, 2019; Wenzel et al., 2020). Today, the proportion of impervious surface and vegetation cover within a given radius can be relatively easily calculated using freely available satellite imagery, which allows for reproducible studies to be conducted irrespective of location and availability of local data (Seress et al., 2014).

The effects of urbanisation on pollinating bees and wasps (hereafter referred to as pollinators) vary greatly across the urban landscape. Compared to natural areas, urban areas tend to be characterised by reduced species diversity (Wenzel et al., 2020). However, patterns become more nuanced when looking at the composition of urban pollinator communities. A pollinator community can be defined not only by its species but also by its functional groups, i.e., species that can be grouped into guilds based on ecological traits such as nesting strategy, social structure, or feeding requirements. Evidence suggests that the urban landscape can act as a filter, promoting species with ecological traits that facilitate colonisation and survival whilst filtering out species with unfavourable traits (Aronson et al., 2016). Therefore, different guilds are likely to be affected in different ways. For example, 75% of all bee species nest in the ground (Wenzel et al., 2020), but urban landscapes are dominated by hard surfaces such as concrete and lawns which are impermeable to ground-nesting species. Conversely, cavity-nesting species could benefit from the large number of cracks and crevices provided by urban structures. For these reasons, several studies have found an increase in the proportion of cavity-nesters in more densely urbanised areas (Banaszak-Cibicka & Żmihorski, 2012; Hinners et al., 2012; Cardoso & Gonçalves, 2018). Other traits that are thought to be beneficial in urban areas are increased sociality and generalist foraging strategies as these can facilitate survival across heterogeneous urban landscapes (Banaszak-Cibicka & Żmihorski, 2012; Hinners et al., 2012; Cardoso & Gonçalves, 2018; Wenzel et al., 2020).

Urban pollinator communities are also influenced by the composition and configuration of suitable habitats (landscape drivers), habitat size and the availability of floral and nesting resources (local drivers), as well as temperature and pollution (abiotic drivers) (Wenzel et al., 2020). The observed diversity of pollinators is likely a product of multiple interacting drivers. For example, Stewart et al. (2018) found that both the size of and floral abundance within a habitat patch promote greater pollinator richness and abundance. Wojcik & McBride (2012) found that pollinator richness and abundance were similar in both wildland and urban habitats, but community composition was different and driven by completely different factors. In the wildlands, patch size and density of resources had the biggest effect on all pollinator species, whereas in urban areas, large and small-bodied species were affected differently. Like in the wildlands, large-bodied species were mostly affected by patch size and density of resources, while smaller-bodied species were more affected by the distance of the resource patch to the urban-wildland interface and riparian areas (Wojcik & McBride, 2012). The success of pollinators in urban areas is therefore likely to be determined by a mixture of their intrinsic ecological traits and the characteristics of the underlying urban matrix.

Given that urbanisation takes many shapes, it is perhaps unsurprising that research into the effects of urbanisation on pollinators has produced conflicting results, ranging from negative to positive. It has been suggested that these conflicting results arise from (i) variation between studies in the extent of urban densification and (ii) whether the chosen non-urban control habitat is natural or agricultural (Wenzel et al., 2020). Generally, the greater the extent of urban densification, the lower the pollinator diversity (e.g. Sing et al., 2016; Lagucki et al., 2017). Conversely, study areas dominated by urban sprawl tend to show higher pollinator diversity than more densely urbanised areas (e.g. Sing et al., 2016). Compared to natural areas, urban spaces tend to have lower pollinator diversities (e.g. McIntyre & Hostetler, 2001; Tonietto et al., 2011; Verboven et al., 2014). Relative to agricultural areas though, areas with urban sprawl tend to have higher pollinator diversity (e.g. Wilson & Jamieson, 2019). As such, some research suggests that urban landscapes could, in fact, serve as refugia for important pollinator diversity, especially when urban areas border agricultural land (Wenzel et al., 2020). The idiosyncrasies associated with each study, and the fact that each study has its own biases, methods, and baselines also likely play important roles.

1.3 Urban pollinators in South Africa

Africa is the most rapidly urbanising continent globally; currently, more than 50% of people live in urban areas, and since 1950 the urban population has increased by approximately 2000% (OECD et al., 2020b). By 2050 the African urban population is predicted to grow from 567 million people to 950 million people (OECD et al., 2020b). Within southern Africa, South Africa is home to some of the largest African cities and has the highest level of urbanisation (70% urbanised; OECD et al., 2020a, b, c). South Africa is also one of the most biodiverse countries in the world and is home to three of the 35 global biodiversity hotspots (Myers, 1988; Mittermeir et al., 2004; Skowno et al., 2019). South Africa has been identified as a globally significant centre of bee diversity with high degrees of endemism (Kuhlmann, 2009). Despite this, approximately 98% of the country has received minimal survey effort with respect to bee diversity (Melin & Colville, 2019). Generally, little is known about invertebrate taxonomy and biology in South Africa (Rebelo et al., 2011; Skowno et al., 2019; Scholtz et al., 2021). Some groups, such as butterflies and invasive insect species, are relatively well studied, whereas other groups, including bees, have been critically understudied (Melin & Colville, 2019; Skowno et al., 2019; van Wilgen et al., 2020). Nonetheless, the significant importance of and potential for pollination services from wild pollinators has been recognised at the national scale, and work is being done to assess the status of these pollinator groups and include them in future National Biodiversity Assessments (Melin et al., 2014; Geslin et al., 2016b; Skowno et al., 2019).

One of the most important centres of biodiversity in South Africa is the Cape Floristic Region (CFR), which is the only area in the world where bee and plant diversity hotspots coincide (Kuhlmann, 2009). Approximately 70% of the CFR's 9400 plant species and 44.5% of the CFR's 317 bee species are endemic (Kuhlmann, 2009; Manning & Goldblatt, 2012). The CFR holds 65% of the country's threatened taxa (all groups), the majority of which are found within the lowland areas where most urban and agricultural development has happened and is continuing to do so (Rouget et al., 2003; van Wilgen et al., 2016). Urban and agricultural development have been identified as major threats to the CFR's biodiversity (Rouget et al., 2003; Skowno et al., 2019; Ntshanga et al., 2021; Skowno et al., 2021).

The largest urban centre in the CFR is the City of Cape Town, whose population of 4.5 million people is projected to grow to about 5.1 million by 2030 (City of Cape Town Policy and Strategy Department, 2021). Cape Town is a diverse city comprising a complex mosaic of urban sprawl, densification, natural and semi-natural areas, and urban agriculture. Most people live in either formal (79.1%) or informal (19.3%) dwellings, with the most growth being seen in the informal sector in the lowland areas of the city (Rebelo et al., 2011; City of Cape Town Policy and Strategy Department, 2021). The most recent estimate available states that three-quarters of the Cape Town metropole is transformed, of which approximately 60% is used for agriculture (Rebelo et al., 2011). It is important to note that this estimate may be outdated and current values are likely much higher. Natural remnants cover approximately 36% of the city, though much of this is not well protected (Holmes & Pugnalin, 2016).

Some research on the effect of urbanisation on pollinators in Cape Town has been done, however, much of this has focused on non-bee or non-insect pollinating taxa such as beetles and birds, the importance of which have been recognised at both the global and local level (Geerts, 2016; Rader et al., 2016; Brom, 2021; du Plessis et al., 2021; Mnisi et al., 2021). Results from these studies were varied. Most indicated negative effects of urbanisation on their respective taxa, although results tended to vary between species. For example, several studies showed that reduced abundance of the oil-collecting bee, *Redeviva peringuey*, in transformed urban landscapes has in turn led to a decrease in the abundance and seed set of specialist plant species in Cape Town, such as non-clonal orchids (Coryciinae), which can only be pollinated by specific bee species (Pauw, 2007; Pauw & Hawkins, 2011). On the other hand, Brom (2021) showed that monkey beetle (Hopliini) guilds can respond differently, with some species being negatively and others positively influenced by urbanisation. Similarly, several studies on nectarivorous sunbird pollinators have shown that certain species, such as the long-billed Malachite sunbird, are less able to penetrate the urban matrix than shorter-billed species (Pauw & Louw, 2012; Geerts, 2016; Coetzee, Barnard & Pauw, 2018). For both monkey beetles and sunbirds, artificial and natural nectar sources, such as artificial nectar feeders, and stepping-stone gardens (planted with native, beneficial, pollinator-attractive plant species) have been shown to increase pollinator abundance within the urban matrix (Coetzee, Barnard & Pauw, 2018; du Plessis et al., 2021; Mnisi et al., 2021). Given the high species diversity, levels of endemism and intensity of threats to biodiversity loss, understanding the effects of urbanisation on other insect pollinators, like bees and wasps, in Cape Town is imperative.

The present study focused on the impacts of urbanisation and agriculture on pollinating bees and wasps in the Durbanville area of Cape Town. Durbanville is primarily dominated by formal dwellings with areas of both high- and low-density infrastructure and development. It directly borders farmland, and several protected natural areas and natural remnants exist within the area. I aimed to investigate the following questions:

1. Do urban, natural, and agricultural areas harbour different bee and wasp communities?

I hypothesised that due to differences in available floral and nesting resources and land management, urban, natural, and agricultural areas would harbour distinct bee and wasp communities.

2. Does bee and wasp diversity differ between urban, natural, and agricultural areas?

I hypothesised that there would be a greater diversity in natural areas compared to urban areas, and a reduced diversity in agricultural areas compared to urban areas.

3. How do different nesting guilds (ground vs cavity nesters) respond to urbanisation?

I hypothesised that with increasing urban intensification, and the associated increase in impermeable surfaces, there would be reduced diversity and abundance of ground-nesting species due to reductions in suitable nesting habitat. Conversely, cavity-nesting species would likely benefit from urban intensification due to the increased availability of cracks and crevices suitable for nesting.

2. METHODS

2.1 Study area

This study was conducted in the Durbanville area of Cape Town, South Africa (33°51'S 18°37'E), in austral Spring-Summer 2019 and 2020 (Figure 1; Appendix A). Cape Town has a Mediterranean climate and is located within the Cape Floristic Region (CFR) austral winter rainfall region where rain primarily falls between May and August and summers tend to be dry and warm (Mucina & Rutherford, 2006). The CFR is largely congruent with the Fynbos biome, which accounts for approximately 83% of the vegetation types in the area (Manning & Goldblatt, 2012). Out of the 435 vegetation types identified across South Africa, Lesotho and Eswatini (formerly Swaziland), the Fynbos Biome alone has 119 different vegetation types, each associated with unique characteristics and floral diversity (Mucina & Rutherford, 2006). The underlying vegetation type for all sampling sites in this study was Swartland Shale Renosterveld. However, four out of the 18 sites were adjacent to other underlying vegetation types, namely Cape Flats Sand Fynbos, Cape Winelands Shale Fynbos, and Swartland Granite Renosterveld (Figure 2). Swartland Shale Renosterveld is characterised by mean annual precipitation of 270-670mm (average: 430mm), mean low-high temperatures of 6.3-29.6°C, clay soils and altitudes between 50-350m (Mucina & Rutherford, 2006). Vegetation is predominantly low to moderately tall shrubland or low and open renosterbos-dominated shrubland, with heuweltjies (raised mounds of soil which can differ in their dominant vegetation) also being common (Mucina & Rutherford, 2006).

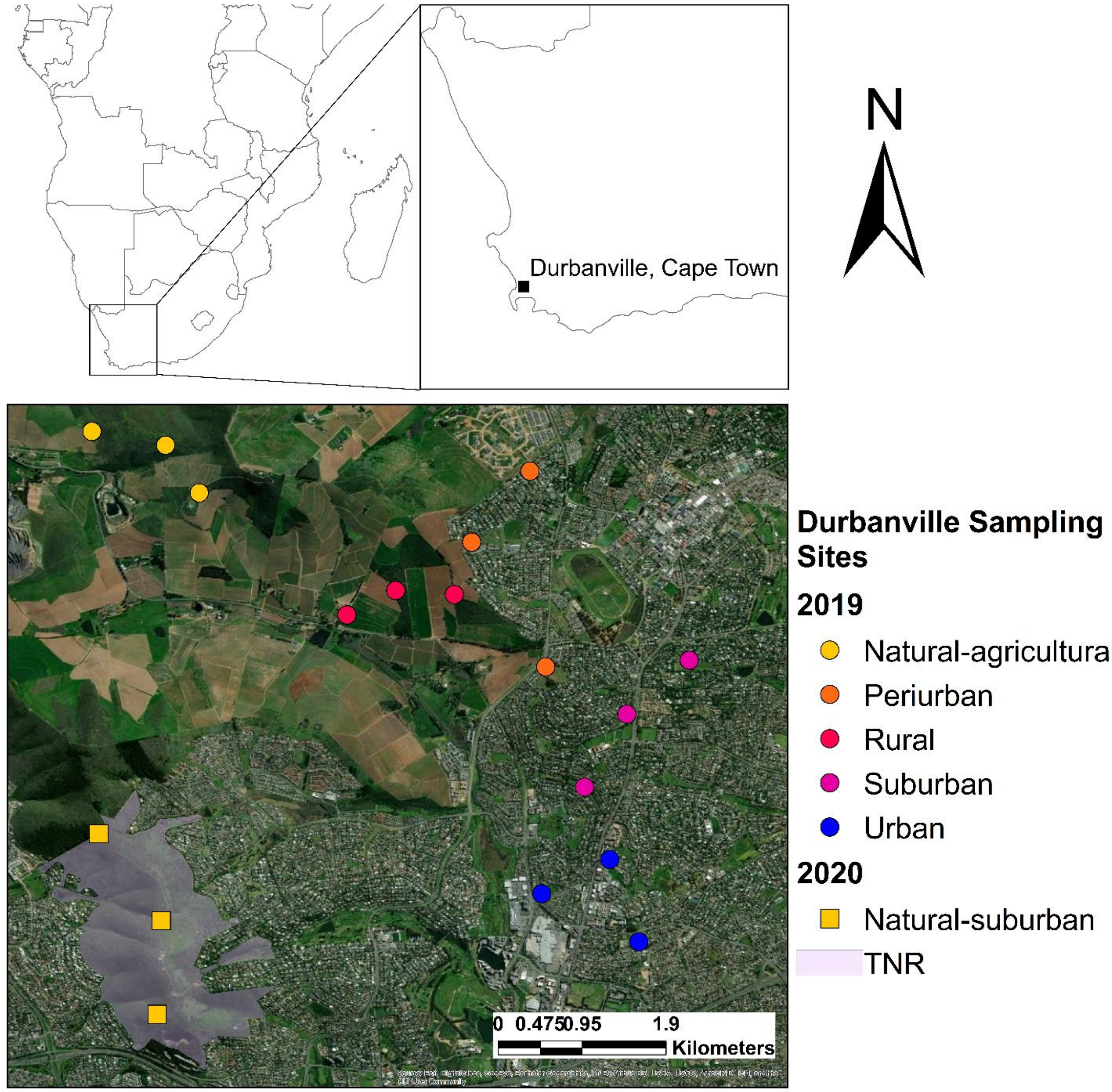

Figure 1. Map indicating study sites where sampling occurred in austral spring, 2019 and 2020. Refer to text for site descriptions. TNR: Tygerberg Nature Reserve.

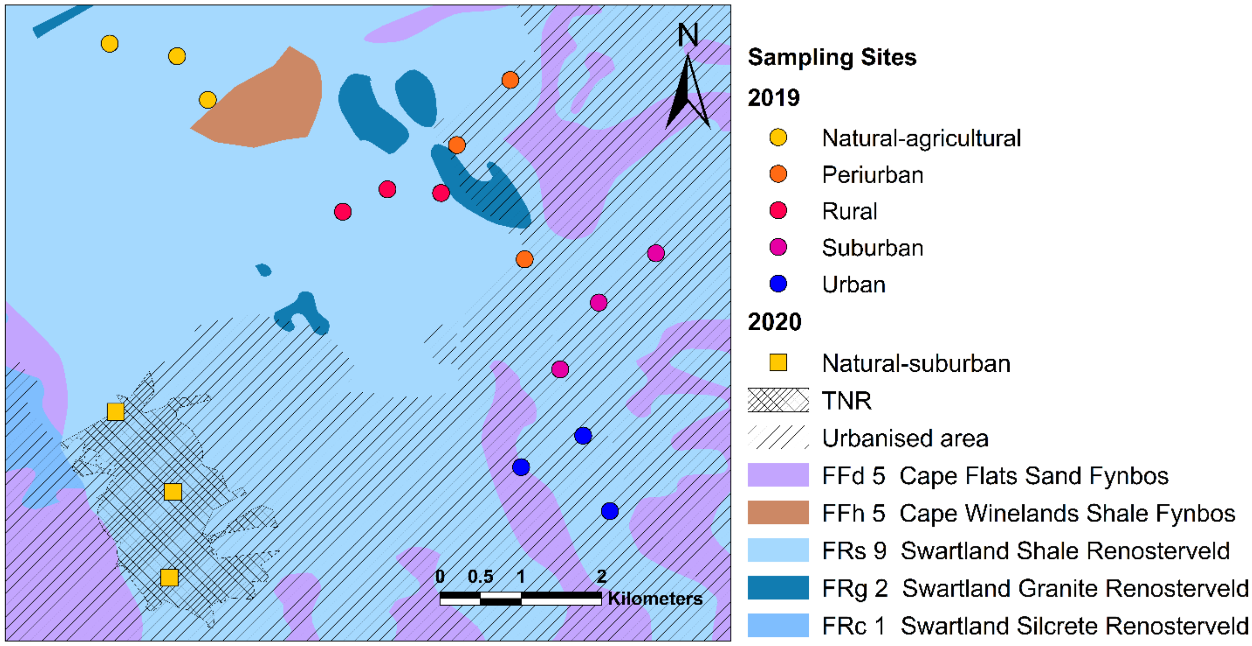

Figure 2. Map showing the study sites where sampling occurred, overlayed on underlying historical vegetation types. Refer to text for site descriptions. TNR: Tygerberg Nature Reserve.

2.2 Sample site selection

Samples from two years were used in this study, 2019 and 2020. The 2019 samples were collected as part of a separate assessment investigating the effects of urbanisation on monkey beetles (Brom, 2021). The traps are designed to collect any pollinating insects, including the bee and wasp specimens used in this study (which were considered bycatch from Brom (2021)). A total of 15 sampling sites, spanning the five different urban zones found along an urban gradient (namely urban, suburban, peri-urban, rural, and natural) were selected using a stratified selection method. Here, urban, and suburban zones refer to areas within the City of Cape Town (hereafter referred to as 'the city' or Cape Town) dominated by urban densification with impervious surface >60%, and urban sprawl with impervious surface <50%, respectively. Peri-urban zones were located directly along the urban edge. Rural zones refer to land found outside the city dominated by agriculture, and natural zones refer to areas dominated by remnant patches of intact vegetation. By doing a layered analysis using zoning schemes and vegetation maps, three representative sites per urban zone were selected. Within the city, all sampling sites were in publicly accessible open spaces such as city parks and road verges.

As illustrated above, the conclusions drawn about the effects of urbanisation on pollinators can vary greatly depending on whether agricultural or natural areas are used for comparison. Therefore, sites from both zones were used for comparative purposes in this study. Due to time and logistical constraints, Brom (2021) was only able to sample natural sites that very closely bordered agricultural land (approximately 35-135m away from the agricultural edge). To account for the possible influence of edge effects on pollinator diversity and abundance (such as pesticides being blown into the natural areas), additional sampling of natural sites bordering a suburban area was conducted in 2020 in Tygerberg Nature Reserve. Note: due to time and logistical constraints the 2019 study sites could not be re-sampled in 2020, however sampling conditions were kept as constant as possible between all sampling events. How these sites were used in analyses is address in the '*2.7 Statistical analysis'* section below.

To minimise possible altitudinal effects, the elevation of all sites was kept below 100m above sea level. Sites were also located between 500m-1km apart.

2.3 Bee and wasp sampling

All 2019 and 2020 samples were collected in austral spring (September-November). Each site was sampled twice, approximately five weeks apart. At each sampling site, for each sampling event, five sets of three different coloured UV-painted pan traps (blue, yellow and white) were placed at ground level in open areas where they were easily visible to pollinators, preferably near to blooming flower patches. Each set of three traps was placed approximately 1.5-3m apart in a zig zag or linear pattern, depending on the available space at the sampling site. Three different colours were used in order to maximise the diversity of insects attracted to traps as different insects are attracted to different colours (Vrdoljak & Samways, 2012; Shrestha et al., 2019). The pan traps (7.5cm in diameter x 4cm deep) were filled with approximately 75ml (2/3 full) of 50% propylene glycol solution and left for 48 hours (Figure 3). Upon collection, traps of the same colour at each site were combined, strained and transferred to vials containing 70% ethanol for further processing in the laboratory.

Figure 3. Example of pan traps used to sample pollinators.

2.4 Collection of floral data

To account for the possible influence of floral resources on pollinating bee and wasp communities, two floral metrics were recorded at each site during each sampling event: flowering plant species richness and open flower abundance. For species such as those in the family Asteraceae, the number of open inflorescences rather than individual flowers were counted i.e., one inflorescence = one open flower. Both metrics were collected from within 10, 1m^2 quadrats, spaced 2m apart along a transect. For areas where there was insufficient space for a 20m transect, the quadrats were placed in a randomised grid. Species that were uncommon but present outside of the quadrats were also recorded.

2.5 Hymenoptera identification

In the laboratory, specimens were identified to order level, and all bees and wasps were separated. To facilitate ease of identification, all individuals were cleaned and pinned following the USGS Bee Inventory and Monitoring lab methodologies (https://www.usgs.gov/media/files/how-catch-and-identify-bees-and-manage-a-collection). When required, Plant & Dubitzky (2008) methods were followed to relax specimens and reposition them to make diagnostic features more easily visible. Individuals were identified to genus, and, where possible, species-level using available keys (primarily Goulet & Huber, 1993; Michener, 2007; Eardley et al., 2010; see Appendix B for others), or expert opinion. Where it was not possible to identify the species, they were identified to morphospecies level. Where required, specimens stored in the entomology dry collection at the Iziko South African Museum (ISAM) were used for reference and comparative purposes.

Information about nesting guild, sociality and feeding strategy were also collated for each species (see Appendix B and C). Where information was not available or multiple strategies exist within a group, the most common or ancestral state for that genus or family was used. For example, Halictids have varied social strategies from strictly solitary to eusocial (Timmermann & Kuhlmann, 2008a). However, solitary is the ancestral state, and so all *Patellapis* sp. were recorded as solitary ground-nesters. Similarly, unless a species was strictly social (such as *Apis mellifera*), they were classified as solitary. For example, communal and cleptoparasitic species were classified as solitary. Limited information was available for several wasp species' nesting strategy. Unless a nesting strategy, such as ground-nesting, was clearly stated in the literature, their nesting guild was classified as unknown.

2.6 Quantifying urbanisation

Bees and wasps are known to be sensitive to certain landscape features, such as the proportion of impervious surface and small patches of vegetation (Wenzel et al., 2020), that are not easily detectable in existing classification schemes such as the South African National Land-Cover Dataset (DFFE, 2020). I present here a 5m-scale landscape classification based on Sentinel-2 imagery and a supervised machine learning model implemented in Google Earth Engine (Gorelick et al., 2017). This classification allows for finer-scale, more accurate calculations of the amount of impervious surface and, therefore, the degree of urbanisation around each site. The output from these calculations were then used as predictor variables in analyses of the observed variation in pollinator diversity and community composition. The classification model and calculations were conducted as follows:

2.6.1 Building the classification model

Sentinel 2 MSI: MultiSpectral Instrument, Level-2A images were accessed through Copernicus/S2_SR between 23rd June 2015 (Sentinel 2 launch) and 30th November 2019. November 2019 was chosen as the upper limit for image selection as this was when the last 2019 samples were collected. As Cape Town is a growing, developing city, extending the image selection period beyond November 2019, could have led to incorrect land-use classifications that were not representative of the situation under which the samples were collected. The samples collected in 2020 were from Tygerberg Nature Reserve (where no development is allowed), thus it is assumed that little changed occurred in that area between November 2019 and November 2020. Images with cloudy pixel counts of higher than 10% were excluded. This left a total of 71 usable images.

Normalised difference vegetation index (NDVI) and normalised difference moisture index (NDMI) were then calculated for each image. NDVI correlates with the photosynthetic capacity of plants and can estimate green vegetation density. NDMI correlates with plant moisture content and estimates plant water stress. The inclusion of both NDVI and NDMI significantly improved the ability of the model to accurately distinguish between and classify different land-use types such as cultivated land and natural vegetation. Similar results have been observed in other studies (Rahman & Mesev, 2019). NDVI was calculated by taking the B8 band (Near Infrared) and B4 band (Red) and applying the following formula:

$$NDVI = \frac{B8 - B4}{B8 + B4}$$

NDMI was calculated by taking the B8A band (Red Edge 4) and B11 band (SWIR 1) and applying the following formula:

$$NDMI = \frac{B8A - B11}{B8A + B11}$$

The median NDVI, NDVI variance, median NDMI and the median values for bands B2-9, B11 and B12 were then used as the input layers for the land-use classification model.

To develop the model, a training set of 249 GPS points were collated using Google Earth Pro V7.3 (Google Earth, 2021) and knowledge of the area obtained during field sampling. A minimum of 20 training points were selected for the following seven land-use categories: cultivated (30 points), impervious surfaces (roads (30 points), buildings (44 points), other (20 points)), natural vegetation (20 points), trees (45 points), urban vegetation (40 points), and waterbodies (20 points). 'Other' impervious surface points included features such as car parks and tennis courts. Urban vegetation refers to the variety of green spaces found within the urban environment, such as gardens, parks, and other publicly available open green spaces. Together with the input layers outlined above, these training points were used to run one of Google Earth Engine's inbuilt classifier models, Gradient Tree Boost Classifier, with 30 trees and default parameters. A confusion matrix was run to validate the model's classification accuracy, which gave an accuracy of 0.97 and kappa of 0.96 (Landis & Koch, 1977; Appendix D). Using 70 validation GPS points (10 per land-use classification category) selected by an independent assessor using Google Earth Pro V7.3, a second validation test was performed on the model using Google Earth Engine. This supported the finding that the model sufficiently classifies the different land-uses (confusion matrix accuracy of 0.83 and kappa of 0.8; Appendix D).

2.6.2 Calculating proportions of each land-use type

Finally, to characterise the landscape surrounding each sampling site in terms of the proportion of impervious surface and vegetation, the pixels corresponding to each category within a 500m radius buffer surrounding each site were counted. Using R V4.1.2 (R Core Team, 2021), the *raster* (Hijmans, 2021) and *rgdal* (Bivand et al., 2021) packages were used to draw the 500m radius buffer around each sampling site and clip the land-use classification raster layer. This distance was used because previous studies have found that a 500m radius buffer was best at explaining variation in bee diversity, and a distance greater than this could result in too much overlap between sampling sites as they were only 500m-1km apart (Wilson & Jamieson, 2019). The proportion of each land-use type within each 500m radius was calculated by taking the total number of pixels per land-use category and dividing them by the total number of pixels within the 500m radius circle. The proportion of cultivated, natural, trees and urban vegetation were combined to give a single vegetation score (i.e. sum of all percentages) as these were all assumed to contain suitable habitat for bees and wasps. This left three categories: impervious surface, vegetation and waterbodies (Figure 4).

2.7 Statistical analysis

2.7.1 Assessing possible climatic variation between 2019 and 2020

As highlighted above, the urban, suburban, periurban, rural, and natural-agricultural sites were only sampled in 2019 and the natural-suburban sites were only sampled in 2020. Due to time and logistical constraints, the re-sampling of 2019 sites were not possible. Combining data from different years can introduce doubt as to whether the results observed are due to location, or temporal (e.g. climatic) variation. As such, the following tests were done to assess the extent of variation in climatic variables between the two years.

Firstly, daily rainfall was obtained for the four weeks preceding each sampling event from the Tygerberg weather station which is located between 3-10km from each site (Appendix E, Figure B; data obtained from the CSAG website: https://www.csag.uct.ac.za/current-seasons-rainfall-in-cape-town/). Each site was sampled twice, once in early spring and once in late spring. Using R, three t-tests were performed: one comparing early spring 2019 with early spring 2020, a second comparing late spring 2019 and late spring 2020, and a third comparing all downloaded 2019 and 2020 rainfall data (i.e. early spring and late spring combined).

Secondly, pollinator abundance and species richness were collated for all sampling sites for each sampling event. Each site was sampled twice, once in early spring and once in late spring. In Cape Town, early spring is generally wetter and cooler than late spring, which tends to be drier and warmer (see figure B for rainfall trends). If the bees and wasps were consistently affected by these climate variables, then we would expect to see some consistent difference in the abundance and diversity of pollinators sampled in early spring and late spring (e.g., always higher in early spring than late spring). To test whether there were significant differences between pollinator abundance and diversity in early and late spring, ANOVA and post-hoc Tukey tests were performed using the aov() and TukeyHSD() functions in base R (R Core Team, 2021).

2.7.2 Pollinator response variables

Five pollinator response variables were calculated for each site: total abundance, total species richness, two different diversity indices, and evenness. Using the *vegan* package (Oksanen et al., 2020), the two diversity metrics calculated were, the exponent of Shannon-Weiner index (ESI), and the inverse Simpson index (ISI). These diversity indices provide a measure of the effective number of species, which is more accurate and easier to interpret than the traditional versions (i.e. Shannon-Weiner and Simpson index) (Jost, 2006). Pielou's evenness index (J'), which gives "the amount of evenness relative to the maximum and minimum possible for a given richness", was calculated as a measure of species evenness across sites (Jost, 2010: pg 207). To test the effect of urbanisation on pollinator functional groups across sites, the following indices were calculated: species richness, abundance, ESI, ISI, and evenness (J') for both cavity- and ground-nesters. To test nesting guild partitioning more generally across sites the ESI, and ISI were calculated using a site by nesting guild matrix, which used species richness as the unit rather than abundance.

Apis mellifera was removed from the dataset because it is a managed species and is, therefore, less likely to have been affected by urbanisation in the same way as wild species. Also, many parasitic wasp and bee species are still known to visit flowers (Gess & Gess, 2014), therefore, may still provide some pollination. Thus, no parasitic species were removed from the dataset in any analysis.

2.7.3 Species accumulation curves

The specaccum() function in the *vegan* package (Oksanen et al., 2020) was used to calculate species accumulation curves for both the full dataset and each individual urban zone, to examine the degree of sampling efficiency. Sampling is considered adequate when the curve reaches an asymptote (Soberon & Llorente, 1993).

2.7.4 Non-metric Multidimensional Scaling (NMDS), Cluster Analysis, and Analysis of Similarities (ANOSIM)

To investigate the composition of pollinator species across the different urban zones, an NMDS analysis was performed in PRIMER V6 (Clarke & Gorley, 2006) using a site by species matrix with abundance per trap colour and month combined into a single abundance measure per site and using urban zone as a factor. The data was first square root transformed then a Bray-Curtis dissimilarity matrix was calculated. Next a CLUSTER analysis was performed, and the results overlaid on the NMDS plot.

To test whether there is a difference in community composition between the different urban zones, an Analysis of Similarities (ANOSIM) test was performed. This analysis was performed using the anosim() function in the *vegan* R package, set to 999 permutations, on a Bray-Curtis dissimilarity matrix, and using urban zone as the grouping factor.

2.7.5 Redundancy analysis

To investigate the influence of continuous variables on community composition, I used redundancy analysis (RDA) and a backward selection model comparison approach, with floral variables (abundance, diversity, richness) and impervious surface coverage as explanatory variables. The RDA was done using the rda() function in the *vegan* package and the best fit model was selected using the stepAIC() function in the *MASS* package (Venables & Ripley, 2002). To make the results more easily comparable, the continuous explanatory variables were scaled using the scale() function in base R. To test the significance of the RDAs, permutation tests were conducted using the anova() function in the *vegan* package. RDAs were plotted using type-2 scaling (correlation plots), which focus on the response variable.

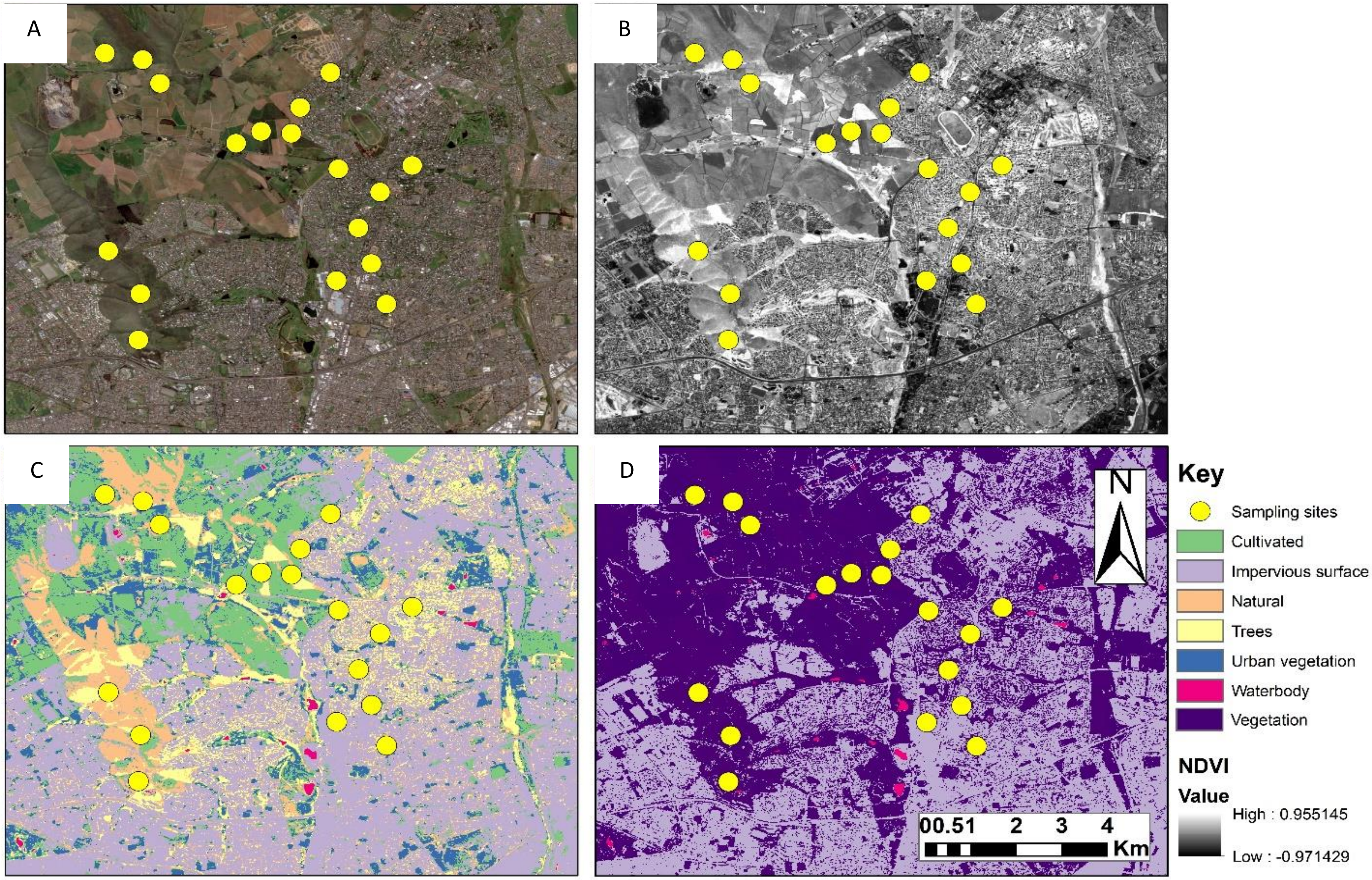

Figure 4. A) An example of a Sentinel image used to create NDVI (this image just shows bands B2, B3 and B4 i.e., RGB); B) Shows median NDVI created using 71 Sentinel images from 23rd June 2015 - 30th November 2019; C) Land-use classifications at a more fine-scale level; D) Final urban land-use classification with 3 categories (impervious surface, waterbodies and vegetation).

2.7.6 Analysis of variance

To test whether there was a statistically significant difference between pollinator abundance and diversity across the different urban zones, Analysis of Variance (ANOVA) and post-hoc Tukey tests were performed. Using the aov() and TukeyHSD() functions in base R (R Core Team, 2021), pollinator abundance, species richness, exponent of Shannon-Weiner index and inverse Simpson index were compared across urban zones. To obtain the compact letter display from the Tukey test, the multcompLetters4() function in the *multcompView* package (Graves et al., 2019) was used.

2.7.7 General linear models

General linear models were run to test the influence of the degree of urbanisation (measured as the percentage of impervious surface within a 500m radius of the sampling site), floral abundance, floral species richness, floral diversity, and floral evenness on the pollinator response variables outlined above in section 2.7.2. To assess whether *Apis mellifera* should be included in the final models as a confounding variable, general linear models were run for each pollinator response variable with *A. mellifera* abundance as the explanatory variable (Table 1). Pollinator species richness, abundance, and exponent of Shannon-Weiner index were all significantly positively correlated with *A. mellifera* abundance (Table 1). This suggests that *A. mellifera* is likely to respond to any explanatory variables similarly to wild species. As such, *A. mellifera* was not included as a confounding variable in any of the final best-fit models. A backwards selection approach was then used, using the stepAIC() function in the *MASS* package (Venables & Ripley, 2002), to identify the best fit model for each of the pollinator and nesting-guild (functional group) response variables. This model selection approach was performed on a dataset containing only the sites sampled in 2019 and was repeated for a dataset containing both the 2019 and 2020 sampling sites. This was done to test whether the inclusion of the 2020 sites would significantly affect or change the results.

2.7.8 Additional notes on programs and packages used

Unless otherwise specified, statistical analyses were performed in R V4.1.2 (R Core Team, 2021). The packages *tidyr* (Wickham, 2021) and *dplyr* (Wickham et al., 2021) were used for data tidying and wrangling, and *ggplot2* (Wickham, 2016) was used to assist in creating figures.

All maps (Figures 1, 2, 4 and A/Appendix A) were created using ArcGIS Desktop V10.7.1. The South African national vegetation map, VEGMAP (http://bgis.sanbi.org/SpatialDataset/Detail/18) (Mucina & Rutherford, 2006), was used to make Figure 2. The 2017 City of Cape Town Biodiversity Network layer was used to create Figure A (Holmes & Pugnalin, 2016; City of Cape Town, 2017).

Table 1. Results from general linear models run for all pollinator community and nesting guild response variables with *Apis mellifera* abundance as the explanatory variable. Also note: ESI = exponent of Shannon-Weiner index, ISI = inverse Simpson index. Significance codes for p-values: *** = p< 0.001, ** = p< 0.01, * = p<0.05.

	Response variable	Explanatory variables	Adjusted R^2	Estimate	Standard error	t-value	F-statistic	DF	p-value
Pollinator response variables	Species richness	*Apis mellifera* abundance	0.3833	1.731	0.509	3.401	11.57	1&16	**
	Species abundance	*Apis mellifera* abundance	0.352	7.447	2.328	3.199	10.23	1&16	**
	Diversity (ESI)	*Apis mellifera* abundance	0.191	0.5393	0.2409	2.239	5.013	1&16	*
	Diversity (ISI)	*Apis mellifera* abundance	-0.007011	0.1582	0.1685	0.939	0.8816	1&16	0.362
	Evenness (J')	*Apis mellifera* abundance	0.1141	-0.02334	0.01307	-1.786	3.189	1&16	0.0931
Nesting guild response variables	Diversity (ESI)	*Apis mellifera* abundance	0.05991	0.09089	0.06297	1.443	2.083	1&16	0.1682
	Diversity (ISI)	*Apis mellifera* abundance	-0.0219	0.03699	0.04639	0.797	0.6357	1&16	0.437

3. RESULTS

3.1 Summary of pollinator abundance and species richness

Across all sampling sites, 488 bee and wasp individuals were collected. Of these individuals, 443 were bees, and only 45 were wasps. A total of 45 morphospecies (hereafter referred to as species) of bee and 27 species of wasp were identified (Appendix C). Bees in the family Halictidae were most common, with 14 species and 258 individuals found across all sites (Figures 5A, B; Appendix C). The next most common families were Apidae and Megachilidae with 13 and 10 species and 71 and 64 individuals, respectively (Figures 5A, B; Appendix C). The family Colletidae had the least number of individuals, with only 18 individuals found, however these all were from seven species within the genus *Scrapter* (Figures 5A, B; Appendix C). Only one species within the family Andrenidae, *Andrena* cf. *notophila*, was collected, however, there were 32 individuals found across all sites (Figures 5A, B; Appendix C). Three of the most common species, *Seladonia* sp. 1, *Seladonia* sp. 2 and *Patellapis* sp. 2, with 72, 44 and 50 individuals found respectively, are all from the subfamily Halictinae (Figures 5A, B; Appendix C). Another common halictid was *Nomioides* cf. *maculiventris* (57 individuals collected), in the subfamily Nomioidinae (Figures 5A, B; Appendix C). Other relatively common species were *A. mellifera* and *Andrena* cf. *notophila* with 53 and 32 individuals identified, respectively (Figures 5A, B; Appendix C). Except for *Lasioglossum* sp. 4 (14 individuals), *Afranthidium* cf. *concolor* (22 individuals) and *Afranthidium* sp. 2 (29 individuals), 10 or fewer individuals were collected for all other species of bees and wasps (Figures 5A, B; Appendix C). A total of 39 species of bees and wasps had only one individual, while a further 22 species had five or fewer individuals (Figures 5A, B; Appendix C).

A total of four different nesting guilds were identified, namely ground-nesters, cavity-nesters, carder bees, and dauber/resin bees. Ground-nesting bees were the most common with 68.9% (31 species), followed by cavity-nesting bees (15.5%, seven species), dauber/resin bees (11.1%, five species), and carder bees (4.4%, two species) (Figures 5C, D; Appendix C). Nesting guilds could only be identified for seven wasp species which were all ground-nesters (Figures 5C, D; Appendix C). Ground-nesting species were found at all urban zones, however, only seven sites had species with a nesting guild other than ground-nesting. One urban site and one rural site had both ground- and cavity-nesters. Two of the natural-agricultural sites had both ground-nesters and carder bees. Only the three natural-suburban sites within Tygerberg Nature Reserve had species from all four nesting guilds.

Except for *A. mellifera*, which is a social honey producer, all other bee species were solitary (Figure 6B, Appendix C). Seven wasp species were identified as solitary, and the rest are unknown (Figure 6B, Appendix C). Collecting pollen from flowers was the most common feeding strategy within the bees (86.7%, 39 species), followed by cleptoparasitism (only 13.3%, six species) (Figure 6A, Appendix C). Of the wasps, all but the pollen wasps (*Celonites* sp. 1 and 2, and *Quartinia* sp.) exhibited some form of parasitism on other insects (Figure 6A, Appendix C).

3.2 Floral abundance and species richness

Floral abundance was highest in the natural-suburban zone with 3072 open flowers and lowest in the peri-urban zone with 643 open flowers (Figure 7A). The natural-agricultural zone had the second-highest abundance of flowers (1715) followed by suburban (1453), rural (1240) and urban (1186) (Figure 7A). Conversely, floral species richness was highest in the rural zone (32 species), followed by natural-suburban (30 species), suburban (22 species), peri-urban (18 species), natural-agricultural (17 species), and urban (12 species) (Figure 7B).

3.3 Pollinator community composition across the urban land-use gradient

The NMDS with overlaid CLUSTER analysis displays the relative similarities between different sampling sites based on their pollinator community composition. The sites were grouped into four distinct clusters (stress = 0.17; Figure 8), however, these clusters only exist at very low similarity levels (best at similarity = 20%). At this level, all three natural-suburban sites cluster together. The other three clusters are made up of sites from a mixture of different urban zones (Figure 8). At 30% similarity seven smaller clusters are seen, and at 40% similarity, this is increased to 12 clusters, many of which comprise of only one site (Figure 8).

These patterns are supported by the ANOSIM analysis results. When all urban zones are considered, there is a statistically significant difference between the pollinator communities in the different urban zones ($p = 0.016$, $R = 0.3016$). However, the relatively low R statistic (closer to 0 than 1) shows that there is a relatively low level of similarity between sites within an urban zone category, and slightly higher similarity between sites from different urban zone categories. To test the influence of the natural-suburban sites on this result, a second ANOSIM analysis was run on all sites except the three natural-suburban sites. In this case, no statistically significant difference between pollinator communities from sites within the different urban zones were observed ($p=0.127$, $R=0.1615$). This suggests that the natural-suburban zone is the only urban zone which can be distinguished from other urban zones based on its pollinator community.

For the RDA, including all sites and all explanatory variables, the constrained axes explained 37% of the variance in pollinator community composition, though this was not significant (ANOVA: $F = 1.3854$, $df = 5$, $p = 0.305$). For the best fit model, which only included floral diversity (exponent of Shannon-Weiner index), floral abundance and floral evenness, 32% of the variance in pollinator community composition was explained by the constrained axes, and this was near-significant ($F = 2.2406$, $df = 3$, $p = 0.065$). The first two constrained axes, RDA1 and RDA2, explained 21.6% and 8.4% of the variance, respectively. The ordination plot (Figure 9A) shows that the explanatory variables which contributed most to the variance were floral abundance and floral diversity (indicated by the length of the arrows). It also shows that sites NS1 (natural-suburban) and NS2, and species *Seladonia* sp. 1 and *Afranthidium* cf. *concolor* tended to be associated with elevated floral abundance, whereas species *Afranthidium* sp. 2 tended to be associated with higher floral evenness. Additionally, it shows that site NS3 and species *Nomioides* cf. *maculiventris* were most closely positively correlated with floral diversity, however, the association is less strong than for the aforementioned sites and species. Finally, the plot showed that the natural-suburban sites were the main drivers of the relationship between floral variables and community composition, and this, in turn, was driven by variation in abundance of a few highly influential bee species.

To account for the strong influence of the natural-suburban sites, a second RDA with natural-suburban sites excluded was conducted. For the best fit model, which included all explanatory variables except for floral abundance, 50% of the variance in pollinator community composition was explained by the constrained axes, and this was significant ($F = 2.4721$, $df = 4$, $p = 0.014$). The first two constrained axes, RDA1 and RDA2, explained 31.3% and 8.9% of the variance, respectively. The ordination plot (Figure 9B) shows that the explanatory variables contributed a similar amount to the variance, with impervious surface contributing slightly more than the other three. The patterns here are less clear than for the previous plot. However, the plot suggests that: sites S1 and S2 (suburban) were positively correlated with impervious surface; sites P2, P3 (peri-urban) and *Syzeuctus* sp. were positively correlated with floral richness; sites NA1 and NA3 (natural-agricultural) were negatively correlated with floral diversity, and *Andrena* cf. *notophila* was negatively associated with floral richness; site U1 (urban) was negatively correlated with both floral diversity and richness. Finally, it shows that site U3, *Patellapis* sp. 2 *and Seladonia* sp. 2 were most closely positively correlated with floral evenness, however, the association is less strong than for the aforementioned sites and species.

3.4 Patterns in pollinator abundance and diversity across the urban land-use gradient

A significant difference in average pollinator species richness (ANOVA: $F= 23.3$, $df=5$, $p< 0.001$) and abundance (ANOVA: $F= 12.69$, $df= 5$, $p<0.001$) was observed between the different urban zones. For both pollinator variables, average species richness and abundance were significantly higher in the natural-suburban zone compared to all other zones which were not significantly different from one another (Figures 10A, B). When measured as the exponent of Shannon-Weiner index, a statistically significant difference in average pollinator diversity between the different urban zones was also observed (ANOVA: $F= 4.454$, $df=5$, $p= 0.0158$). The natural-suburban zone had the highest average diversity and was significantly different to both suburban and natural-agricultural zones, which had the lowest mean diversity (Figure 10C). The average pollinator diversity of the urban, peri-urban, and rural zones was significantly similar to both natural-suburban, suburban, and natural-agricultural zones (Figure 10C). Conversely, when measured as inverse Simpson index, the difference in average pollinator diversity between the different urban zones was not statistically significant (ANOVA: $F= 2.434$, $df= 5$, $p= 0.096$; Figure 10D).

3.5 Response of nesting guilds to urbanisation

Impervious surface cover, which was used as a proxy for the degree of urbanisation, did not have a significant effect on pollinator species richness, abundance, diversity, or evenness at both the community and nesting guild level (see table E, Appendix D for impervious surface cover values).

Instead, floral indices had the biggest influence on pollinator community variables. At the pollinator community level, floral abundance positively influenced pollinator species richness, and diversity. Floral evenness and richness positively affected pollinator abundance and evenness, respectively. Conversely, floral diversity had a slight negative effect on pollinator evenness. Floral abundance positively influenced nesting guild diversity. The same was observed for species richness, abundance, and diversity of cavity-nesters. Floral diversity also had a positive effect on cavity-nester diversity. The statistics associated with each linear model can be seen in Table 2.

3.6 A note on the use of the 2019-2020 combined dataset and the implication for interpretation of results

For the following reasons, it seems unlikely that the results observed in this study are due to temporal/climatic effects. Firstly, whether the 2019 samples were analysed alone, or whether they were combined with the 2020 sites did not significantly change any of the conclusions drawn. For example, the linear model outputs were similar, irrespective of which dataset was used; even when the 2020 sites were excluded, floral resources still had the biggest positive effect on pollinator diversity and abundance (Appendix E, Tables F and G). Secondly, climatic variables such as rainfall, were not significantly different between the two years. For all three t-tests performed (comparing 1) early spring 2019 and 2020, 2) late spring 2019 and 2020, and 3) combined early spring and late spring 2019 and 2020) the results showed that there was no significant difference between rainfall in 2019 and 2020 ($p>0.05$). Lastly, results from an ANOVA and post-hoc Tukey test show that for both pollinator abundance and pollinator species richness there is a significant difference between the natural-suburban zone and all other sampling zones, but not between early and late spring at each site (Appendix E, Figure C; ANOVA, abundance: $F= 7.998$, $df= 11$, $p<0.001$; ANOVA, richness: $F= 8.674$, $df= 11$, $p<0.001$). There is no general pattern that can be drawn either; within some zones, pollinator abundance and richness were higher in early spring, and others were higher in late spring (Appendix E, Figure C). As such, it is unlikely that the results observed in this study are due to slight differences in climate between 2019 and 2020. It is much more likely, based on the trends observed in the data, that the larger pollinator abundance and species richness seen in the natural-suburban sites was due to their being located within a more pristine environment and due to the floral resources available.

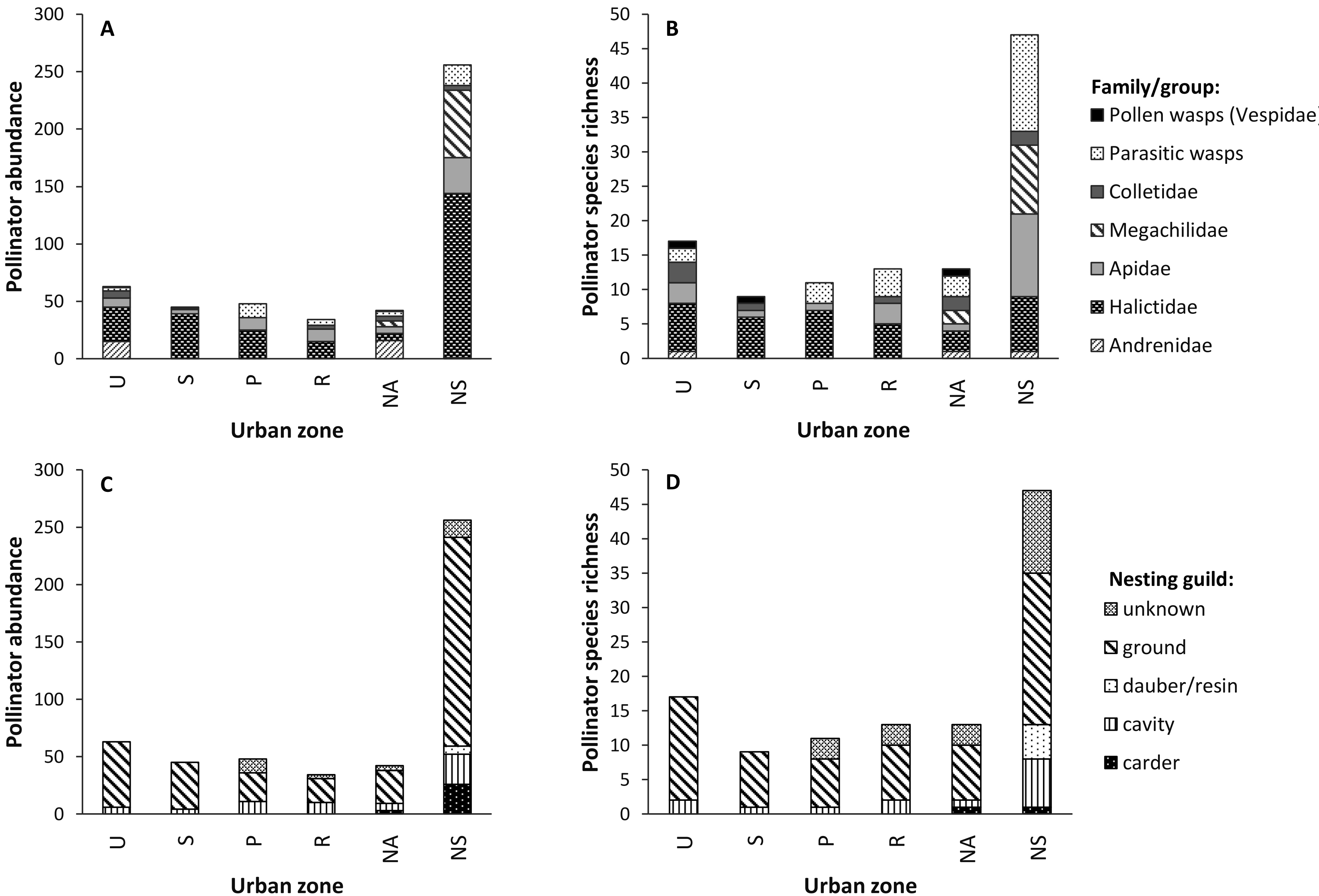

Figure 5. Total pollinator (bees and wasps) abundance (A, C) and species richness (B, D), categorised by family/group (A, B) and nesting guild (C, D), from urban (U), suburban (S), peri-urban (P), rural (R), natural-agricultural (NA), and natural-suburban (NS) sites in the Durbanville area, Cape Town. Note: all wasps were placed into two categories: pollen wasps from the family Vespidae (known pollinators), and parasitic wasps from 12 different families.

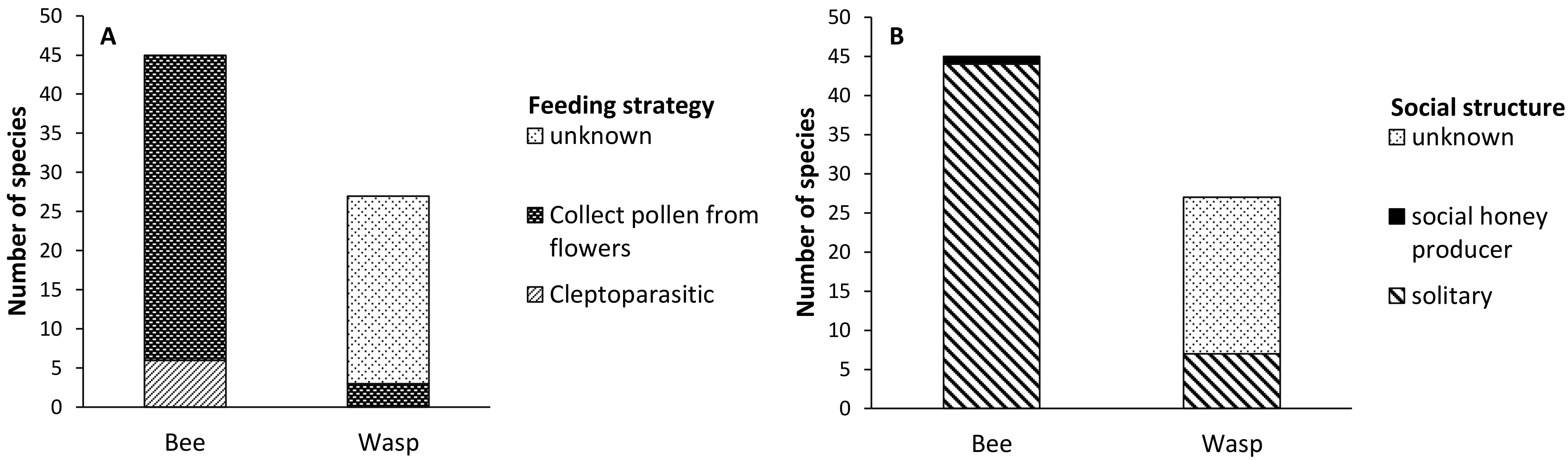

Figure 6. Total number of morphospecies (hereto referred to as species), categorised by feeding strategy (A) and social behaviour (B) from sites in the Durbanville area, Cape Town.

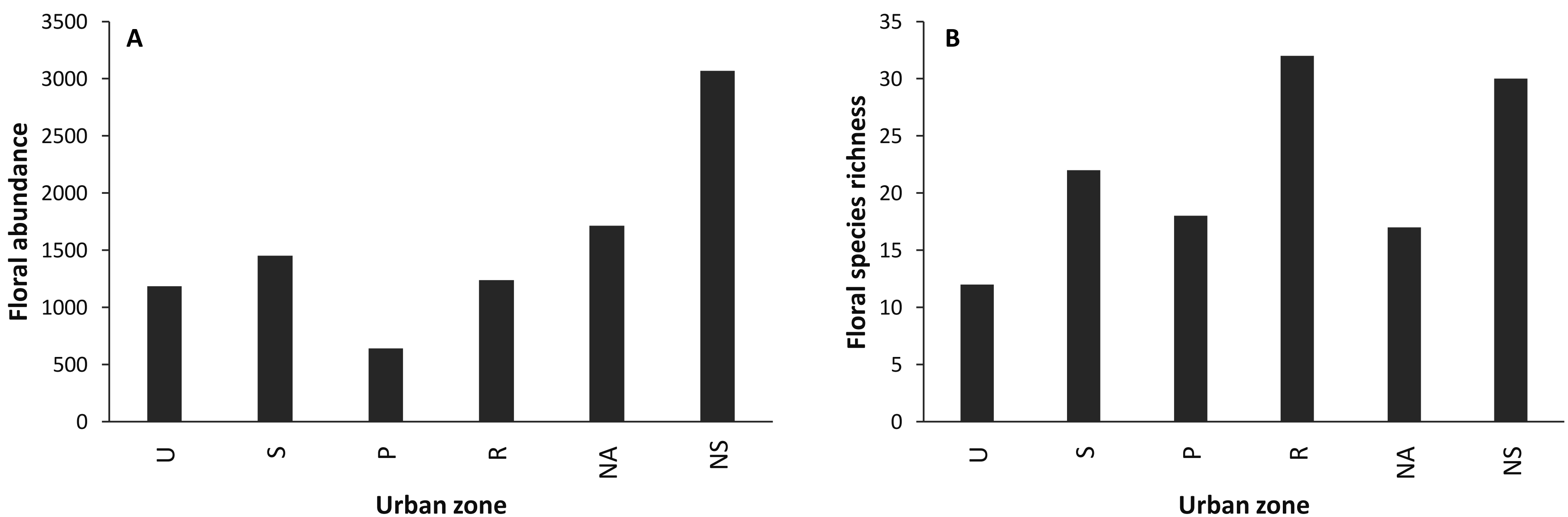

Figure 7. Total floral abundance (A) and species richness (B) from urban (U), suburban (S), peri-urban (P), rural (R), natural-agricultural (NA), and natural-suburban (NS) sites in the Durbanville area, Cape Town.

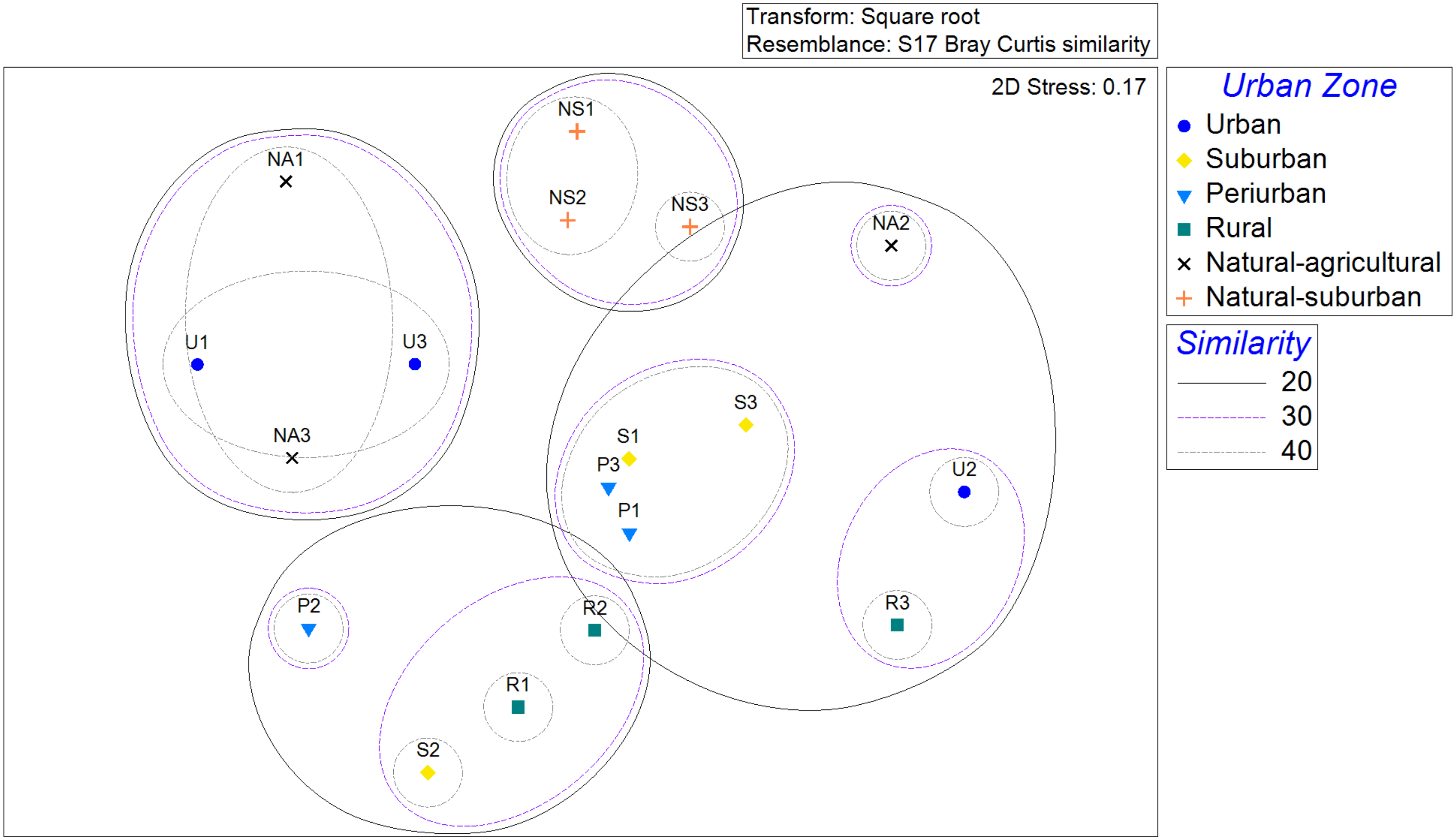

Figure 8. NMDS of sample sites using species abundance matrix (which was square root transformed and converted to a Bray-Curtis dissimilarity matrix) with urban zone as a factor. Results of the CLUSTER analysis are overlayed (i.e., similarity values).

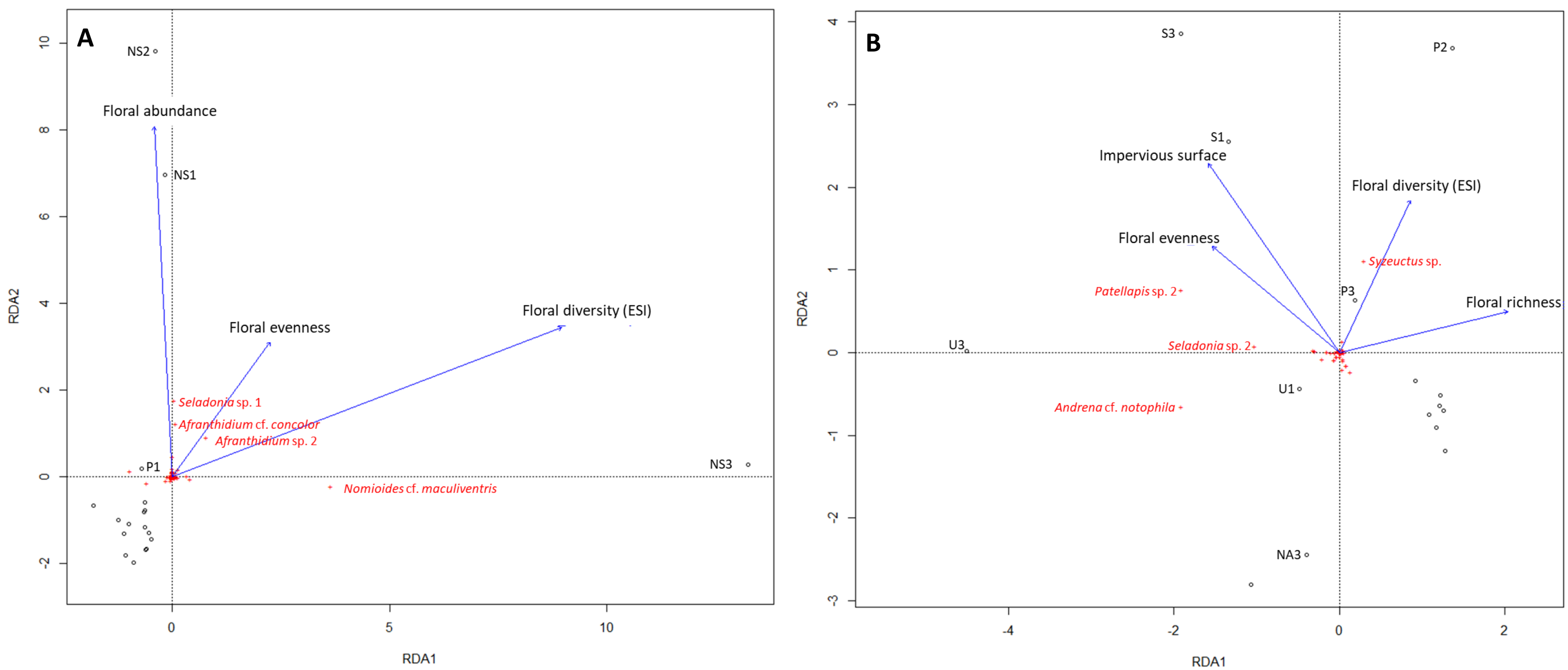

Figure 9. Redundancy analysis plots based on the best fit model for (A) both the full dataset with all urban zones included (p = 0.065), and (B) the subset dataset with natural-suburban sites excluded (p = 0.014). For both plots, red crosses show species, and black circles show sites. Blue arrows represent the explanatory variables.

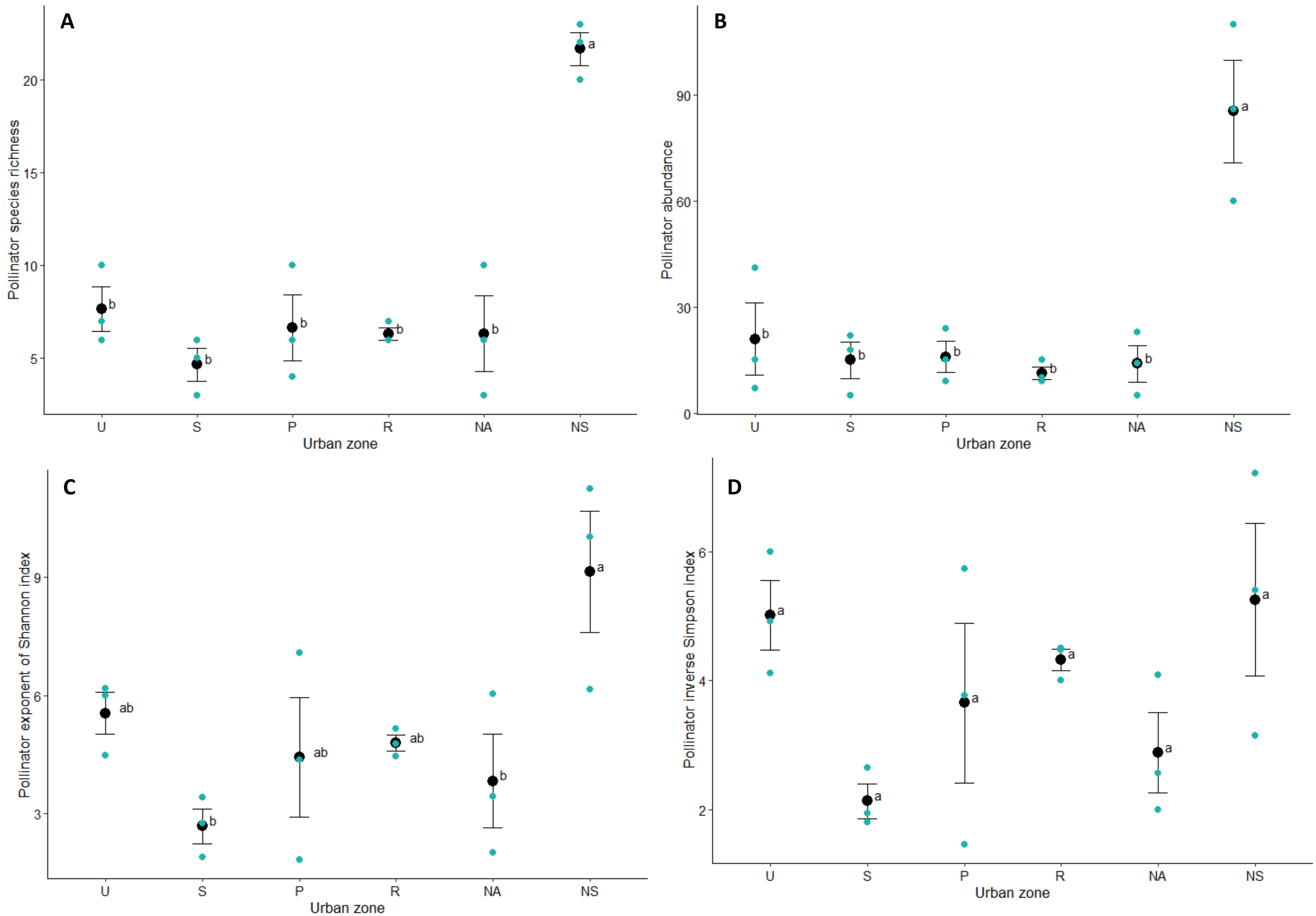

Figure 10. Mean (+/- SE) pollinator species richness (A), abundance (B), exponent of Shannon-Weiner index (C), and inverse Simpson index (D) across all urban zones are show by the black points and lines. Blue circles indicate raw data points from each replicate (3 total) for urban (U), suburban (S), peri-urban (P), rural (R), natural-agricultural (NA), and natural-suburban (NS) sites sampled in the Durbanville area, Cape Town. The letters to the right of each bar indicate the results of ANOVA and post-hoc Tukey tests.

Table 2. Results from general linear models run for all pollinator community and nesting guild response variables with the best fit explanatory variables. These best fit models were selected using a backwards selection approach, starting with impervious surface (%), floral abundance, floral richness, floral evenness, and floral Shannon-Weiner exponent response variables. Note: indices such as floral evenness are scaled between 0-1, whereas floral abundance is scaled between 0-2222, which makes it hard to compare the estimates in the final best fit model summary. Therefore, floral abundance was calculated as floral abundance/maximum abundance (which changes the scale to between 0-1). This does not affect the p-values, t-values, multiple R^2, F-statistic or DF. Also note: ESI = exponent of Shannon-Weiner index, ISI = inverse Simpson index. Significance codes for p-values: *** = p<0.001, ** = p<0.01, * = p<0.05.

Pollinator response variables	Explanatory variables	Adjusted R^2	F-statistic	DF	Estimate	Std error	t-value	p-value
Community level models								
Species richness	**Floral abundance**	0.312	4.852	2&15	**17.930**	**6.273**	**2.858**	*
	Floral evenness				**20.518**	**9.010**	**2.277**	*
Species abundance (log10(x+1))	Floral abundance	0.250	3.833	2&15	0.739	0.420	1.760	0.0989
	Floral evenness				**1.605**	**0.603**	**2.663**	*
Diversity (ESI)	**Floral abundance**	0.257	3.937	2&15	**7.522**	**2.694**	**2.792**	*
	Floral evenness				5.300	3.869	1.370	0.1909
Diversity (ISI)	**Floral abundance**	0.175	4.615	1&16	**3.504**	**1.631**	**2.148**	*
Evenness (J')	Floral abundance	0.637	10.930	3&14	-0.189	0.114	-1.661	0.11891
	Floral richness				**0.025**	**0.008**	**3.240**	**
	Floral diversity (ESI)				**-0.084**	**0.015**	**-5.488**	***
Functional group models								
Nesting guild:								
Diversity (ESI)	Impervious surface (%)	0.528	10.510	2&15	-0.007	0.004	-1.665	0.1167
	Floral abundance				**1.873**	**0.488**	**3.842**	**
Diversity (ISI)	Impervious surface (%)	0.599	13.710	2&15	-0.005	0.003	-1.686	0.112489
	Floral abundance				**1.431**	**0.317**	**4.509**	***
Ground-nesters:								
Species richness	Floral abundance	0.120	2.157	2&15	6.073	3.779	1.607	0.1288
	Floral evenness				10.029	5.427	1.848	0.0844

Pollinator response variables	Explanatory variables	Adjusted R^2	F-statistic	DF	Estimate	Standard error	t-value	p-value
Species abundance (log10(x+1))	Floral evenness	0.054	1.974	1&16	0.956	0.681	1.405	0.179
Diversity (ESI)	Floral evenness	-0.046	0.260	1&16	1.251	2.454	0.510	0.6173
Diversity (ISI)	Floral diversity (ESI)	-0.005	0.908	1&16	-0.136	0.143	-0.953	0.354742
Cavity-nesters:								
Species richness	**Floral abundance**	0.479	8.810	2&15	**2.982**	**0.742**	**4.019**	**
	Floral diversity (ESI)				0.125	0.082	1.523	0.14845
Species abundance (log10(x+1))	**Floral abundance**	0.609	14.220	2&15	**3.942**	**0.764**	**5.163**	***
	Floral diversity (ESI)				0.147	0.085	1.736	0.102992
Diversity (ESI)	**Floral abundance**	0.604	13.960	2&15	**1.703**	**0.362**	**4.711**	***
	Floral diversity (ESI)				**0.111**	**0.040**	**2.756**	*

4. DISCUSSION

4.1 Patterns in pollinator community composition and diversity

The results of this study supported the predictions that pollinator diversity would be greater and community composition would be distinct in natural areas relative to urban and rural areas, which is in line with previous work (McIntyre & Hostetler, 2001; Tonietto et al., 2011; Verboven et al., 2014; Wenzel et al., 2020). However, this was only true for sites in the natural-suburban zone, which had higher pollinator species richness and abundance. For sites in the natural-agricultural zone, pollinator diversity was not significantly different from the rural or urban zones (Figures 10A, B, and C). Similarly, pollinator communities could not be clearly distinguished between zones along the urban-rural/natural gradient, except for sites within the natural-suburban zone (Figure 8). One possible explanation lies in the natural-suburban zone's greater floral diversity and abundance relative to the natural-agricultural zone (Figure 7). This is consistent with previous studies which have demonstrated that greater floral diversity and abundance positively influence urban pollinators (Ahrné et al., 2009; Everaars et al., 2011; Hülsmann et al., 2015; Quistberg et al., 2016; Wenzel et al., 2020).

The natural-suburban zone may also be a haven for rare pollinator species. The correlation between urban zone and pollinator diversity was strongly affected by the choice of diversity index. According to the exponent of Shannon-Weiner index, the effective number of pollinator species was approximately 3.4 and 2.4 times greater in the natural-suburban zone than suburban and natural-agricultural zones, respectively (Figure 10C). Conversely, according to the inverse Simpson index, pollinator diversity was not significantly different between zones (Figure 10D). The inverse Simpson index is less sensitive to rare species than the exponent of Shannon-Weiner index (Jost, 2006), which likely explains this inconsistency, as most of the species sampled in this study were rare ($\leq$ 5 individuals, Appendix C). As such, the natural-suburban sites are likely to provide refuge to rare species.

The natural-agricultural, rural, and other urban zones did not differ from each other in their community composition or diversity. One possible explanation is that the degree of urbanisation poorly predicts pollinator community composition in this area (Everaars et al., 2011; Shwartz et al., 2013; Hülsmann et al., 2015; Quistberg et al., 2016). This is supported by the findings showing that floral resources, rather than impervious surface area, explained much of the variation in pollinator diversity and community composition (Figure 9, Table 2). However, for the full pollinator community and the sub-set community with natural-suburban sites removed, only 32% and 50% of the variation was explained by the constrained RDA axes, respectively (i.e., explained by the explanatory variables) (Figures 9A, B). Only the latter model was statistically significant, with the former being near-significant. Therefore, the low percentages associated with the constrained axes suggest that there were explanatory variables that were not accounted for in this study.

One such unmeasured variable may be linked to the locations of the sampling sites within the natural habitat patches and could explain the observed differences in community composition and diversity between the natural-agricultural and natural-suburban zones. Both types of natural zone were under some form of protection. The natural-suburban sites were all located within Tygerberg Nature Reserve, which is protected in perpetuity (Appendix A, Figure A), and the natural-agricultural sites were located within privately owned nature reserves. However, the natural-suburban sites were all located within the centre of the reserve, as far away from the neighbouring suburban area as possible. In contrast, all three natural-agricultural sites were located along the edge of the natural vegetation and surrounded by an agricultural matrix made up of a combination of vineyards and rye. The pesticides used in agriculture are known to negatively affect pollinators, and can affect pollinators in neighbouring natural areas due to drift or being carried in the wind (Muratet & Fontaine, 2015; Cardoso et al., 2020; Samways et al., 2020). Given their close proximity to the agricultural fields, the natural-agricultural sites were more likely to suffer from the detrimental effects of pesticide use.

An additional variable that could account for some of the unexplained variance in pollinator community composition is urban warming (Hamblin et al., 2018). The rising urban temperatures associated with climate change are known to negatively impact insects through alterations to their physiology, fitness and abundance, with observed declines in bee abundance of about 41% for every 1°C rise in temperature in some parts of the world (Hamblin et al., 2018). In the North Carolina, USA, Hamblin et al. (2018) found urban warming to be a stronger predictor of both bee abundance and community composition than the proportion of impervious surface, or availability of floral resources. It is important to note that this observation may not apply to all parts of the world, especially areas that are currently colder, as rising temperatures may in fact make those areas more habitable to bees. However, the temperatures reported by Hamblin et al. (2018) are within temperature ranges seen in Cape Town. As such, one may expect temperature to play an influential role in negatively impacting bees and wasps in this city.

4.2 The response of nesting guilds to urbanisation

The response of ground and cavity nesting pollinators to the proportion of impervious surface was also unexpected. There were very few cavity nesters observed, even at the highly urbanised sites in the urban zone. Floral resources, rather than the proportion of impervious surface, showed stronger positive correlations with pollinator nesting guilds at both the community and individual guild level (Table 2). Particular characteristics of the floral communities, such as the presence of specific plant species, may partly explain this. The natural-suburban zone was the only area that housed all four nesting guilds identified in this study: ground nesters, cavity nesters, carder bees, and dauber/resin bees. Carder bees require plant fibres to line their nests, and dauber/resin bees require mud or resin to aid in nest construction (Gess & Gess, 2014). Other species depend on certain petals to line their nest cells or stems and leaves from specific plant species/families on which to build their nests (Gess & Gess, 2014). Some bee species even exclusively nest in snail shells (Gess & Gess, 2014). Thus, species within each nesting guild were likely responding to more nuanced aspects of floral communities and nesting habitats, than those captured in this study.

4.3 The importance of floral resources and habitat connectivity

The finding that floral resources have a stronger influence on pollinator community composition and diversity than the proportion of impervious surface is consistent with other studies. Several studies from the northern hemisphere also found that local scale variables, such as floral resources, were stronger predictors of pollinator diversity than landscape level variables, such as impervious surface (Ahrné et al., 2009; Everaars et al., 2011; Shwartz et al., 2013; Hülsmann et al., 2015; Quistberg et al., 2016). In this study, it is possible that particular sites, such as natural-suburban 1 (NS1), which had much higher floral abundance than all other sites, were strongly influential on the analyses. However, the RDA results suggest that floral variables were still important determinants of pollinator community composition, even when the natural-suburban sites were removed. Due to the strong influence of floral resources on pollinator communities, many studies have concluded that the negative landscape-scale effects associated with urbanisation could be mitigated by the inclusion of floral-rich, bee-friendly green spaces within a city (Wojcik et al., 2008; Williams & Winfree, 2013; Blackmore & Goulson, 2014; Hülsmann et al., 2015), and the results of this study support this.

The components that contribute to bee-friendly green spaces are also important. For example, floral community composition, which includes factors such as the proportion of native and non-native plant species, as well as the presence of particular species or families, has been shown to have a strong influence on pollinators (Hülsmann et al., 2015; Wenzel et al., 2020; Brom, 2021). Investigating these factors was beyond the scope of this study. However, other studies have shown that whilst pollinators generally do not have a preference for native or non-native flowering plants (Hinners & Hjelmroos-Koski, 2009; Matteson & Langellotto, 2011; Martins et al., 2017; Rollings & Goulson, 2019; Wilson & Jamieson, 2019), certain ornamental or non-native plant species are more attractive to pollinators than others, resulting in higher pollinator abundance (Garbuzov & Ratnieks, 2014; Garbuzov et al., 2015). In some cases native plant species can attract a higher diversity of pollinators (Rollings & Goulson, 2019). Other work has demonstrated that native plants are associated with higher pollinator visitation rates and shorter decision time at the flower site (Chrobock et al., 2013; Fukase & Simons, 2016), and that the presence of certain plant species benefit some pollinators more than others. For example, Hülsmann et al. (2015) showed that the presence of Fabaceae species had disproportionately large effects on bumblebee abundance due to their preferential feeding on Fabaceae flowers In the City of Cape Town, Brom (2021) showed that within a dominant pollinator group, monkey beetles (Hopliini), different guilds showed preferences for different floral groups ranging from mass-flowering annuals to rare bulbs. Gess & Gess (2014) have catalogued the floral preference of many bee and wasp species in southern Africa. Similarly, in South Africa, the relationships between various pollinator groups and invasive plant species have been fairly well documented (van Wilgen et al., 2020; Adedoja et al., 2021; Geerts & Adedoja, 2021). However, it is not currently known how these floral preference observations relate to pollinators in the urban context.

The size and degree of connectivity between suitable habitat and floral resources is a further factor that has been shown to be important for maintaining diverse pollinator communities. Larger green spaces tend to support a greater abundance and species richness across taxonomic classes (Quistberg et al., 2016; Stewart et al., 2018). However, with enough floral resources, even small public gardens can support pollinator communities (Ahrné et al., 2009; Shwartz et al., 2013). In addition to habitat size, how habitats are configured throughout the urban matrix is also important. Banaszak-Cibicka et al. (2016) showed that the close proximity and continued connectivity of bee-friendly green spaces throughout the urban matrix (from the urban edge to the urban centre) can facilitate movement of pollinators throughout the city and promote higher pollinator diversity within the central urban areas. They also highlighted that disconnected green spaces can act as important stepping-stones for certain pollinator species. However, because pollinator flight distance is dependent on body size (Wenzel et al., 2020), smaller species are less able to travel between the green spaces, thus leading to overall reductions in pollinator diversity in urban centres.

Habitat connectivity associated with different types of urban development, such as land sharing and land sparing, can strongly influence pollinator communities. For example, Soga et al. (2014) showed that different insect groups benefit from the alternative developmental approaches in contradicting ways. They found that abundance of beetles was highest under land sparing, but abundance of butterflies was highest under land sharing. In the present study, most urban zones fall under the land-sharing category, except for the natural-suburban zone, which is an example of land sparing. The finding that pollinator diversity was highest at sites under the land-sparing model suggests that land sparing facilitates higher pollinator diversity in the Durbanville area. It is also important to note that factors affecting pollinators may be interdependent (Wojcik & McBride, 2012; Stewart et al., 2018). Therefore, floral resources need to be considered together with habitat size, connectivity, and quality.

4.4 Limitations of the sampling scheme

There were some inherent biases associated with the insect trapping method which limited the pollinator species collected. The small size of the pan traps limited the pollinators caught to those of a smaller size as big individuals and species could escape more easily (Wilson et al., 2016). Thus, larger, but prevalent, species such as those in the genus *Xylocopa* could have been missed. Additionally, not all pollinators are equally attracted to pan traps. Certain groups tend to be trapped more often than others. Therefore, using only pan traps can lead to overrepresentation of particular pollinator groups, such as halictids, and the underrepresentation of others, such as honey bees and *Colletes* species (Roulston et al., 2007). This study's high abundance of halictids may be due to the sampling method used, not because they are more abundant in the urban matrix. As such, it is generally recommended that use of pan traps is accompanied by sweep netting (Roulston et al., 2007). Sweep netting was not done here because the samples from this study were bycatch from the study by Brom (2021), where trapping methods were designed to primarily attract and trap monkey beetles. However, the pan traps used by Brom (2021) are also commonly used to attract bees and wasps and the samples were therefore also appropriate for this study (e.g. Fischer et al., 2016; Guenat et al., 2019; Wilson & Jamieson, 2019). Although the pollinator community was not sampled to completion (Appendix F, Figure D), this is not uncommon for entomological studies (Shwartz et al., 2013; Cardoso & Gonçalves, 2018; Lerman et al., 2018). An increase in sample size, e.g. through increasing sampling effort at each site or the number of sampling sites, could result in clearer patterns.

4.5 Conservation implications and future research recommendations

The results of this study illustrate the importance of protecting and enhancing the availability of floral resources within the city, and support the findings that the inclusion of floral-rich, bee-friendly spaces can greatly benefit urban pollinators (Wojcik et al., 2008; Williams & Winfree, 2013; Blackmore & Goulson, 2014; Hülsmann et al., 2015). Certain pollinator species may be more sensitive to the floral species present (Gess & Gess, 2014; Hülsmann et al., 2015; Brom, 2021) and there is still much research to be done in order to understand which floral species and characteristics are preferred by pollinators in Cape Town. Conducting field observation studies to determine which and how often pollinators are visiting the available plant species would be a valuable future exercise. Due to the strong dependence of certain pollinator species on plants and other natural resources for nesting (Gess & Gess, 2014), investigating the connections between nesting materials and pollinator diversity would also be a beneficial addition. Given the high levels of plant diversity, endemism and threat status within the Cape Floristic Region (Rouget et al., 2003; Manning & Goldblatt, 2012; van Wilgen et al., 2016), studying the roles of different plant groups in influencing pollinator communities is imperative. However, many studies suggest that an increase in floral abundance and diversity results in increased diversity and abundance of pollinators, regardless of whether the plants are native or exotic (Hinners & Hjelmroos-Koski, 2009; Matteson & Langellotto, 2011; Martins et al., 2017; Rollings & Goulson, 2019; Wilson & Jamieson, 2019; Wenzel et al., 2020). Whilst use of native plant species is preferable, this implies that any policies to increase floral resource availability may be beneficial to urban pollinators in Cape Town.

Conservation efforts can start with improved management of existing green spaces within the city, including publicly open spaces such as parks and gardens, road verges, and private gardens. One management-related solution is to alter mowing practices to facilitate maximum floral diversity, as has been suggested by several studies (Shwartz et al., 2013; Wastian et al., 2016; Lerman et al., 2018; Samways et al., 2020; Watson et al., 2020; Brom, 2021). In Cape Town, Brom (2021) highlighted the need to stop municipal lawnmowing between mid-August and mid-November to allow important spring flowers to bloom and set seed. This facilitates completion of the plants' lifecycle, allowing important floral species, such as flowering bulbs, to persist (Brom, 2021), providing the potential for these populations to grow in a relatively short space of time. Therefore, reducing mowing frequency is a cost-effective way to positively support pollinators and plant-pollinator relationships and can be undertaken at both the municipal and individual household level (Watson et al., 2020; Brom, 2021).

Additional actions that would benefit pollinators and can be applied in both public and private green spaces include increasing floral abundance and diversity of grass lawns through simple measures, such as the development of small-scale patches of flowers (Simao et al., 2018), and the provisioning of wildflower seed mixes (Blackmore & Goulson, 2014). In particular, having small-scale patches of flowers supports habitat connectivity, and therefore the movement of pollinators across the urban landscape, by creating stepping-stones. The management of urban spaces requires input from a wide variety of stakeholders (Goodness, 2018; Brom, 2021). Providing opportunities to engage with these stakeholder groups is key to the successful implementation of pollinator conservation initiatives. A stepping-stones project which aims to reconnect people with plants and birds through the development of gardens in schools has already been successfully established in Cape Town (Mnisi et al., 2021; also see https://www.fynboscorridors.org/about/our-organisations/). Expanding on or collaborating with this project to also include insect-pollinator friendly plant species into these gardens could provide an invaluable opportunity to engage with and educate young learners on the importance of insect pollinators, whilst simultaneously providing floral-rich habitats to act as stepping-stones.

In the longer term, research suggests a need to increase habitat connectivity within urban spaces. Ultimately, this would benefit not only bees and wasps, but also many other insect groups and even small to large mammals (Brom, 2021; Deacon & Samways, 2021; Schnetler et al., 2021). Small-scale initiatives such as those mentioned above could provide a starting point for future conservation efforts. However, much more research needs to be done to fully understand the situation in Cape Town. Cape Town is a large and heterogeneous city, and it is unknown whether the observed patterns from this study apply to the city as a whole. As such, there is a need to study how habitat size and fragmentation apply to currently observed patterns and expand on the current research to include other city areas.

4.6 Conclusion

When compared to larger areas of intact natural vegetation such as Tygerberg Nature Reserve, pollinator communities were negatively impacted by both the effects of urbanisation and agriculture. However, sites within the urban and agricultural matrices (both rural and natural-agricultural sites) were equally depauperate in pollinator diversity. This lack of significant difference suggests that urbanisation is neither beneficial nor detrimental to pollinators. These contrasting results highlight the importance of including comparative sites from a diversity of land uses when assessing impacts of urbanisation on pollinators. The finding that floral resources explained more variation in pollinator communities than the proportion of impervious surfaces supports the findings of other studies (Wenzel et al., 2020). This suggests that there are several cost-effective and achievable conservation initiatives that could be started immediately, which would support and promote expansion of available floral resources. These include the adoption of no-mow periods during austral spring (Brom, 2021) and development of small-scale bee-friendly floral-rich patches, which can be established and maintained by existing municipal structures and private landowners alike. Urban spaces in Cape Town have the potential to support important pollinator diversity, but more research is needed. Future research should focus on understanding the ways that 1) individual floral species and characteristics, 2) the size, shape, location of habitat, and specifically how floral patches can provide connectivity, and 3) the effects of urban warming, influence pollinator diversity and community composition.

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APPENDIX A. Critical biodiversity network and sampling sites in Durbanville, Cape Town

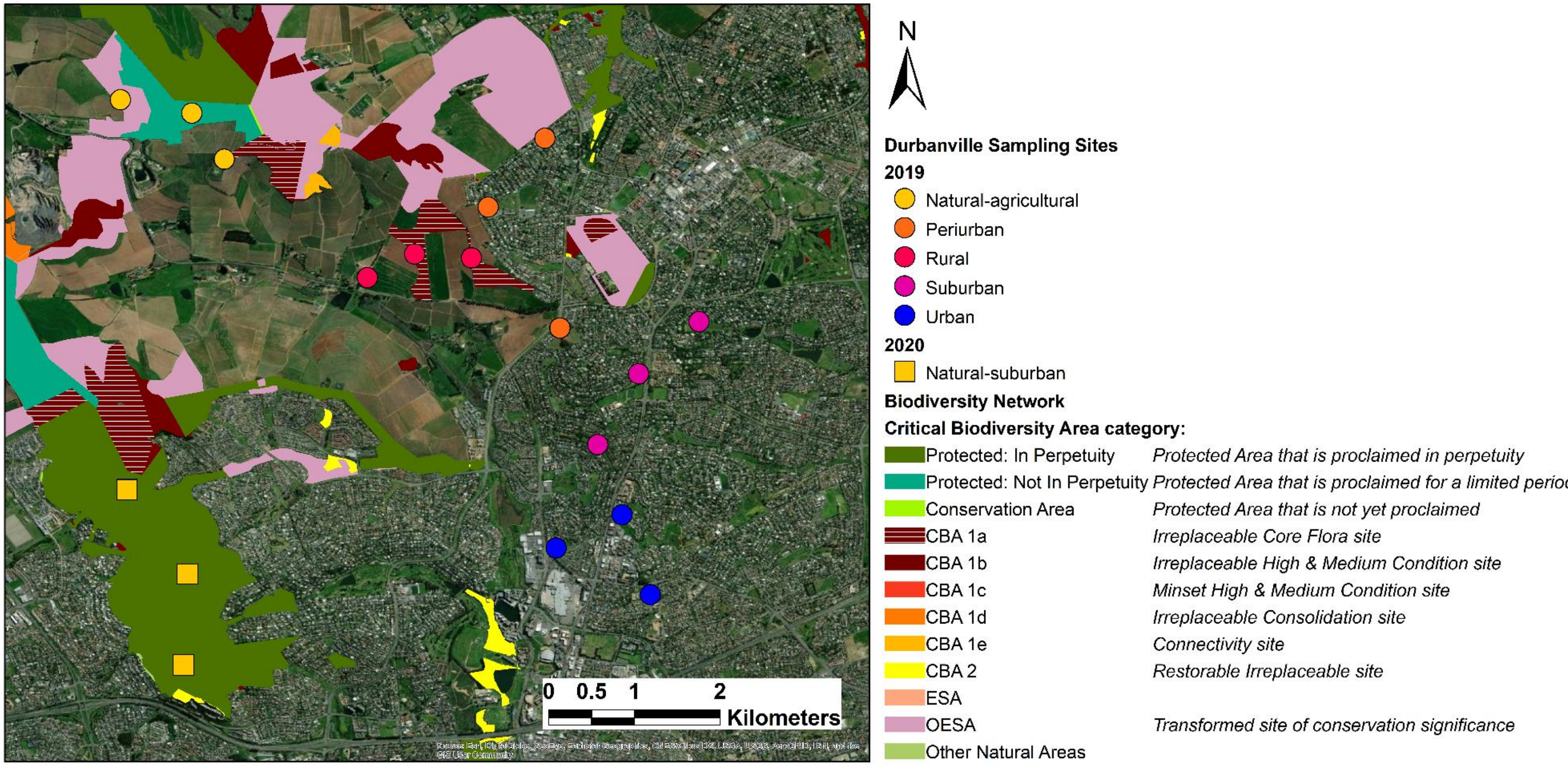

Figure A. Map showing the critical biodiversity network structure in the Durbanville area of Cape Town.

APPENDIX B. Morphospecies reference papers

Table A. List of morphospecies and reference papers used for identification and to obtain ecological information/information on their biology.

Morphospecies	Reference papers
Bees:	
Afranthidium cf. *concolor*	Michener (2007); Eardley et al. (2010); Gess & Gess (2014); Litman et al. (2016)
Afranthidium sp. 2	Michener (2007); Eardley et al. (2010); Gess & Gess (2014); Litman et al. (2016)
Afroheriades sp. 1-2	Michener (2007); Eardley et al. (2010); Gess & Gess (2014)
Allodapula cf. *variegata*	Michener (1975); Eardley et al. (2010)
Amegilla sp.	Eardley et al. (2010)
Andrena cf. *notophila*	Eardley (2006); Michener (2007); Eardley et al., 2010)
Apis mellifera	Eardley et al. (2010)
Ceratina sp. 1-4	Eardley & Daly (2007); Eardley et al. (2010)
Ceylalictus cf. *halictoides*	Pesenko & Pauly (2005); Eardley et al. (2010)
Hoplitis sp. 1-2	Michener (2007); Eardley et al. (2010); Gess & Gess (2014)
Lasioglossum sp. 1-4	Eardley et al. (2010); Gess & Gess (2014)
Lipotriches sp.	Eardley et al. (2010); Gess & Gess (2014)
Nomioides cf. *maculiventris*	Pesenko & Pauly (2005); Eardley et al. (2010)
Othinosmia sp. 1-2	Michener (2007); Eardley et al. (2010); Gess & Gess (2014)
Patellapis sp. 1-3	Timmermann & Kuhlmann (2008a,b); Timmermann & Kuhlmann (2009); Eardley et al. (2010); Gess & Gess (2014)
Scrapter sp. 1-7	Eardley (1996); Eardley et al. (2010); Gess & Gess (2014)
Seladonia sp. 1-3	Eardley et al. (2010); Gess & Gess (2014)
Sphecodes sp.	Eardley et al. (2010); Gess & Gess (2014)
Sphecodopsis sp. 1-5	Eardley et al. (2010); Gess & Gess (2014)
Stenoheriades sp.	Michener (2007); Eardley et al. (2010); Gess & Gess (2014); Müller & Trunz (2014)
Tetraloniella sp.	Eardley et al. (2010)
Wainia sp.	Michener (2007); Eardley et al. (2010); Gess & Gess (2014)
Wasps:	
Aphidiinae sp. 1-2	van Noort (2021)
Campopleginae sp.	van Noort (2021)
Celonites sp. 1-2	Gess & Gess (2014); van Noort (2021)
Chalcididae sp.	Gess & Gess (2014); van Noort (2021)
Chrysidinae sp. 1-2	Gess & Gess (2014); van Noort (2021)
Coptera sp.	van Noort (2021)
Dryinidae sp.	van Noort (2021)
Encyrtidae sp. 1-2	Gess & Gess (2014); van Noort (2021)
Enicospilus sp.	van Noort (2021)

Morphospecies	**Reference papers**
Heliconinae sp.	van Noort (2021)
Larra sp. 1-2	Bohart & Menke (1976); Gess & Gess (2014); van Noort (2021)
Liris sp.	Bohart & Menke (1976); Gess & Gess (2014); van Noort (2021)
Macrocentrus sp.	van Noort (2021)
Mymaridae sp.	Gess & Gess (2014); van Noort (2021)
Oraseminae sp.	Gess & Gess (2014); van Noort (2021)
Pompilidae sp. 1-2	Gess & Gess (2014); van Noort (2021)
Quartinia sp.	Gess & Gess (2014)
Syzeuctus sp.	van Noort (2021)
Tiphia sp.	Gess & Gess (2014); van Noort (2021)

APPENDIX C. Morphospecies metadata

Table B. Morphospecies metadata. * = parasitic wasp species (here, parasitic is a catch-all term for multiple forms of parasitism including endoparasites, ectoparasites, and parasitoids); [R] = rare/uncommon

Morphospecies	Subfamily	Genus	Species	Sex	Nesting guild	Sociality	Feeding	Total Abundance
BEES:								
Andrenidae								
Andrena cf. *notophila*	Andreninae	*Andrena*	*notophila*	f	ground	solitary	Pol	32
Halictidae								
Lasioglossum sp. 1[R]	Halictinae	*Lasioglossum*	U	f	ground	solitary	Pol	2
Lasioglossum sp. 2[R]	Halictinae	*Lasioglossum*	U	f	ground	solitary	Pol	5
Lasioglossum sp. 3[R]	Halictinae	*Lasioglossum*	U	f	ground	solitary	Pol	5
Lasioglossum sp. 4	Halictinae	*Lasioglossum*	U	f	ground	solitary	Pol	14
Patellapis sp. 1[R]	Halictinae	*Patellapis*	U	f	ground	solitary	Pol	2
Patellapis sp. 2	Halictinae	*Patellapis*	U	f	ground	solitary	Pol	50
Patellapis sp. 3[R]	Halictinae	*Patellapis*	U	m	ground	solitary	Pol	2
Seladonia sp. 1	Halictinae	*Seladonia*	U	f	ground	solitary	Pol	72
Seladonia sp. 2	Halictinae	*Seladonia*	U	f	ground	solitary	Pol	44
Seladonia sp. 3[R]	Halictinae	*Seladonia*	U	m	ground	solitary	Pol	2
Sphecodes sp.[R]	Halictinae	*Sphecodes*	U	f	ground	solitary	Clep	1
Lipotriches sp.[R]	Nomiinae	*Lipotriches*	U	m	ground	solitary	Pol	1
Ceylalictus cf. *halictoides*[R]	Nomioidinae	*Ceylalictus*	*halictoides*	f	ground	solitary	Pol	1
Nomioides cf. *maculiventris*	Nomioidinae	*Nomioides*	*maculiventris*	f	ground	solitary	Pol	57
Apidae								
Amegilla sp.[R]	Apinae	*Amegilla*	U	f	ground	solitary	Pol	1
Apis mellifera	Apinae	*Apis*	*mellifera*	f	cavity	SHP	Pol	53
Tetraloniella sp.[R]	Apinae	*Tetraloniella*	U	m	ground	solitary	Pol	1
Sphecodopsis sp. 1[R]	Nomadinae	*Sphecodopsis*	U	f	ground	solitary	Clep	1
Sphecodopsis sp. 2[R]	Nomadinae	*Sphecodopsis*	U	f	ground	solitary	Clep	1
Sphecodopsis sp. 3[R]	Nomadinae	*Sphecodopsis*	U	f	ground	solitary	Clep	1

Morphospecies	Subfamily	Genus	Species	Sex	Nesting guild	Sociality	Feeding	Total Abundance
Sphecodopsis sp. 4[R]	Nomadinae	*Sphecodopsis*	U	m	ground	solitary	Clep	2
Sphecodopsis sp. 5[R]	Nomadinae	*Sphecodopsis*	U	m	ground	solitary	Clep	2
Allodapula cf. *variegata*[R]	Xylocopinae	*Allodapula*	*variegata*	f	cavity	solitary	Pol	2
Ceratina sp. 1[R]	Xylocopinae	*Ceratina*	U	f	cavity	solitary	Pol	2
Ceratina sp. 2[R]	Xylocopinae	*Ceratina*	U	f	cavity	solitary	Pol	2
Ceratina sp. 3[R]	Xylocopinae	*Ceratina*	U	f	cavity	solitary	Pol	1
Ceratina sp. 4[R]	Xylocopinae	*Ceratina*	U	m	cavity	solitary	Pol	2
Megachilidae								
Afranthidium cf. *concolor*	Megachilinae	*Afranthidium*	*concolor*	f	ground (carder)	solitary	Pol	22
Afranthidium sp. 2	Megachilinae	*Afranthidium*	U	m	carder	solitary	Pol	29
Afroheriades sp. 1[R]	Megachilinae	*Afroheriades*	U	f	D/R	solitary	Pol	2
Afroheriades sp. 2[R]	Megachilinae	*Afroheriades*	U	m	D/R	solitary	Pol	1
Hoplitis sp. 1[R]	Megachilinae	*Hoplitis*	U	f	ground	solitary	Pol	2
Hoplitis sp. 2[R]	Megachilinae	*Hoplitis*	U	f	ground	solitary	Pol	3
Othinosmia sp. 1[R]	Megachilinae	*Othinosmia*	U	m	D/R	solitary	Pol	2
Othinosmia sp. 2[R]	Megachilinae	*Othinosmia*	U	m	D/R	solitary	Pol	1
Stenoheriades sp.[R]	Megachilinae	*Stenoheriades*	U	f	cavity	solitary	Pol	1
Wainia sp.[R]	Megachilinae	*Wainia*	U	f	D/R	solitary	Pol	1
Colletidae								
Scrapter sp. 1[R]	Colletinae	*Scrapter*	U	f	ground	solitary	Pol	1
Scrapter sp. 2	Colletinae	*Scrapter*	U	f	ground	solitary	Pol	9
Scrapter sp. 3[R]	Colletinae	*Scrapter*	U	f	ground	solitary	Pol	1
Scrapter sp. 4[R]	Colletinae	*Scrapter*	U	f	ground	solitary	Pol	1
Scrapter sp. 5[R]	Colletinae	*Scrapter*	U	f	ground	solitary	Pol	1
Scrapter sp. 6[R]	Colletinae	*Scrapter*	U	m	ground	solitary	Pol	1
Scrapter sp. 7[R]	Colletinae	*Scrapter*	U	m	ground	solitary	Pol	4
						Total abundance:		**443**

Morphospecies	Subfamily	Genus	Species	Sex	Nesting guild	Sociality	Feeding	Total Abundance
WASPS:								
Crabronidae								
Dryudella sp.*[R]	Astatinae	*Dryudella*	U	U	ground	U	U	1
Larra sp. 1*[R]	Crabroninae	*Larra*	U	U	ground	solitary	U	1
Larra sp. 2*[R]	Crabroninae	*Larra*	U	U	ground	solitary	U	1
Liris sp.*[R]	Crabroninae	*Liris*	U	U	ground	solitary	U	2
Crabronidae sp.*[R]	U	U	U	U	U	solitary	U	1
Chalcididae								
Chalcididae sp.*[R]	U	U	U	U	U	U	U	1
Encyrtidae								
Encyrtidae sp. 1*[R]	U	U	U	U	U	U	U	1
Encyrtidae sp. 2*[R]	U	U	U	U	U	U	U	1
Eucharitidae								
Oraseminae sp.*[R]	Oraseminae	U	U	U	U	U	U	1
Mymaridae								
Mymaridae sp.*[R]	U	U	U	U	U	U	U	1
Chrysididae								
Chrysidinae sp. 1*[R]	Chrysidinae	U	U	U	U	U	U	2
Chrysidinae sp. 2*[R]	Chrysidinae	U	U	U	U	U	U	1
Dryinidae								
Dryinidae sp.*[R]	U	U	U	U	U	U	U	1
Diapriidae								
Coptera sp.*[R]	Diapriinae	*Coptera*	U	U	U	U	U	2
Braconidae								
Aphidiinae sp. 1*[R]	Aphidiinae	U	U	U	U	solitary	U	1
Aphidiinae sp. 2*[R]	Aphidiinae	U	U	U	U	solitary	U	1
Heliconinae sp.*[R]	Helconinae	U	U	U	U	U	U	1
Macrocentrus sp.*[R]	Macrocentrinae	*Macrocentrus*	U	U	U	solitary	U	1

Morphospecies	Subfamily	Genus	Species	Sex	Nesting guild	Sociality	Feeding	Total Abundance
Ichneumonidae								
Syzeuctus sp.*	Banchinae	*Syzeuctus*	U	U	U	U	U	10
Campopleginae sp.*R	Campopleginae	U	U	U	U	U	U	1
Enicospilus sp.*R	Ophioninae	*Enicospilus*	U	U	U	U	U	1
Pompilidae								
Pompilidae sp. 1*R	U	U	U	U	U	U	U	1
Pompilidae sp. 2*R	U	U	U	U	U	U	U	1
Tiphiidae								
Tiphia sp.*R	U	*Tiphia*	U	U	U	U	U	1
Vespidae								
Celonites sp. 1R	Masarinae	*Celonites*	U	U	ground	U	Pol	4
Celonites sp. 2R	Masarinae	*Celonites*	U	U	ground	U	Pol	4
Quartinia sp.R	Masarinae	*Quartinia*	U	U	ground	U	Pol	1
							Total abundance:	**45**

Key:

D/R – dauber/resin

Clep - Cleptoparasitic

Pol – collect pollen from flowers

SHP – social honey producers

f/m – female/male

U – unknown

APPENDIX D. Confusion matrices and model output

Table C: Confusion matrix for the model training set.

		Predicted values					
		Cultivated	**Impervious**	**Natural Vegetation**	**Trees**	**Urban Vegetation**	**Waterbody**
Actual values	**Cultivated**	28	0	0	1	1	0
	Impervious	0	94	0	0	0	0
	Natural Vegetation	0	0	17	3	0	0
	Trees	0	0	0	45	0	0
	Urban Vegetation	0	0	1	0	39	0
	Waterbody	0	1	0	1	0	18

Table D. Confusion matrix for the validation set.

		Predicted values					
		Cultivated	**Impervious**	**Natural Vegetation**	**Trees**	**Urban Vegetation**	**Waterbody**
Actual values	**Cultivated**	8	2	0	0	0	0
	Impervious	0	10	0	0	0	0
	Natural Vegetation	0	0	7	3	0	0
	Trees	1	0	1	8	0	0
	Urban Vegetation	4	3	0	1	2	0
	Waterbody	0	0	0	0	0	10

Table E. Proportion (%) of impervious surfaces and vegetation found within a 500m radius around each of the sampling sites. The mean proportion per zones is also given. Note: impervious surface represents the proportion of built up or developed area surrounding the sampling sites, this may be in the form of buildings, roads, or any other kind of impervious surface; vegetation is assumed to represent the proportion of available above and below ground space available to bees and wasps for nesting and resource acquisition.

Sample	Zone	Impervious Surface (%)	Vegetation (%)	Mean Impervious Surface (%)	Mean Vegetation (%)
DUR_UR_1	Urban	64	36	70.3	29.3
DUR_UR_2		72	27		
DUR_UR_3		75	25		
DUR_SU_1	Suburban	47	53	45.3	54.7
DUR_SU_2		48	52		
DUR_SU_3		41	59		
DUR_PU_1	Peri-urban	32	68	41	59
DUR_PU_2		51	49		
DUR_PU_3		40	60		
DUR_RU_1	Rural	7	91	7.7	91.7
DUR_RU_2		2	98		
DUR_RU_3		14	86		
DUR_NA_1	Natural-Rural	6	94	4	96
DUR_NA_2		2	98		
DUR_NA_3		4	96		
TYG_NA_1	Natural-Suburban	18	82	10	90
TYG_NA_2		7	93		
TYG_NA_3		5	95		

APPENDIX E. CSAG rainfall data, early-/late-spring comparison, and additional model outputs

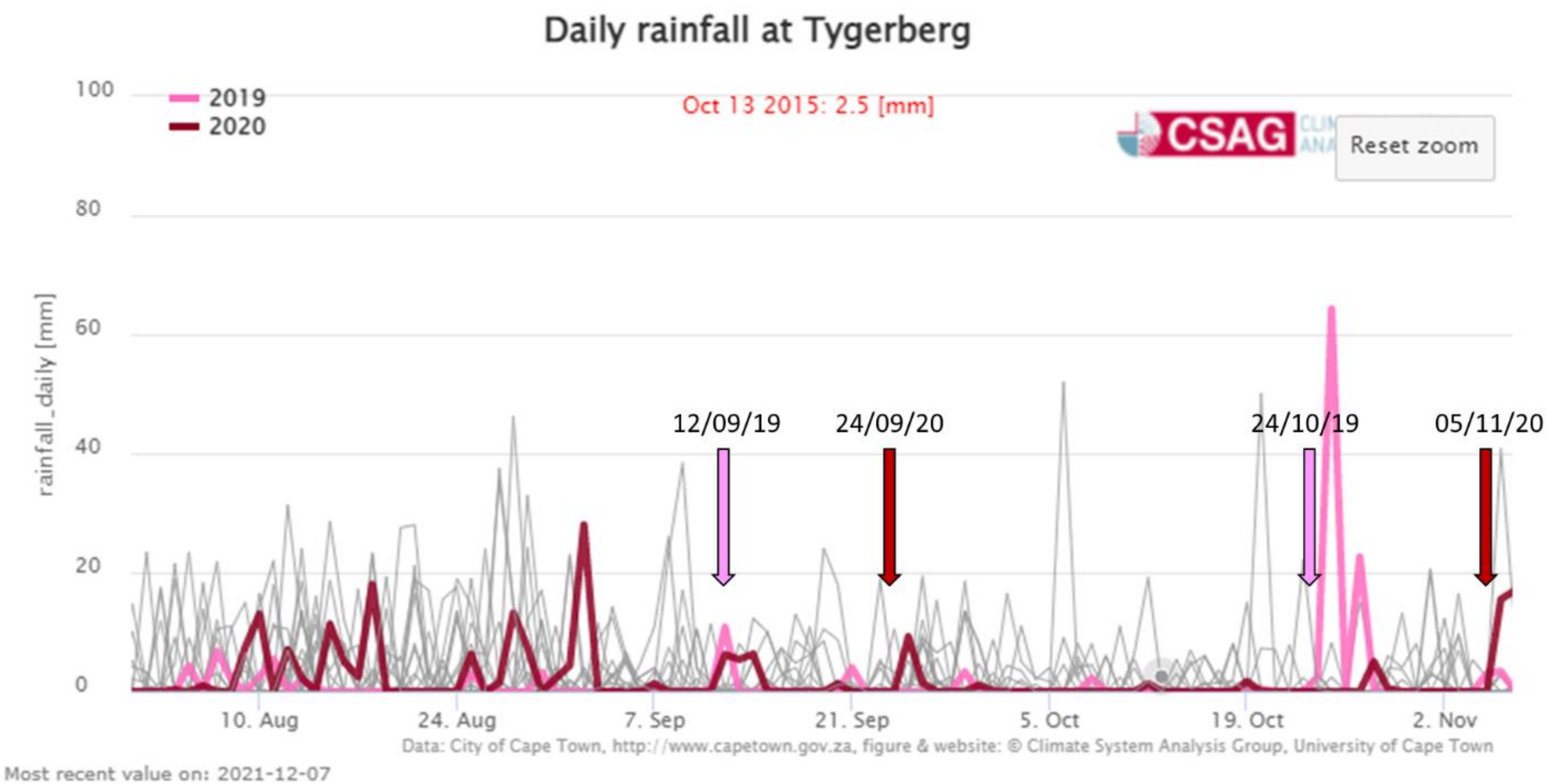

Figure B. Daily rainfall (mm) measured at Tygerberg weather station between 01/08 and 06/11 in 2019 (pink line) and 2020 (red line). The arrows indicate when each sampling event occurred (pink, 2019: 12/09 and 24/10; red, 2020: 24/09 and 05/11. Note: the grey lines represent daily rainfall from previous years. The base figure was obtained from the CSAG website: https://www.csag.uct.ac.za/current-seasons-rainfall-in-cape-town/.

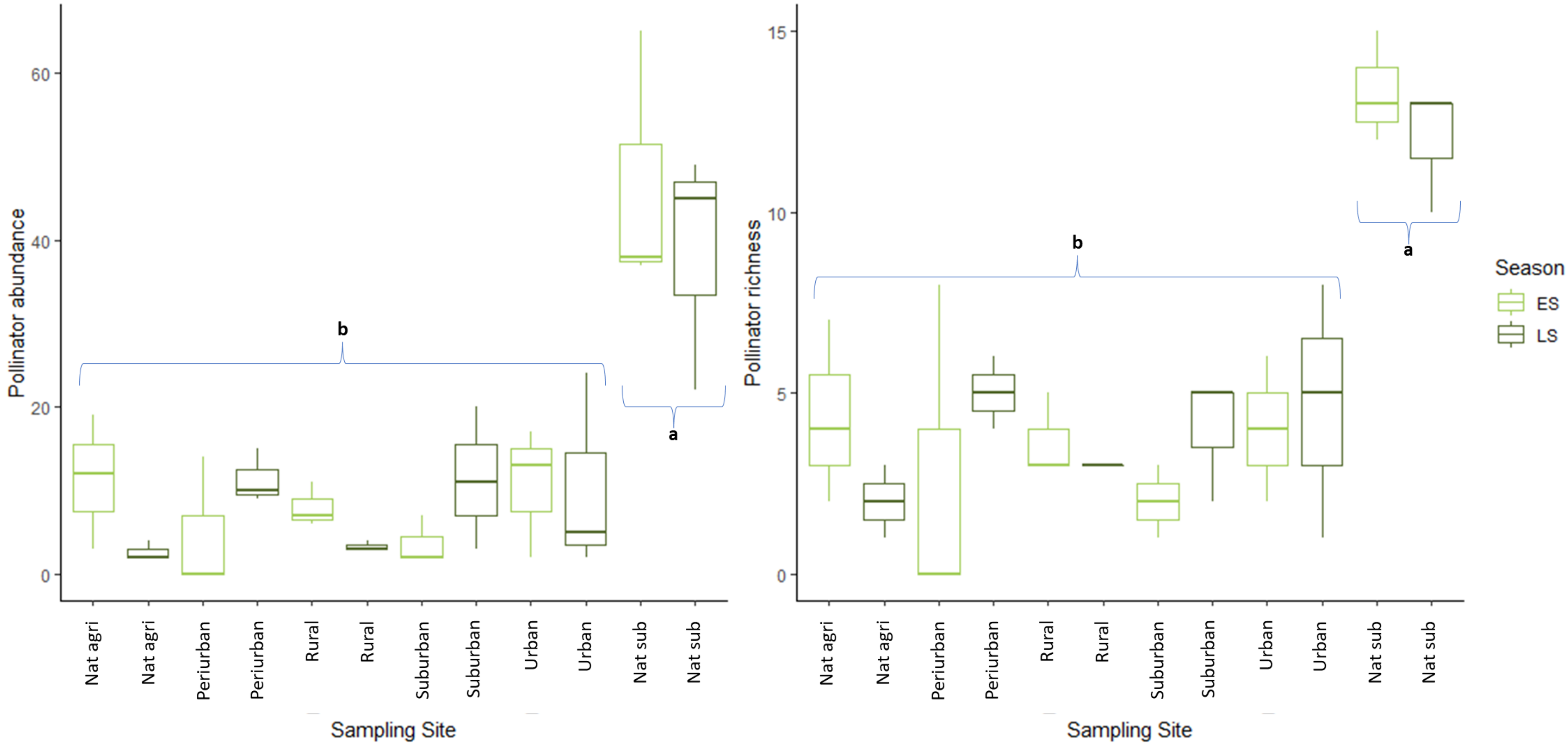

Figure C. Pollinator abundance (A), and species richness (B) across all urban zones based on sites sampled in the Durbanville area, Cape Town, during early spring (ES) and late spring (LS). The letters above/below each boxplot indicate the results of ANOVA and post-hoc Tukey tests.

Table F. Results from general linear models run for all pollinator community and nesting guild response variables with the best fit explanatory variables, using data from sites sampled in 2019 only. These best fit models were selected using a backwards selection approach, starting with impervious surface (%), floral abundance, floral richness, floral evenness, and floral Shannon-Weiner exponent response variables. Note: indices such as floral evenness are scaled between 0-1, whereas floral abundance is scaled between 0-2222, which makes it hard to compare the estimates in the final best fit model summary. Therefore, floral abundance was calculated as floral abundance/maximum abundance (which changes the scale to between 0-1). This does not affect the p-values, t-values, multiple R^2, F-statistic or DF. Also note: ESI = exponent of Shannon-Weiner index, ISI = inverse Simpson index. Significance codes for p-values: *** = p<0.001, ** = p<0.01, * = p<0.05.

	Pollinator response variables	Explanatory variables	Adjusted R^2	F-statistic	DF	Estimate	Std error	t-value	p-value
	Community level models								
1)	Species richness	Floral abundance	-0.073	0.521	2&12	-1.147	3.352	-0.342	0.738
		Floral evenness				2.454	5.425	0.452	0.659
2)	Species abundance (log10(x+1))	Floral abundance	0.184	2.573	2&12	-0.317	0.349	-0.910	0.3806
		Floral evenness				0.484	0.564	0.859	0.4074
3)	Diversity (ESI)	Floral diversity (ESI)	0.057	1.841	1&13	-0.320	0.236	-1.357	0.197928
4)	Diversity (ISI)	Floral diversity (ESI)	0.134	3.157	1&13	-0.347	0.195	-1.777	0.098997
5)	Evenness (J')	**Floral richness**	0.587	10.940	2&12	**0.024**	**0.007**	**3.182**	**
		Floral diversity (ESI)				**-0.071**	**0.015**	**-4.660**	***
	Functional group models								
	Nesting guild:								
6)	Diversity (ESI)	Impervious surface (%)	0.688	11.300	3&11	-0.004	0.002	-2.084	0.061293
		Floral abundance				**0.900**	**0.194**	**4.645**	***
		Floral richness				**-0.043**	**0.014**	**-2.964**	*
7)	Diversity (ISI)	Impervious surface (%)	0.610	8.289	3&11	-0.004	0.002	-1.859	0.08989
		Floral abundance				**0.758**	**0.190**	**3.987**	**
		Floral richness				**-0.034**	**0.014**	**-2.413**	*
	Ground nesters:								
8)	Species richness	Floral diversity (ESI)	0.120	1.954	2&12	-0.628	0.359	-1.749	0.1059
		Floral evenness				7.833	4.131	1.896	0.0823
9)	Species abundance (log10(x+1))	**Floral diversity (ESI)**	0.305	4.070	2&12	**-0.153**	**0.059**	**-2.584**	*
		Floral evenness				**1.831**	**0.679**	**2.695**	*

	Pollinator response variables	Explanatory variables	Adjusted R^2	F-statistic	DF	Estimate	Std error	t-value	p-value
10)	Diversity (ESI)	Floral abundance	0.105	1.824	2&12	-2.616	1.480	-1.768	0.1024
		Floral diversity (ESI)				-0.287	0.208	-1.379	0.19317
11)	Diversity (ISI)	Floral abundance	0.091	1.698	2&12	-0.857	0.467	-1.835	0.09135
		Floral evenness				-1.054	0.756	-1.394	0.18851

For both Table F above and Table G below the coloured cells indicate the following:

(green)	Similarities between Table F and Table G
(orange)	Differences between Table F and Table G
(grey)	Where there is an extra explanatory variable present in one or other of the models

Note: This colour coordination was only done for the seven best fit models (models 1, 2, 5, 6-9) which had identical or near-identical explanatory variables.

Also note: in Table F, models 12-14 are not present because there were too few pollinator specimens to make these analyses meaningful.

Table G. Results from general linear models run for all pollinator community and nesting guild response variables with the best fit explanatory variables, using data from the sites sampled in 2019 and the sites sampled in 2020. These best fit models were selected using a backwards selection approach, starting with impervious surface (%), floral abundance, floral richness, floral evenness, and floral Shannon-Weiner exponent response variables. Note: indices such as floral evenness are scaled between 0-1, whereas floral abundance is scaled between 0-2222, which makes it hard to compare the estimates in the final best fit model summary. Therefore, floral abundance was calculated as floral abundance/maximum abundance (which changes the scale to between 0-1). This does not affect the p-values, t-values, multiple R^2, F-statistic or DF. Also note: ESI = exponent of Shannon-Weiner index, ISI = inverse Simpson index. Significance codes for p-values: *** = p<0.001, ** = p<0.01, * = p<0.05.

	Pollinator response variables	Explanatory variables	Adjusted R^2	F-statistic	DF	Estimate	Std error	t-value	p-value
	Community level models								
1)	Species richness	**Floral abundance**	0.312	4.852	2&15	**17.930**	**6.273**	**2.858**	*
		Floral evenness				**20.518**	**9.010**	**2.277**	*
2)	Species abundance (log10(x+1))	Floral abundance	0.250	3.833	2&15	0.739	0.420	1.760	0.0989
		Floral evenness				**1.605**	**0.603**	**2.663**	*
3)	Diversity (ESI)	**Floral abundance**	0.257	3.937	2&15	**7.522**	**2.694**	**2.792**	*
		Floral evenness				5.300	3.869	1.370	0.1909
4)	Diversity (ISI)	**Floral abundance**	0.175	4.615	1&16	**3.504**	**1.631**	**2.148**	*
5)	Evenness (J')	Floral abundance	0.637	10.930	3&14	-0.189	0.114	-1.661	0.11891
		Floral richness				**0.025**	**0.008**	**3.240**	**
		Floral diversity (ESI)				**-0.084**	**0.015**	**-5.488**	***
	Functional group models								
	Nesting guild:								
6)	Diversity (ESI)	Impervious surface (%)	0.528	10.510	2&15	-0.007	0.004	-1.665	0.1167
		Floral abundance				**1.873**	**0.488**	**3.842**	**
7)	Diversity (ISI)	Impervious surface (%)	0.599	13.710	2&15	-0.005	0.003	-1.686	0.112489
		Floral abundance				**1.431**	**0.317**	**4.509**	***
	Ground-nesters:								
8)	Species richness	Floral abundance	0.120	2.157	2&15	6.073	3.779	1.607	0.1288
		Floral evenness				10.029	5.427	1.848	0.0844

	Pollinator response variables	Explanatory variables	Adjusted R^2	F-statistic	DF	Estimate	Standard error	t-value	p-value
9)	Species abundance (log10(x+1))	Floral evenness	0.054	1.974	1&16	0.956	0.681	1.405	0.179
10)	Diversity (ESI)	Floral evenness	-0.046	0.260	1&16	1.251	2.454	0.510	0.6173
11)	Diversity (ISI)	Floral diversity (ESI)	-0.005	0.908	1&16	-0.136	0.143	-0.953	0.354742
	Cavity-nesters:								
12)	Species richness	**Floral abundance**	0.479	8.810	2&15	**2.982**	**0.742**	**4.019**	**
		Floral diversity (ESI)				0.125	0.082	1.523	0.14845
13)	Species abundance (log10(x+1))	**Floral abundance**	0.609	14.220	2&15	**3.942**	**0.764**	**5.163**	***
		Floral diversity (ESI)				0.147	0.085	1.736	0.102992
14)	Diversity (ESI)	**Floral abundance**	0.604	13.960	2&15	**1.703**	**0.362**	**4.711**	***
		Floral diversity (ESI)				**0.111**	**0.040**	**2.756**	*

APPENDIX F. Species accumulation curves

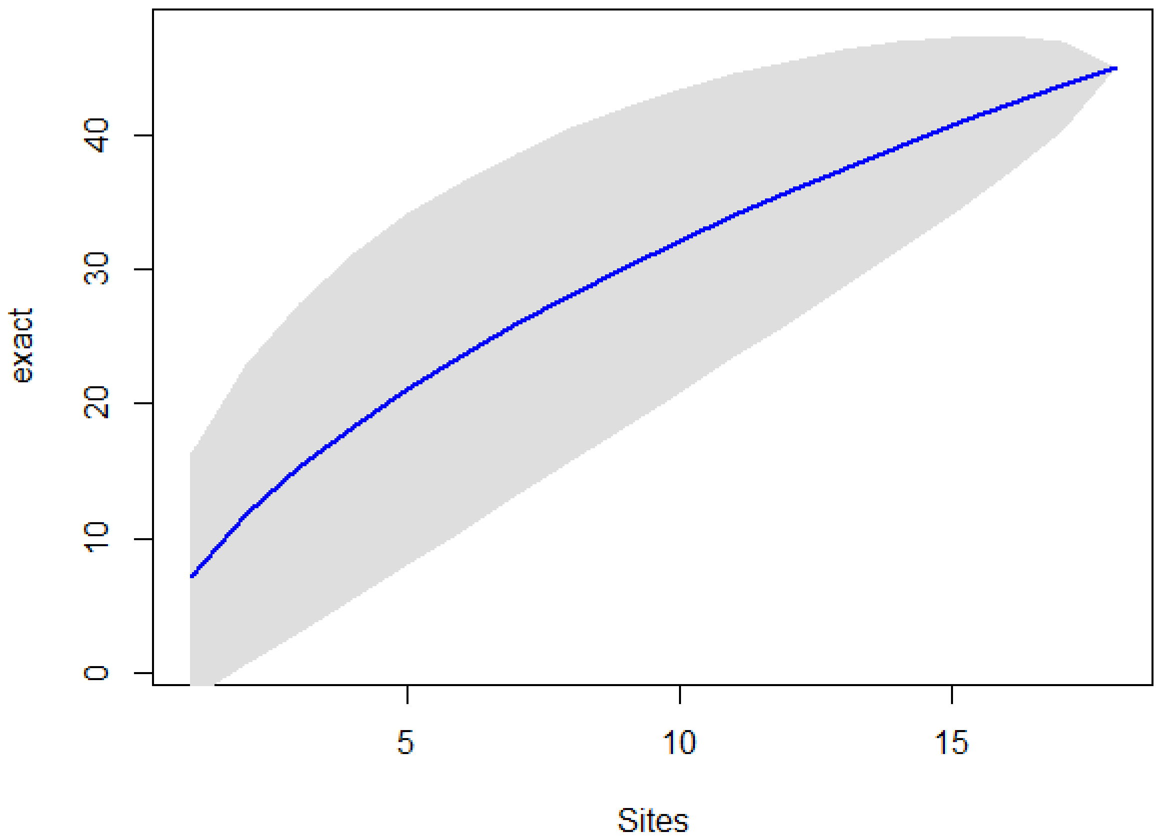

Figure D. Species accumulation curve calculated from the whole sample set.

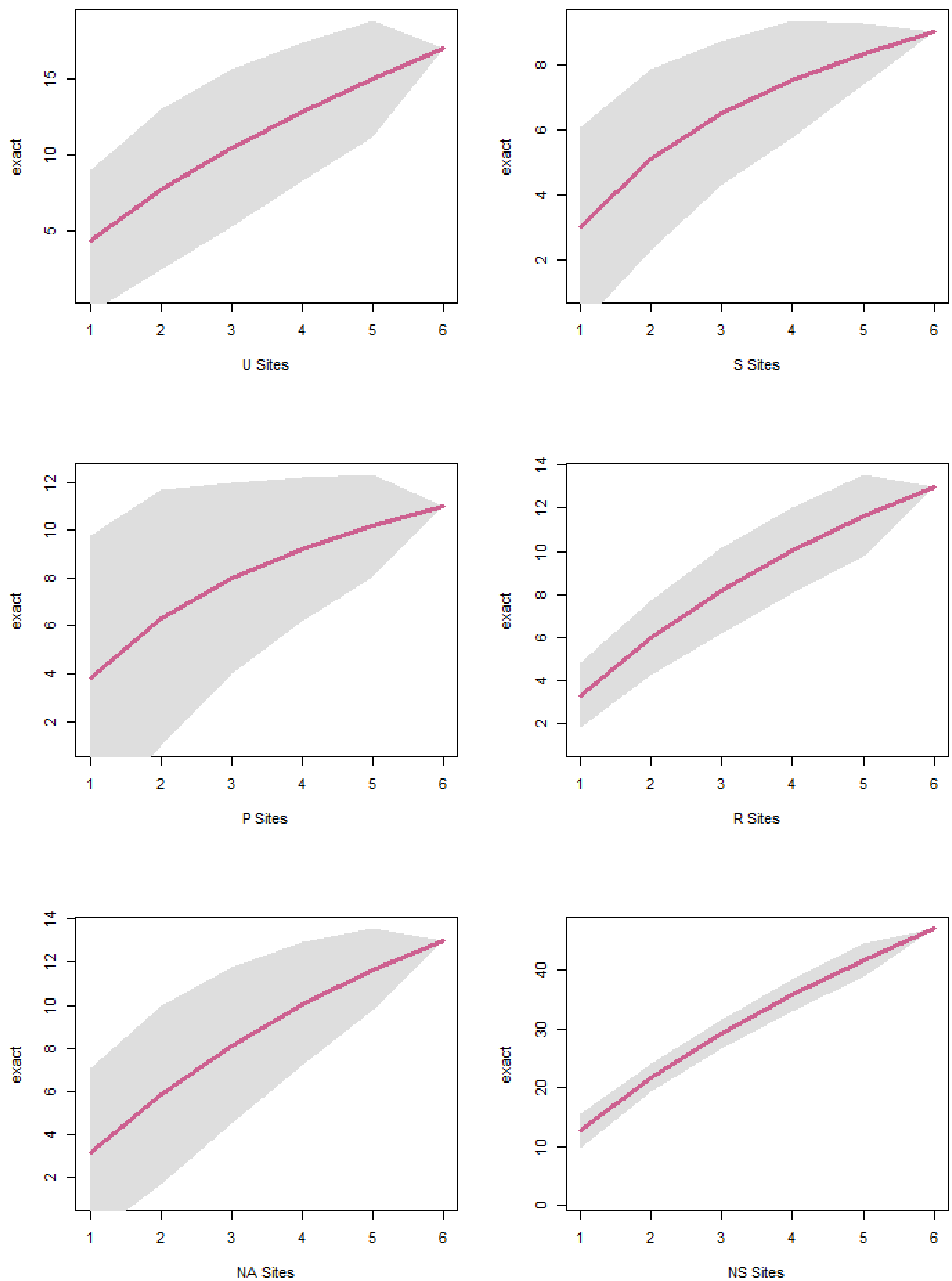

Figure E. Species accumulation curve calculated for each urban zone: urban (U), suburban (S), peri-urban (P), rural (R), natural-agricultural (NA), and natural-suburban (NS) sites.

APPENDIX G. Raw abundance data

Table H. Raw abundance values for all species of bee and wasp across urban (U), suburban (S), peri-urban (P), rural (R), natural-agricultural (NA), and natural-suburban (NS) sites in the Durbanville area, Cape Town. Three sites were sampled within each urban zone.

Urban zone	**U**			**S**			**P**			**R**			**NA**			**NS**		
Repeat	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Bees																		
Afranthidium cf. *concolor*	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	11	7	2
Afranthidium sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	9	4	13
Afroheriades sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Afroheriades sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Allodapula cf. *variegata*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Amegilla sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Andrena cf. *notophila*	4	0	11	0	0	0	0	0	0	0	0	0	9	0	7	1	0	0
Apis mellifera	2	1	2	0	2	2	2	4	5	4	1	4	3	1	2	2	10	6
Ceratina sp. 1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Ceratina sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Ceratina sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ceratina sp. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Ceylalictus cf. *halictoides*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hoplitis sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Hoplitis sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0
Lasioglossum sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Lasioglossum sp. 2	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	1	0	0
Lasioglossum sp. 3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Lasioglossum sp. 4	0	1	0	1	0	2	1	0	1	0	0	1	0	0	0	0	1	6
Lipotriches sp. 1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nomioides cf. *maculiventris*	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	56
Othinosmia sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Othinosmia sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Patellapis sp. 1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Patellapis sp. 2	4	0	11	10	0	14	1	1	3	0	0	0	2	0	1	0	1	2
Patellapis sp. 3	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Scrapter sp. 1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Scrapter sp. 2	0	0	0	0	0	0	0	0	0	1	2	0	1	0	2	0	3	0
Scrapter sp. 3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scrapter sp. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scrapter sp. 5	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Scrapter sp. 6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scrapter sp. 7	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Seladonia sp. 1	0	0	2	2	2	0	3	1	6	4	3	0	0	0	1	15	29	4
Seladonia sp. 2	0	1	7	4	0	2	1	0	3	0	1	1	0	2	0	4	11	7

Urban zone	U			S			P			R			NA			NS		
Repeat	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Seladonia sp. 3	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphecodes sp. 1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Sphecodopsis sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sphecodopsis sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Sphecodopsis sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sphecodopsis sp. 4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphecodopsis sp. 5	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Stenoheriades sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Tetraloniella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Wainia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Wasps																		
Aphidiinae sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Aphidiinae sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Campopleginae sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Celonites sp. 1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0
Celonites sp. 2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0
Chalcididae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Chrysidinae sp. 1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysidinae sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Coptera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Crabronidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Dryinidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Dryudella sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Encyrtidae sp. 1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Encyrtidae sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Enicospilus sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Heliconinae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Larra sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Larra sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Liris sp.	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Macrocentrus sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mymaridae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Oraseminae sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pompilidae sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pompilidae sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Quartinia sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Syzeuctus sp.	0	0	0	0	0	0	0	9	1	0	0	0	0	0	0	0	0	0
Tiphia sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX H. Results from CLUSTER analysis

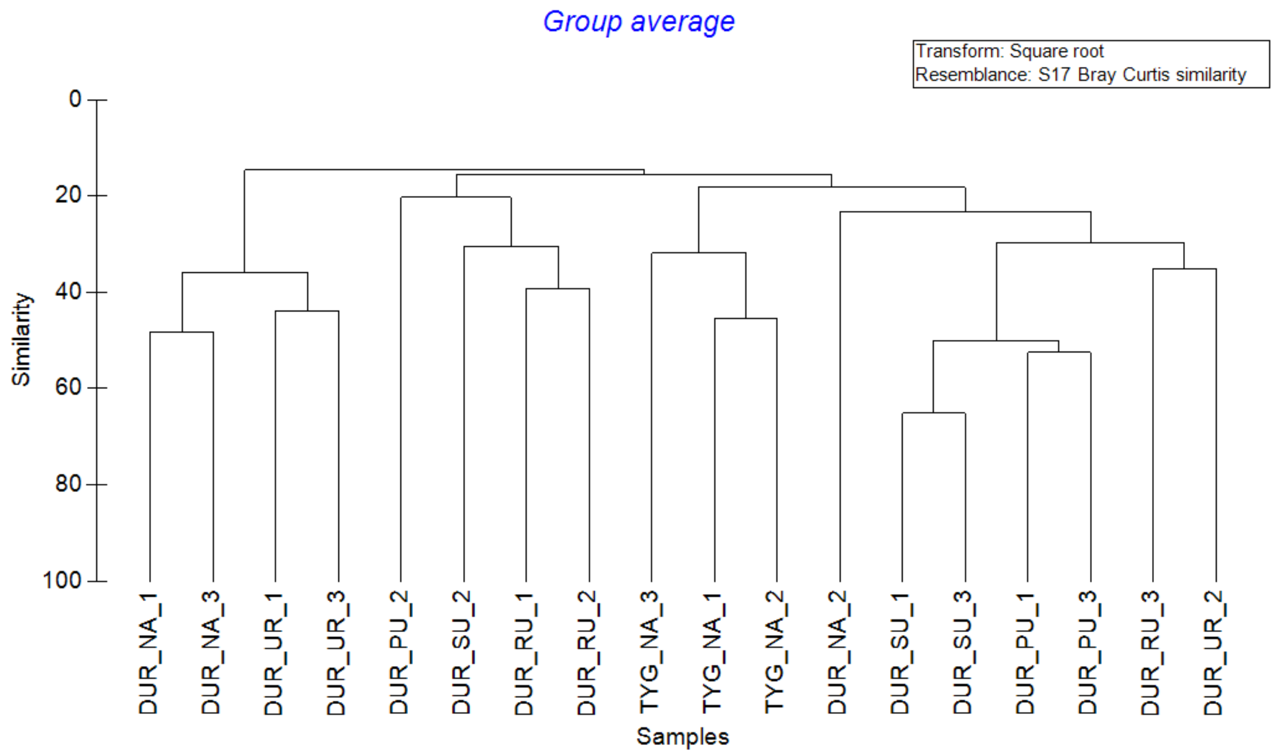

Figure F. Cluster dendrogram for sites NMDS plot (Figure 8 above).

APPENDIX I. Pollinator richness and abundance summary

Table I. Total richness and abundance summaries for all pollinators, *Apis mellifera* only, flowering plants, and percentages for impervious surface and vegetation cover across urban (U), suburban (S), peri-urban (P), rural (R), natural-agricultural (NA), and natural-suburban (NS) sites in the Durbanville area, Cape Town. Three sites were sampled within each urban zone.

Urban zone		**U**			**S**			**P**			**R**			**NA**			**NS**	
Repeat	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Total pollinator richness	6	7	10	5	3	6	6	4	10	7	6	6	10	3	6	22	23	20
Total pollinator abundance	15	7	41	18	5	22	9	15	24	15	9	10	23	5	14	60	86	110
Total *Apis mellifera* abundance	2	1	2	0	2	2	2	4	5	4	1	4	3	1	2	2	10	6
Total floral abundance	139	989	58	431	471	551	385	49	209	522	388	330	466	826	423	2222	495	355
Total floral richness	5	8	4	10	11	12	13	10	7	8	16	18	7	9	9	18	9	17
Impervious surface (%)	64	72	75	47	48	41	32	51	40	7	2	14	6	2	4	18	7	5
Vegetation (%)	36	27	25	53	52	59	68	49	60	91	98	86	94	98	96	82	93	95