Pollination in the Middle East

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Abstract

Pollination networks have traditionally been seen as static, specialised systems. This view has supported the concept of pollination syndromes; the idea that plants evolve particular traits that attract specific pollinator types. However, this view has been challenged in the last few decades as a community level approach has revealed plants are visited by a wide range of taxa. Conversely, xeric environments are rich in oligolectic bee species, suggesting specialism is dominant in this habitat type. This thesis used the Hajar Mountains in Oman as a study site to investigate how visitation networks change temporally and spatially. Specialism appears to be the governing process across all types of flower visitor, not just bee species. However, when a temporal approach is taken, species replacement was extremely high, indicating a constant fluctuation in the composition of the networks in this mountain range, which like in other studies challenges the notions regarding floral syndromes. Species distribution models show a degree of homogenisation in bee communities across the Arabian Peninsula. This contrasts at more local level as seen in the Hajar Mountains. Further studies are now needed to DNA barcode pollen loads from bee specimens collected during the study and region as a whole. This would allow a clearer understanding of network dynamics and help clarify whether the observed specialism seen in this study reflects evolutionary specialism or simply floral constancy.

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Contents

Chapter 1.

General introduction: The importance of studying pollination networks

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Understanding how pollination networks are structured in terms of the levels of generalisation vs. specialisation of insect visitors and their associated plant species is a keystone area of research in evolutionary biology. Specialised plant-pollinator mutualisms have traditionally been held up as evidence supporting natural selection and coevolution (Mayer et al., 2011). While the evolutionary development of these relationships remains an active area of research (Mayer et al., 2011), the global decline in pollinators (Sánchez-Bayo & Wyckhuys, 2019) adds urgency to the need to understand how networks operate in a structural sense. This allows improved predictions to be made of how factors such as pesticides, global warming or habitat fragmentation might affect the collapse of networks (Memmott, 2007; Mayer et al., 2011).

A belief in specialisation within mutualistic interactions has a long history in pollination biology, stretching back to the first observations of proto-biologists such as Aristotle (Darwin, 1876). This belief in tightly linked mutualisms carried through the early years of the true study of pollination. It started at the beginning of the 18th century, first with the recognition by Johann Gottlieb Gleditsch and Philip Miller that insects transferred pollen, followed by the pioneering work of Kölreuter (Olby, 1985) and Sprengel (Waser, 2006). This led to Faegri & Pijl's (1966) description of floral syndromes based on Delpino's earlier 'adaptational groups' (Ollerton & Watts, 2000) and the later work of Vogel (1954).

As demonstrated by Brosi (2016), towards the end of the 20th century two key papers by Jordano (1987) and Waser et al (1996) recognised that at a community level, generalisation in the visitation habits of pollinators is far more common than specialisation. Although rare and geographically more frequent in the tropics, specialisation amongst pollinators does exist across a broad range of taxa, e.g. bats and carrion flies are examples of highly specialised pollinators (Ollerton & Watts, 2000). Evidence suggests that rather than pollinators showing a strict dichotomy of either specialised or generalised visitation habits, species exist along a continuum between the two (Waser, 2006). A small minority of specialist pollinators interact with specialist plants, while the remainder interact with generalists of varying degrees (Vazquez & Aizen, 2004; Chacoff et al., 2012), creating a generally asymmetric pattern to networks (Bascompte et al., 2003). These papers shifted attention away from seeing pollinators as innately predisposed to specialise on one plant species or genus, as represented by Stebbins' (1970) "most effective pollinator" principle of angiosperm evolution. Stebbins' (1970) view was epitomized by the statement '*The characteristics of the flower will be moulded by those pollinators that visit it most frequently and effectively in the region where it is evolving*'. This is more or less the same view held by Darwin just over a hundred years earlier: '*We thus see that the structure of the flowers of*

Orchids and that of the insects which habitually visit them, are correlated in an interesting manner (Darwin, 1862)' (quoted in Grant & Grant, 1965).

Thus there has been a shift in our view of pollinator visitation, from narrow (visiting a handful of plant taxa) to broad, recognising that across populations, plants are visited by a diverse range of animal visitors. Constancy within pollinator individuals or across populations is variable in time and space, a function of resource abundance, as well as other factors (Schiestl & Johnson, 2013). This viewpoint creates a challenge within pollination biology. While an ever-greater number of pollination network studies reveals a diversity of insect visitors to flowers, the physical traits of plants and pollinators suggest specialisation (Amaya-Márquez, 2009).

Although support for the existence of floral syndromes has by no means been abandoned (Fenster et al., 2004; Fenster et al., 2009; Willmer, 2011), criticism of floral syndromes is now mainstream (Ollerton, 2007), and in fact was present from early on in the history of pollination biology. As highlighted by Waser et al (2011), the botanist Hermann Müller (1829-1883), a contemporary of and correspondent with Delpino, attacked belief in adaptational groups/floral syndromes as being teleological. Mayr (1988) has described this type of teleology as 'cosmic teleology', meaning a belief that observed phenomena are not created by natural mechanisms but instead governed by set of laws that lead to perfection determined by a God. While work on floral syndromes since Delpino does not require a belief in teleology, discussion of syndromes can become typological, referring to certain flower types as ‘bee' or ‘fly' flowers, for instance. Müller resisted this view by citing the examples of particular flowers that Delpino suggested as purely bee-pollinated; in fact they are also pollinated by syrphid flies. Thus flower phenotypes can attract various types of pollinator (Waser et al., 2011). This criticism is a forerunner of today’s recognition that most pollinators are generalists and will visit a wide range of floral types.

There is an important counter-argument, however. While many species can visit a particular flower, not every species is equally effective in pollination (Rosas-Guerrero et al., 2014). Although many pollinators are generalists, the selection pressures they exert on flower phenotypes are not equal, and can be antagonistic (Thomson, 2003). For instance, ants are regular visitors to flowers, feeding on nectar (Bleil et al., 2011) and to a lesser extent pollen (Czechowski et al., 2011). In addition ants can destroy pollen due to secretions from their metapleural gland (Beattie et al., 1985) and can physically prevent pollinators from accessing flowers (Lach, 2008). Unless they provide other services, such as protection from herbivores (Palmer & Brody, 2007), ants can be detrimental to plant fitness. Consequently some plant species have evolved ant-repellent substances that discourage ants from visiting flowers while they’re producing and receiving pollen (Gonzálvez et al., 2013).

The idea of the existence of different tiers of potential pollinators, based on pollination efficacy, leads to the suggestion that both primary and secondary pollinators can play a role in pollinating a plant. Floral syndromes can evolve due to selection pressure based predominantly on interactions with the primary pollinator (Stebbins 'most effective pollinator'). Other flowers may not preclude secondary pollinators from access and pollination (Rosas-Guerrero et al., 2014). This two-tier scenario is a possible explanation for the supposed levels of generalism seen in visitors to flowers, while still explaining the role that specialisation plays in shaping floral shapes, colours and scents. This in turn may also explain how plant species maintain populations in the face of year-to-year variation in the relative abundance of pollinators (Fantinato et al., 2019) because they can rely on secondary pollinators in seasons when the primary pollinator species is rare or absent.

Community level studies of pollination networks have been conducted for several decades (Elberling & Olesen, 1999), but there is geographical bias because most of them come from temperate (Petanidou & Ellis, 1993), Neotropical (Chacoff et al., 2018) and North American desert environments (Wilson et al., 2009). Middle Eastern habitats remain vastly underrepresented. This bias may have important ramifications because it might mislead us. Pollinators are declining globally (Sánchez-Bayo & Wyckhuys, 2019), but not all are susceptible to the same processes or are declining at the same rate. Due to this bias in where pollinator studies have predominantly been conducted, most examples of pollinator decline come from temperate environments (Williams, 1982; Kosior et al., 2007; Nieto et al., 2014). Nevertheless, the FAO's (2019) recent report cites Oman as an example of where a perceived decline in wild foods (such as berries) is believed to be due to a loss of pollinators. The report proposes this may be due to high temperatures as a result of climate change reducing pollinator populations (FAO, 2019). This reported decline highlights the importance of studying pollination networks globally and across as many ecoregions as possible.

The research described in this thesis was based in the Hajar Mountains, an arid mountain range that runs along the northern coastline of Oman and the United Arab Emirates. It addresses several aspects of pollinator network structure, including the topology across a range of sampling sites, spatio-temporal changes to abundances over three seasons, and the degree to which abiotic factors influence abundances over two years at a single locality.

I first test whether generalisation in pollinators is central to network structure. The melittological literature stresses that xeric habitats, hotspots in bee diversity (Patiny & Michez, 2007), are composed of communities dominated by oligolectic bees (Michener, 2007). Several suggestions have been proposed to explain this abundance of oligolectic bees in desert environments. Solitary, specialised bees tend to nest in the ground, and while flood-prone, tropical soils may be unsuitable, dry, sandy soils provide excellent conditions for establishing nests (Danforth et al., 2019). Additionally a specialised, solitary lifestyle is an appropriate adaptation in an environment where floral resources are often confined to short time frames, dependent on rainfall. Social species that maintain large colonies require a wide range of flowering plants over several months in order to maintain large colonies (Danforth et al., 2019). This lack of social species in xeric habitats can also result in reduced competition for resources, which would benefit oligolectic species. This challenges the contemporary view that generalisation is the dominant type of interaction, the reason why syndromes supposedly cannot evolve.

In the following chapter, I look at how insect populations visiting *Euphorbia larica* change spatially and temporally through three survey periods. Studying a network through time allows a greater understanding of how mutualistic communities are regulated and how floral phenotypes can evolve. It also allows a greater understanding of plant-pollinator interactions, which can guide conservation planning (Burkle & Alarcón, 2011). At a community level, temporal dynamic study of pollinator networks has been neglected (Burkle & Alarcón, 2011) and only relatively recently have been applied to networks to look for seasonal/annual patterns (Olesen et al., 2008; Burkle & Alarcón, 2011; Lucas et al., 2018). This is partially due to the logistical issues and costs of studying whole communities over multiple seasons (Hegland et al., 2009). Spatio-temporal changes to species richness provide vital information on how networks operate, and thus a greater understanding of how they might respond to habitat fragmentation, pesticides and climate change (Dupont et al., 2009).

I explore changes to other diversity measures, both taxonomic and functional, which could explain how pollinators and visitors shape floral phenotypes (Junker et al., 2015).

In the fourth chapter I record the responses of bees to precipitation, investigating whether pulsed events initiate mass emergence from diapause. This part of the study ran for just less than two years at a single locality in the grounds of the Oman Botanic Garden. Studies of xeric-adapted bees have been contradictory about whether bees respond to rainfall. One study suggested that drought influences the abundance of oligolectic species because they remain in diapause to avoid unfavourable years when resources are low (Minckley et al., 2013). However, another study found that bee abundance was high in a drought year, concluding that precipitation did not trigger bee emergence in synchronization with host plants (Mayer & Kuhlmann, 2004).

Finally, I use records from three museum collections to explore the distribution of species across the Middle East (Figure 1). Throughout this study I define the Middle East in its contemporary political sense and therefore include the following countries: Bahrain, Egypt, Iran, Iraq, Israel, Jordan, Kuwait, Lebanon, Oman, Palestine, Qatar, Saudi Arabia, Syria, United Arab Emirates and Yemen. I exclude Turkey (and Cyprus) as although this country contains xeric habitats, it's bee fauna strongly overlaps with northern, Palearctic temperate faunas. As these are unrepresentative of the fauna's found in desert environments that occur across much of the Middle East, it was most straightforward to exclude all of Turkey. Consequently I feel confident when making generalisations regarding the bee communities found in the Middle East. Using species distribution models, I look at how distributions might change with the climate forecast of the HadGEM2-CC Representative Concentration Pathway (RCP) 8.5 for the year 2070. To date only one study (Silva et al., 2018) has looked at how arid-adapted bees might respond to future climate change.

The study site: The Hajar Mountains

The fieldwork was carried out in the Hajar Mountains of northern Oman. This mountain range, reaching a maximum height of ~3000 m (Garcia-Porta, 2017), runs for approximately 700 km (Lippard et al., 1982) through northern Oman and the UAE, ending in Oman's enclave, the Musandam Peninsular. To the north the range is bordered by the Gulf of Oman, and to the south by the sand sea desert of the Sharqiya Sands and extensive hyper arid gravel deserts, areas low in plant diversity but rich in endemic species (Borrell et al., 2019).

The mountains are intercut with wadis and wider depressions such as the Samail and Dibba gaps (Lippard et al., 1982). Most of the plants are clustered within these dry riverbeds. Outside the wadis on rock faces and scree slopes, plant diversity is low, although certain species such as

Euphorbia larica and *Blepharis ciliaris* can tolerate the extremely thin soils (Monks et al., 2019), and as a result can be locally abundant.

The Hajar Mountains are situated between the Indo-Asian and Afro-European phytogeographical regions, and are floristically diverse (El-Keblawy et al., 2016). A potential explanation for this high diversity is the topographic complexity of the mountain range, with the potential for species to become isolated, leading to allopatric or peripatric speciation (Garcia-Porta, 2017). At the highest altitudes of the Jebel Akhdar massif of the Western Hajar, the juniper, *Juniperus seravschanica*, dominates the plant community. This species also occurs in other mountainous areas in Iran and Pakistan (Gardner & Fisher, 1996).

While the flora of Oman is now well documented (Ghazanfar, 1997; Ghazanfar, 1998; Patzelt & Knees, 2014; Borrell et al., 2019), there have been no studies of pollination *per se*, something also true for the Arabian Peninsula as a whole. The bee fauna is believed to be rich (Patiny & Michez, 2007) based on specimens held in museum collections (Baker, 2004), but little is known about community structure or how species are distributed. The scarcity of detailed data on bees is ubiquitous across the Arabian Peninsula, although examples of relevant recent papers includes species lists for the UAE (van Harten, 2009) and the Socotra Archipelago (Straka et al., 2017), a survey of some of the bee visitors to plants within the Dubai Desert Conservation Reserve (Gess & Roosenschoon, 2016), and a series of papers describing new bee records and species found in Saudi

Arabia (Alqarni et al., 2012a; Alqarni et al., 2012b; Alqarni et al., 2013; Engel et al., 2017). A partial explanation for the paucity of studies is the lack of keys to the species. For instance the last key describing the Anthophorini of the region was published in 1957 (Priesner, 1957) and although this taxon forms an important element of the fauna, most collections only hold a few specimens of each species (Engel, 2007). Taxonomy of bees in the Peninsula is held back by these two factors: a lack of specimens and a lack of keys to identify them by.

This thesis aims to improve both the knowledge of bee distributions in the Arabian Peninsula and to improve our understanding of how networks operate in a little studied region.

Figures

Figure 1. Map showing the Middle East. The red rectangle highlights the Hajar Mountains in Oman, where the fieldwork for this study was conducted.


TURKEY
SYRIA
LEBANON
PALESTINE
ISRAEL
JORDAN
IRAQ
IRAN
KUWAIT
BAHRAIN
QATAR
UNITED ARAB EMIRATES
EGYPT
SAUDI ARABIA
OMAN
YEMEN

Fig. 1

Chapter 2.

Does specialisation dominate flower interactions in a xeric visitation network?

Does specialisation dominate flower interactions in a xeric visitation network?

Abstract

The classical view of plant-pollinator interactions is one of close mutualism resulting in pollination syndromes based on shared morphology and/or phylogeny. This view has been contested in the last few decades as community studies have shown pollinators tend to visit a wide range of host plants and thus generalisation is common. Desert pollination networks are relatively unstudied at a community level and so offer an opportunity to test this view especially in the light of the melittology literature, which describes xeric habitats as being particularly rich in oligolectic species of solitary bee. A total of 124 insect and 22 plant species comprised the visitation network. Network architecture was examined for centrality, nestedness and modularity. There appeared to be limited modularity, whereas the network was significantly nested. At the individual level, specialisation comprised the majority of species interactions across all four pollinating groups including Hymenoptera, Diptera, Coleoptera and Lepidoptera. This may suggest generalism within networks is not universal as previously suggested, and outside of temperate systems other network patterns may be more common.

Introduction

The traditional view of plant-pollinator interactions amongst pollination biologists until the end of the 1980s was of one of communities composed of tightly linked mutualists within highly specialised systems (Petanidou & Potts, 2006). Though now recognised as rare, a classic representation of this view is seen in the pollination systems of both invertebrates and vertebrates. For instance, Agaonidae wasps and *Tegeticulla* (Prodoxidae) moths are the only pollinators of the plant genera *Ficus* (Moraceae) and *Yucca* (Asparagaceae) (Kjellberg et al., 1987; Pellmyr et al., 1996). This type of extreme specialisation is also recorded in the relationship between the marsupial *Tarsipes* and species of *Banksia* (Proteaceae) in Australia (Faegri, 1978).

This idea of intense specialisation of pollinators onto one or a few host plants was seen as evidence of the driving force behind the high levels of speciation within the angiosperms through the biotic pollination hypothesis i.e. angiosperm diversity was driven by coevolution with pollinating insects (Gorelick, 2001). Interspecific competition drives flower phenotypes to evolve to attract specific pollinators (Waser, 1998), thus creating pollination syndromes (Fenster et al., 2004). An example used to represent this view is that of species within the genus *Digitalis* evolving isolating mechanisms such as tubular flowers and guard hairs that prevent small, short-tongued bees from entering the flower, and thus the flowers can only be pollinated by a suite of long-tongued bees (O'Toole

& Raw, 1991). Conversely Simonin & Roddy (2018) have suggested an alternative hypothesis of how angiosperm dominance arose in the Cretaceous period. The authors suggest genome downsizing (resulting in smaller but more abundant cells) increased CO_2 uptake and lead to dominance over the-then omnipresent gymnosperms and ferns. This suggests a physiological rather than mutualistic explanation to angiosperm speciation, downplaying the role of syndromes in driving diversification. Gorelick (2001) also highlights the family Formicidae as an example of a species-rich group (~11,700 species: AntWeb, 2018) that plays little role in pollination but has a close association with the angiosperms. He suggests that if flowering plants had caused a co-radiation in insect diversity, groups not involved in pollination should not show high levels of diversification. Instead Hölldobler & Wilson (2009) suggest ant speciation is partly a result of new niche opportunities created by an increased build-up of leaf litter during the Eocene as the angiosperms diversified. While ant species richness may be an indirect result of angiosperm diversity, there is no coevolutionary feedback to further diversification of flowering plants, supporting Gorelick (2001).

Over the last three decades, a different view has developed: that direct specialisation between one plant and one pollinator is extremely rare (Popic et al., 2013). By specialisation, I mean simply that a plant receives only one or a few pollinators/insect visitors within a pool of potential interactions, while generalization is a plant receiving multiple insect visitors (Armbruster, 2006). Thus, I refer to specialisation in terms of *ecological specialisation.*

The view that a few specialised insect visitors drive plant speciation has become more difficult to justify in the context of the community level approach, which has shown generalisation of resource/feeding patterns to be common (Burkle & Alarcon, 2011). Not only is specialisation considered rare, but most recently the idea of temporal dynamicism has been applied to pollination networks (Burkle & Alarcon, 2011). This has revealed that network composition is fluid, with the potential for high species turnover between years (Petanidou et al., 2008), and that pollinator behaviour is plastic (Burkle & Alarcon, 2011). The effects of temporal dynamics on pollinator diversity will be explored further in the next chapter. This view of networks as dynamic, mostly generalised systems contrasts with the views of melittologists in the taxonomic and biogeographic literature, who suggest that the bee fauna found particularly in xeric habitats is predominately composed of oligolectic species (Michener, 2007; Danforth et al., 2019). Bees specialised to a few specific plant species/genera would suggest constancy to specific plant species in a network, which is not what studies including a temporal element suggest.

In order to understand how networks are structured, several approaches can be taken. This includes the calculation of various indices aimed at understanding how nodes (species) are connected within a network, such as connectance, 'links per species' and web asymmetry (Dormann et al., 2009). These give an indication of how specialised or generalised the species are. A further step is the use of null models, allowing an assessment of whether patterns of linkages in networks are random, or in fact controlled by universal mechanisms such as 'nestedness' (Vazquez & Aizen, 2006). Nestedness and modularity are two properties of networks believed to be geographically universal (Martin Gonzalez et al., 2012).

Nestedness is a concept originally used in island biogeography (Atmar & Patterson, 1993), first applied to mutualistic networks by Bascompte et al (2003). In the island scenario, a chain of islands would each contain a smaller subset of the species contained on the nearest island to the mainland. In a highly nested network, the network would contain many specialist insects that only use a subset of the plants that the more generalised insect visitors interact with (Gresty et al., 2018). The more generalist species interact with both specialist and generalist partners and therefore if some of the specialist species are lost, a core of generalist species remain that maintains the interactions necessary to keep a network functioning (Fantinato et al., 2019). This type of pattern is believed to be common in mutualistic networks (Bascompte & Jordano, 2007) and may help create stability within the system and reduce inter-specific competition, allowing a large number of species to coexist (Fantinato et al., 2019).

While nestedness is common, it is not necessarily guaranteed to occur and other patterns may exist. More recently the concept of modularity or compartmentalization (Olesen et al., 2007; Fortuna et al., 2010) has been applied to mutualistic networks, the idea that certain sets of species (of both plants and animals) interact more closely amongst themselves within the network, thus creating compartments or modules (Dicks et al., 2002). Species can still interact with those of other modules, but they show a preference for species within their own module, implying a degree of specialisation. Within the literature these types of species are known as 'hubs', while species connected to several modules are termed 'connectors' (Martin Gonzalez et al., 2012). The idea of compartments comes from work done on food webs in the 1970s and 1980s (May, 1972; Pimm & Lawton, 1980). Membership of compartments is believed to be influenced by phylogenetic relatedness and body size (Martin Gonzalez et al., 2012). This might provide evidence to support the existence of pollination syndromes because, for instance, a module containing mainly Diptera would suggest flies are attracted to particular flower types/shapes/scents evolved to attract them (i.e. fly-flowers). The debate over the existence of pollination syndromes is still not decided (Rosas-Guernero, 2014), and therefore the quantification of modularity offers an opportunity to test pollination networks for such syndromes. If the prediction is true, that oligolecty dominates in the foraging behaviour of solitary bees, then I would expect to see the network highly compartmentalised and composed mostly of hub species with few connectors.

An issue to consider when determining levels of specialisation/generalisation within a community is that the fidelity or flower constancy of an insect to a particular plant may change temporally and spatially in response, for example, to the availability of flowers. Conspecific plants that grow closely together, or individual plants with abundant flowers, may encourage insect fidelity.

Short-term fidelity to a specific flower is a useful adaptation for a pollinator such as a bee. Although pollinator fidelity increases the likelihood of a plant receiving conspecific pollen, it may also be detrimental by raising the risk of geitonogamy (Mitchell et al., 2004). One advantage is that by focusing on a single flower type, the bee is able to forage more efficiently by learning how to handle it, reducing handling times. This is beneficial because their alleged limited cognitive abilities means it is hard to learn to use multiple flower types at the same time (Darwin, 1876; Gegear & Thomson, 2004). This short-term behavioural specialisation should not be confused with true evolutionary specialisation, which prevents a pollinator being able to use other plant species. A good example of this is the total reliance by agaonid fig wasps on *Ficus*, and vice versa. It is more common for a pollinator to vary its use of flower types through the flowering season, depending on current resource availability. For instance, Lucas et al (2018) noted that specialisation of syrphid flies in fen-meadow grasslands in Wales declined through the summer. This was perhaps because of an increase in the number of flowering plants later in the season, which encouraged more generalised feeding behaviour. Surveying solely in the spring would give a false impression of intense specialisation by syrphid flies. Likewise, sampling a network in too few sites at any given time may suggest an intense specialisation by a pollinator that also can be false. Repeated surveys of the same plant assemblage in multiple sites are necessary to record as many possible links between individual plant species and their pollinators.

A final consideration when studying the degree of specialisation within a habitat is how individual plant species are distributed within a habitat. This is because this may also have an important role in influencing the degree of specialisation/ generalisation. Using a population genetic model to examine the evolution of floral phenotypes, Sargent & Otto (2006) suggest that plant species that are abundant within a habitat should evolve floral traits to become generalists, whilst rare or very dispersed plants would evolve to be specialists. When abundant, it is likely that visiting insects are carrying conspecific pollen and so the plant does not need to discriminate among pollinator species, encouraging generalisation (Sargent & Otto, 2006). Plants in desert habitats tend to be clustered into small areas where water is available, such as in wadi beds and alluvial fans (Patzelt, 2015). Such localised abundance could favour a plant community composed of generalists.

Although some studies have investigated the specialisation of bees in the deserts of the southwestern United States (Danforth, 1999; Minckley et al., 2000), mid-latitude deserts remain a relatively under-surveyed region (Chacoff et al., 2012) in terms of processes controlling pollination networks. As xeric environments within this latitudinal band are believed to harbour some of the world's richest oligolectic bee faunas (Michener, 1979a; Michener, 2007), it is important to understand the networks found within these regions. In the deserts of North America, over 60% of bee species are recorded as oligolectic (O'Toole & Raw, 1991), suggesting that specialisation in desert bees is a common adaptation.

While pollen is an important source of carbohydrates for many flower-visiting insects (Willmer, 2011), apart from bees, pollen wasps (Vespidae: Masarinae) and a few species of beetles (Tepedino, 1979), no other plant visitors are totally reliant on pollen to feed their larvae. For example, Bombyliidae regularly visit flowers as adults for nectar, but as larvae are parasitoids of other insects (Yeates & Greathead, 1997). Thus synchronisation and specialisation with a particular plant is not necessary for many insect visitors. In a system where nectar and pollen resources are only available for a short period, generalization appears to be more obviously preferable.

Desert environments thus offer an interesting opportunity to look at the structure of pollination networks. Contemporary thinking regarding networks suggests specialisation is rare. However, the bee literature records xeric habitats, as being particularly rich in oligolectic bees, creating a challenge to the view that generalisation is the dominant force shaping pollination networks.

Study aims

I explore here the topology of the flower visitation network of the lowland areas of the Hajar Mountains of northern Oman, identifying structure in the network for comparison with other networks (Bascompte et al., 2003; Jordano et al., 2006). I ask the following question: *how is the network structured*? From the melittological literature, I predict that oligolectic bees should dominate, creating a highly modularized network. As for the other flower visitors (Coleoptera, Diptera and Lepidoptera), since they collect floral resources for themselves rather than for their offspring, I predict that these species should form the majority of the generalised interactions.

Methods

1. Study Site

The study was conducted in thirteen localities within the lowlands of the Hajar Mountains, northern Oman in March 2018 (see Fig. 1), an arid habitat, rich in plant species diversity (Patzelt & Knees, 2014) but with a short flowering season (Ghazanfar, 1997) peaking in January-March. The study sites fall within the plant communities called ‘open drought *Euphorbia larica-Vachellia tortilis* woodland (northern Oman; 0-450m)’ and the ‘*Euphorbia larica-Moringa peregrina* community (northern Oman; 300-1500m)’ (Patzelt, 2015). These plant communities show considerable overlap in species, and are estimated to contain ~211 and ~133 species, respectively (Patzelt, 2015). The Western Hajar Mountains, the most species rich section of the mountains in terms of plant diversity, contains an estimated 485 species (Patzelt, 2015).

The lowland Hajar Mountains have similar climatic conditions throughout the range, with a mean average temperature of 28.4°C (Patzelt, 2015) although rainfall can be extremely localised. In order to control for climatic variables while assessing the visitation network, I sampled the same plant communities in three different sections of the Hajar Mountains. This included three sites in the Jebel Akhdar range (Western Hajar Mountains), five sites in the Jebel Nakhl range/Samail Gap area, and five sites in the Eastern Hajar Mountains (see Fig. 1). At each site a 50 m x 4 m transect was established. A phytocentric approach to sampling the network was taken. This approach identifies and quantifys species interactions by observing a flower and recording the insects that visit it (Vizentin-Bugoni et al., 2018). Within this transect every flowering plant was recorded. Plants were identified using Ghazanfar (2003), Ghazanfar & Patzelt (2005), and Patzelt (2015).

Each plant was observed for six minutes. Six minutes was chosen as an appropriate time to observe individual plants for two reasons. Firstly as many pollinators appeared to be at low levels of abundance in the environment as a whole, surveying for shorter time periods did not allow enough time for observations to be made as insects were simply missed. However, at certain sites abundance of individual plant species was high. This was an issue as temperatures rose rapidly throughout the morning, which later on may have impacted the flight activity of certain insect species. As only a limited number of plants could be observed accurately at any given time, increasing the observation time beyond six minutes would have meant surveys lasted for too long and the impact that temperature might have on insect activity increased.

Any individual insect that made contact with a flower during these six minutes was recorded. Apart from *Apis mellifera* and *A. florea*, all insect visitors were collected for identification using a hand net. Where possible, insect species were identified to species level, and if not, separated into morpho-species using Goulet & Huber (1993), Michener (2007), and van Harten (2008, 2009, 2010, 2011, 2014, 2017). Identifications were made at the Natural History Museum, London (Hymenoptera), National Museum Wales, Cardiff (Diptera), and by Chris O'Toole, Oxford University Museum of Natural History (Bees).

All surveys were conducted in the morning between 8am-11am. Preliminary observations suggested this was the peak time for insect activity because by noon insect abundance had declined as the temperatures increased. Several plants (such as *Convolvulus* spp.) closed their flowers by noon.

2. Data Analysis

Specialisation

Indices that estimate the degree to which a species is specialised do not all measure the same type of specialisation. For instance, indices that measure the centrality of the distribution of visits (called "degree centrality"), measure specialisation in terms of how many links a species have with other species (Dormann, 2011). A bee that visits two plants is clearly more specialised than one that visits five. However, the results from this index should only be taken as an indication of specialisation, because the strength of the interaction is not recorded. Due to temporary flower constancy influencing specialisation at a specific time, the observed interaction may only be recording temporary specialisation.

Another way of measuring specialisation is to employ methods that look at how important individual species are within a network (Dormann, 2011) such as 'betweenness centrality'. This looks at connections between species and 'modularity' that looks to see if patterns exist within a network that separate species into different modules specialising on specific plants.

Hence I use a range of indices that address different types of specialisation both at the species and network level. As all survey sites contained species of the same plant assemblage, data from all sites were combined in order to assess the lowland Hajar Mountains network as a whole. The analysis used species abundances rather than binary, presence-absence, data.

The following indices and properties were used to look for specialisation at the network level at each site surveyed: connectance, web asymmetry, links per species, H_2, species richness, and niche overlap (Table S15 for a the formulae and range of values of the indices used). The calculations were done using the function *networklevel* in the R (3.5.0 version) package *bipartite* (Dormann & Gruber, 2012). At the species level, degree centrality, normalised degrees, betweenness, closeness and d' were all assessed using the function *specieslevel* in the same *bipartite* package.

The level of specialisation within the network was tested using the two indices, d' (specialisation of individual species) and H_2' (specialisation at the overall network-level) (Bluthgen et al., 2006). d' and H_2' are estimated by the R package *bipartite*. Both d' and H_2' lie between 0 and 1, with 0 meaning no specialisation and 1 meaning complete specialisation (Dormann et al., 2009).

Indices are influenced by the size of a network: Dormann et al (2009) suggested that indices calculated for networks with fewer than 50 species cannot be trusted. The total number of species (plants and insects) in the lowland Hajar Mountains network was 136, minimising this issue.

To visualise the data, the package *bipartite* was used with the function *plotweb* to create bipartite graphs of the whole network as well as at individual sites. This method uses a plant x insect matrix, which depending on the number of visits by the insect, determines the thickness of the link thus allowing a clear visual representation of the strength of interactions within a network.

Centrality distribution

Centrality encompasses several methods that can be used to measure the position of a node (species) within a network in relation to other nodes. These methods include degree centrality, betweenness and closeness. Two centrality measures that can be used to highlight important species within a network are degree centrality and betweenness (Martin Gonzalez et al., 2010).

Degree centrality is a basic measure that determines how generalised a species is by ranking the number of interactions a species has with other species. A high degree indicates a well-connected species (hub species) (Pavlopoulos et al., 2018). While useful as a preliminary step in recording specialisation, this measure has been described as a crude estimation of generalisation as it is simply a measure of the number of links a species has and does not distinguish how often a pollinator visits a particular plant (Martin Gonzalez et al., 2010).

Betweenness centrality offers a different measure, not how many links a node has, but instead how important a node is in connecting to other nodes within the network (Martin Gonzalez et al., 2010). Betweenness describes how well a node acts as a bridge between two well-connected communities within the network. This has implications for the stability of a network. Species with a betweenness score greater than 0 can be considered 'connectors'. Lastly closeness centrality measures how central a node is within a network by ranking species in relation to their position to other species within the network (Russo et al., 2013). When applied to pollination networks, centrality provides a way of visualising the role of a species within a network. This is both in terms of how specialised or generalised a species is, and in the stability a species provides to a network through its connections.

Nestedness

Several methods have been developed to assess the extent to which nestedness exists within a network include the Nestedness Temperature Calculator (NTC) (Atmar & Patterson, 1993), Rodríguez-Gironés & Santamría's (2006) BINMATNEST program and the NODF metric (Almeida et al., 2008). An issue with all these methods is they rely on presence-absence adjacency matrices and thus do not take into account the frequency of interactions between different trophic levels (Galeano et al., 2009). This means an important level of information is lost about the intensity of interactions occurring within a network.

Consequently I used the Weighted-Interaction Nestedness Estimator (WINE) (Galeano et al., 2009), which uses abundance data. WINE was calculated using the *wine* function in the R package *bipartite*. This function returns a weighted-interaction nestedness estimator that varies between zero (indicating a random distribution of species) and 1.0 (meaning maximum nestedness). An associated z-score and p-value are also returned. P-values of $p<0.05$ show a significantly nested network.

Compartmentalization

Compartmentalization/modularity was calculated for individual sites and the network as a whole using the function *compart(web)* in the bipartite package.

β *-diversity between three sections of the Hajar Mountains*

To evaluate whether the β -diversity of insect species varied between the three areas of the study, the Jebel Akhdar range, the Samail Gap (a large wadi separating the western and eastern Hajar Mountains), and eastern

Hajar Mountains, a permutation-based test calculating multivariate homogeneity of group's variances was used. This tested whether the species composition varied between pairwise combinations of the three sections of the mountains sampled in. This was calculated in the R package *vegan* (Oksanen et al., 2014) using the function *permutest.betadisper*

Results

1. Network composition

A total of 22 plant (Table 1) and 124 insect species (Table S1) were recorded interacting within the visitation network resulting in a total of 186 realised links and 671 interactions. Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera visited the flowers: apart from the Hemiptera, these are well-known pollinator groups. The order Thysanoptera was also noted within some flowers, but were ignored because accurately assessing their abundance on plants was not practicable: *Ochradenus aucheri*, for instance, can have 3000 flowers on a single plant.

The Hymenoptera showed the greatest species richness with a total of 75 species, of which 41 were bees. Four bee families were recorded: Megachilidae (21 species), Halictidae (12 species), Colletidae (five species), and Apidae (three species). Apart from three species (*Apis florea* [30 individuals], *A. mellifera* [10] and Nomioidinae sp. 1 [8]), abundance of individual species of bee was low. All of the other 38 species were recorded with six or fewer individuals.

The Coleoptera and Diptera were also relatively species-rich groups, with 18 and 17 species, respectively. While the Hymenoptera were the most species-rich group, the Coleoptera showed the greatest abundance for individual species. For instance, 115 individuals of *Anthelephila multiformis* (Anthicidae, ant-like flower beetles) were recorded. This is considerably more than the 30 individuals of *Apis florea*, the most abundant bee species. The beetle families recorded included Anthicidae (1 species), Buprestidae (3), Chrysomelidae (1), Coccinellidae (1), Dasytidae (1), Dermestidae (1), Malachiidae (3), and Mordellidae (1).

Of the Diptera, I recorded the following families: Bombyliidae (8 species), Calliphoridae (1), Muscidae (2), Mythicomyiidae (1), Sarcophagidae (2), Syrphidae (2), Tachinidae (2) and Tephritidae (1). Of the Bombyliidae (the most species-rich family observed), the subfamily Anthracinae had the greatest number of species (3). While the Diptera was almost as species-rich as the Coleoptera, the number of recorded interactions with plants was the lowest of all visiting orders (ignoring the Hemiptera) across species (mean ± SD= 1.6 ± 0.70). No species was recorded as having more than three interactions, and eight of the 17 species had only one recorded interaction.

Lepidoptera species richness was also low with only 11 species recorded including the families Hesperiidae (one species), Lycaenidae (5), Pieridae (4), and Nymphalidae (1). Whilst species richness was low, abundance was high in two of the species*,* *Pontia glauconome* (29 interactions) and *Tarucus rosaceus* (10)*,* making them an important element within the network in terms of interactions.

14 plant families were recorded, including Asclepiadaceae (1 species), Asphodelaceae (1), Asteraceae (2), Boraginaceae (1), Brassicaceae (3), Capparaceae (1), Convolvulaceae (2), Euphorbiaceae (2), Fabaceae (2), Lamiaceae (1), Nyctaginaceae (1), Resedaceae (2), Rubiaceae (1) and Zygophyllaceae (1).

For the overall network, linkage levels of plants species varied from 1 to 63 (mean ± SD= 8.68 ± 13.41), while for insect species, links ranged from 1 to 7 (mean ± SD= 1.55 ± 1.03). The pattern of a few generalised plants attracting a high number of insect species, while the remaining plants attracting low numbers of species contributed to the network being significantly nested. The most connected plant species included two regional endemics, *Ochradenus arabicus* and *O. aucheri* (Resedaceae) as well as *Taverniera cuneifolia* and *Tephrosia apollinea* (Fabaceae) (Table 2).

A Pearson product-moment correlation coefficient was calculated to assess the relationship between the number of links per insect species and the species total recorded abundance. There appeared to be no correlation between these two variables (r= 0.358, N=123, p= >0.5) indicating more abundant species were not more generalised in their visitation habits than rare species. Specialisation/low linkage levels were common across all species and sites (Table 3 and Tables S2-14 for a breakdown of species linkage levels).

Insect species richness at the thirteen survey sites ranged from 7-36 species (mean ± SD= 16.8 ± 9.2) (Table 4). Plant species richness was low across all sites, ranging from 2-5 species per site (mean ± SD= 3.3 ± 1.2), while total number of individual plants per site varied from 3-65 (mean ± SD= 21.6 ± 19.6) (Table 4). No clear pattern in the dominance of a particular plant species was observed across all sites. For instance at the site Ghubrah Canyon, *Asphodelus fistulosus* (Asphodelaceae) represented 86 % of all recorded plant species. Conversely, at the site nr. Taww Village, the same species only represented 33 % of the recorded plant species. This suggests short term floral constancy at a particular time of the year may not be beneficial as all plant species were only recorded as being abundant at a local level. No plant species appeared to be abundant throughout all of the lowland Hajar Mountains, although all sites appeared seemingly similar in soil type and topography.

A second Pearson product-moment correlation coefficient showed that while insect species richness showed a positive increase with plant species richness, there was no significant correlation between the two groups (r= 0.35, p= 0.24). Instead insect species richness appeared to be influenced by the presence of *O. aucheri.* As numbers of *O. aucheri* at a site increased, there was a significant positive correlation with insect species richness (r= 0.85, p= 0.00). As each *O. aucheri* contained up to an estimated 3000 individual flowers, these plants appear to provide an important source of pollen and nectar to insects in the lowland Hajar Mountains.

2. Network structure and interactions

The WINE value was 0.62 (z = 23.26, $p<0.05$), signifying that the network was nested and hence that there was order within the network and species were not visiting plants randomly (Table 5). The function *compart(web)* showed that two compartments existed at the overall network level (Table 6): Module 1= *Heliotropium longiflorum*- *Celonites yemenensis* (Masarinae), and Module 2= all other plants-all other insects. As only one individual of the plant *H. longiflorum* was surveyed during the study, it is highly likely this division into two compartments is an artificial result due to the under-recording, and not a reflection of a tight specialisation to Masarinae wasps for pollination services. At the level of the three different ranges, both the Eastern and Western Hajar Mountains contained three compartments, while the Samail gap sites contained two modules. At the individual site level, modularity was equally low, with 12 of the 13 sites containing either no compartments or two compartments. Only the site Yiti 1 had three compartments. However, as all four plant species recorded at this site (*Euphorbia larica*, *Morettia parviflora,* *Lavandula subnuda* and *Taverniera cuneifolia*) were visited at other sites by other insect species, this result did not impact on the overall network modularity. These results indicate modularity does exist to some extent within the pattern structuring this network although there is variation depending on which scale it is calculated. Figs. 2-5 show the overall network structure and that of the three ranges. In all graphs *Ochradenus aucheri* was a key component of the network. To explore structure at individual sites, 13 bipartite graphs were constructed (Figs. S1-13), with 11 of the 13 sites displaying an asymmetrical pattern.

The permutation test found β -diversity, expressed as the variation in the composition of the insect communities of the three different sections of the Hajar Mountains (western, central, and eastern), did not differ significantly ($p > 0.05$). Likewise, Tukey's Honest Significant Differences pairwise comparisons of the three areas found no significant differences ($p > 0.05$)(Fig 6).

Discussion

The topology of the lowland Hajar Mountains visitation networks was remarkably similar throughout the whole of the surveyed range with medium to low connectance, mostly asymmetric shaped webs, and communities chiefly composed of specialised insect species. When the individual surveys were combined, the overall network for the lowland Hajar Mountains was significantly nested. This appears to be the natural state for most mutualistic networks, as demonstrated by Bascompte et al's (2003) review that concluded that 75% of 52 networks showed this structure.

Plant species richness was low in all sites (no transect contained more than five species of plant) meaning all but two sites, Lizugh and Wadi Arbein, showed a highly asymmetric shape, a common pattern in mutualistic networks (Russo et al., 2013). The two sites showing a more symmetrical shape contained an equally low number of insect visitors rather than increased plant species richness. The permutation test revealed no significant variability of the insect composition between the three sections of the Hajar Mountains surveyed in the study. This was surprising: although the floral community of the lowland Hajar Mountains is relatively similar throughout the range, at higher elevations the plants of the western and eastern Hajar Mountains are distinct. They contain many endemic species, and the western Hajar Mountains contain almost 30% of the total flora of the country (Patzelt, 2009; Patzelt & Knees, 2014), which therefore could potentially support a more diverse insect fauna. Unless specialisation confines species to different altitudinal bands, leading to strongly compartmentalised networks, it could be expected that the difference in the higher altitude plant communities might lead to differences in the insect communities. In this scenario a third type of network pattern could exist (as opposed to a nested or compartmentalised network), a network gradient. This is a common occurrence in plant communities, creating a situation where species are slowly lost or gained but without serious discontinuities within the network (Lewinsohn & Prado, 2006). While less commonly seen within insect communities, because pollinators tend to show a greater degree of mixing in their interactions rather than displaying neat matching to sequences of plants along a gradient (Lewinsohn & Prado, 2006), this type of network has been recorded in oligolectic bees (Moldenke, 1979; Petanidou et al. 1995; Lewinsohn & Prado, 2006). More data on the visitation networks at higher altitudes would allow a fuller understanding of the total Hajar Mountain visitation network topology and create a better understanding of the reasons behind the lack of variability across the lowlands.

While the Hajar Mountains are recognised as being rich in plant diversity and contain a high number of endemics, at the scale of the transects, 50 x 4 m, plant diversity was low (2-5 plant species per transect). The results of the correlation test looking at whether an association existed between plant species richness and insect species richness found no significant correlation as plant species richness increased. This result suggests that even when insects were exposed to different floral options, most insects were only visiting a limited number of plants. Whether this changes temporally should be investigated. Whether this observation was an indication of true specialism or floral constancy is not clear. However, an increase in plant species richness at a particular site, did not lead to a linear increase in insect species richness.

Regardless of plant species richness in general, sites that contained the highest number of insects were correlated significantly with those that contained the regional endemic *Ochradenus aucheri. O. aucheri* was the most well connected plant with a total of 63 insect species recorded visiting. With each plant containing an estimated 3000 individual flowers that contain abundant and easily accessed pollen, this species appears to play a key role in influencing insect species abundance within the Hajar Mountains.

Two compartments exist for the network as a whole, one consisting of the plant *Heliotropium longiflorum* visited by a species of Masarinae wasp, *Celonites yemenensis*, and then the rest of the insect and plant species existing in a second compartment. Across the three sections of the range, modularity varied from two (Samail gap sites) to three (Eastern and Western Hajar Mountains) modules when the respective sites were combined. This lack of greater compartmentalisation of the local assemblage is not surprising, since strict compartments are believed to be unlikely to arise unless webs occur in distinct sub-habitats within an area (Pimm et al., 1991). Here, the plant local assemblage was similar throughout the surveyed areas. The absence of modules at the overall network level meant there was no evidence for specialisation of related taxa towards particular floral types. Clearly while this study did not investigate how individual insect species responded to particular floral phenotypes, the lack of modularity suggests while specialisation was the standard at species level, at higher taxonomic levels taxa were generalised in their visitation habits. Therefore there was no evidence to support floral syndromes existing within the network.

All networks had low linkage levels per species and high H_2 scores, (apart from the sites Lizugh and Taww), indicating that at the network level communities were highly specialised (Table 3). This was unexpected. I had suggested bee species would be oligolectic and individual species rare, a common observation in multiple studies (Barbola & Laroca, 1993; Potts et al., 2003) including in this study. I had not expected this pattern to be repeated in the other three main orders of pollinating insects. This pattern was particularly clear amongst the Diptera, conventionally considered the second most important order of pollinators after bees (Larson et al., 2001). The results showed the same transience and low abundance of Diptera as for the bees. Apart from the Tephritidae, all the Diptera taxa recorded in this study are normally associated with visiting flowers, and so may play a role in pollination (J. Deeming, personal communication, 10.05.2018). The Anthracinae theoretically may act as important pollinators within the network due to their habit of settling within flowers and hence potentially picking up pollen inadvertently. The Toxophorinae tend to hover above flowers, feeding on nectar using their long proboscis (M. Ebejer, personal communication, 10.05.2018), suggesting a less important role in pollination because they are less likely to come into contact with pollen grains unless visiting specialised or tubular flowers. However, based on the linkage level and low abundance of individuals, and unlike Diptera in Arctic pollination networks (Olesen et al., 2008) or at high altitudes, the low abundance of species recorded indicates that flies do not play a major role in pollination at this point in the flowering season.

The centrality of the individual networks (Tables S2-14) at each site did not wholly conform to the commonly observed pattern seen in many other network types, i.e. a few highly connected nodes and numerous poorly linked ‘peripheral’ nodes (Gómez & Perfectti, 2012). Instead all sites had low degree centrality scores amongst all insect species (one simple indication of specialisation) and only five of the 13 sites contained species with betweenness scores >0. The closeness centrality scores for individual networks showed little variety within networks, reflecting that most insects had few links and therefore this centrality measure showed little variation between species. This implies networks are composed of mostly peripheral species interacting with a limited number of plant species. By being outside of the centre of the network, most species have little influence on the stability and functioning of the system (Gómez & Perfectti, 2012). While the most species-rich group recorded, nearly all the bees formed peripheral nodes in individual networks. Species that were central to individual networks were predominantly butterflies and beetles that showed generalised visitation patterns. Centrality differed spatially, as highlighted by the butterfly *Pontia glauconome*, which only acted as a central node in two of the six sites it was recorded. It would be interesting to record how centrality measures varied temporally. The study was carried out towards the end of the blooming period, and therefore the lack of annual flowers with which solitary bees are commonly associated may be one reason why bees (and flies) played such marginal roles in individual networks.

Other extrinsic factors that may have influenced bee abundance include the distance from nest sites to suitable foraging areas as well as parasite pressure (Danforth et al., 2019). Several cleptoparasitic genera, such as *Sphecodes* (Halictidae), *Coelioxys, Stelis* (Megachilidae), and *Thyreus* (Apidae) are present in Oman. However, cleptoparasitic species are often very rare (Larsson & Franzén, 2008; Danforth et al., 2019) and their impact on bee populations in the Hajar Mountains, and how this varies temporally, is completely unknown. The accessibility of bare ground, natural or man-made cavities, and plants with pithy stems are all factors that influence nesting success and therefore abundance of bees (Potts et al., 2005). Most solitary bee species will only forage up to 500 m from their nest (Danforth et al., 2019). Therefore, low numbers of certain species that have specific nesting requirements may be an indication of poor nesting resources in a local area rather than indicating a lack of specific floral resources. While the aim of this study was to look at whether specialisation was key to influencing network structure, future studies should aim to combine an assessment of floral abundance with an evaluation of nesting resources and presence of cleptoparasitic species at the survey site in question, in order to gain a fuller undstanding of the factors determing bee abudance.

A theme to investigate further is whether the physical conditions experienced by insects in wadis leads to the floral constancy observed. Several of the wadi sites surveyed in this study were deep, steep-sided canyons, several kilometres long. An insect entering this environment would be confined to the few plant species available, especially if it is a weak flyer, thus enforcing floral constancy. Although plant species richness was low, the abundance of particular species was not necessarily limited, allowing floral constancy to be advantageous. Consequently the high H_2 scores may represent temporary specialisation/floral constancy due to the habitat conditions and may not represent true specialisation. The two sites Lizugh and Taww with low H_2 scores, and therefore containing generalised insect species, were both open sites on the periphery of the Hajar Mountains. This open environment may allow insects more opportunities to move further distances to visit a wider range of floral resources from a more diversified community of plants, encouraging a lower degree of floral constancy.

Lucas et al (2018) suggested that generalism in hoverflies recorded in meadows in Wales increased during the summer months as more plants came into flower, thus offering a greater abundance of potential resources. The surveys in this study were carried out in March, towards the end of the flowering season and after the majority of annuals had flowered, and hence it is possible that a decline in floral choices has resulted in an apparent increase in specialisation. Further surveys are needed earlier in the blooming period to see whether specialisation levels change temporally amongst insect visitors.

The majority of community level studies of pollination networks are very different in structure, being composed predominately of generalist visitors, believed to be a result of high plant diversity offering multiple resources (Devoto et al., 2011; Baldock et al., 2015). A temporal approach is now necessary in order to clarify if the results of this study indicate true specialisation across all orders of insect. Alternatively the results show specialisation increasing through the blooming season as plant flowering diversity starts to decline.

Conclusions and future research

Throughout the lowland Hajar Mountains, plants are visited by a set of predominantly specialised insects. The visitation network shows a significantly nested pattern with low modularity and no significant variation in local species assemblage between different sections of the range. This general pattern is based on a visitation network which treated all visitors equally in their assumed potential ability to act as pollinators. This therefore may mask certain properties of the true pollination network, which will be influenced by a subset of the visitors recorded in this study.

As the study of whole networks has advanced over the last few decade's different approaches to recording network structure have been made. An example other than visitation networks includes pollen transport netwoks (Forup & Memmott, 2005; Alarcón, 2010). Here data is gathered from the pollen loads found on insects and an assessment of the importance of that insect to a specific species of plant can be made in relation to the composition of pollen found on different insects. A further step is pollen importance networks (Ballantyne et al., 2015). This type of approach combines information on pollinator effectiveness, whether an insect deposits pollen on a virgin stigma (Ne'eman et al., 2010; King et al., 2013), as well as the frequency of visits to a plant species (Ballantyne et al., 2015). All approaches have advantages and disadvantages. Like records of visitation, pollen found on an insect still does not guarantee that insect acts as a pollinator of a particualr plant, although it allows a history of interactions to be constructed, which is not possible from purely observing which insect visits which plant as many interactions may not be observed. Likewise pollinator importance networks, while giving the most detailed information on network structure, are time consuming to construct and may be impractical when recording networks composed of large numbers of species. Therefore, the type of question being asked dictates the type of network approach most appropriate (Ballantyne et al., 2015). As this study was the first attempt in the Arabian Peninsul to simply quantify which insect species visit which plant species, a visitation network was sufficient to answer this fundamental question.

Further studies are now needed to investigate whether the high levels of specialisation observed vary temporally throughout the whole of the Hajar Mountains flowering season. Here a pollen transport network or pollen importance network would provide more detailed answers.

Figures and Tables

Figure 1. Location of the study sites within the Hajar Mountains. Green squares show sites in the Jebel Akhdar range, orange circles the Jebel Nakhl/Samail Gap sites, and red stars the Eastern Hajar Mountain sites.

Figure 2. Overall lowland Hajar Mountain visitation network

Figure 3. Eastern Hajar Mountains network

Figure 4. Samail Gap network

Figure 5. Western Hajar Mountains network.

Figure 6. Tukey's Honest Significant Differences pairwise comparisons of the three sections of the Hajar Mountains: Eastern, Western & Central Hajar Mountains

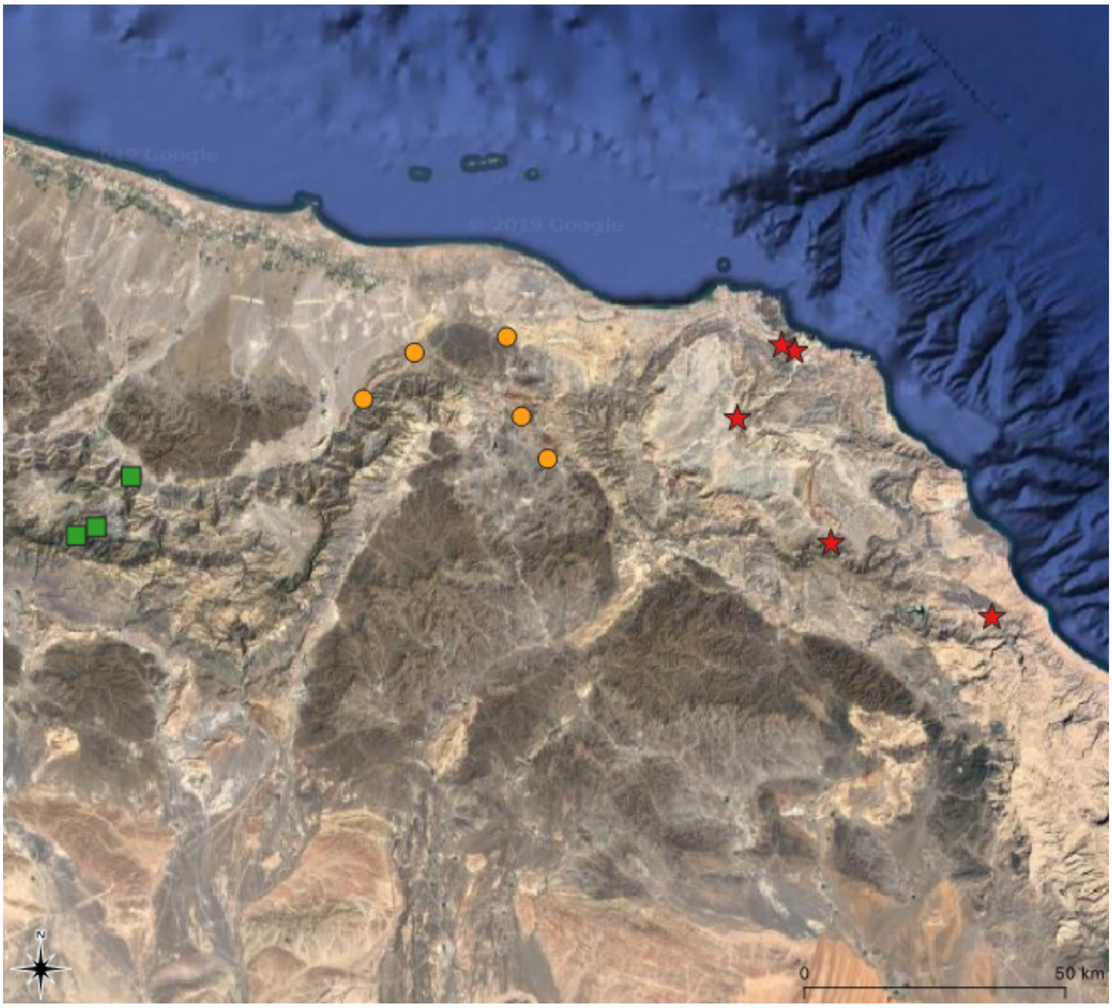


Fig 1.

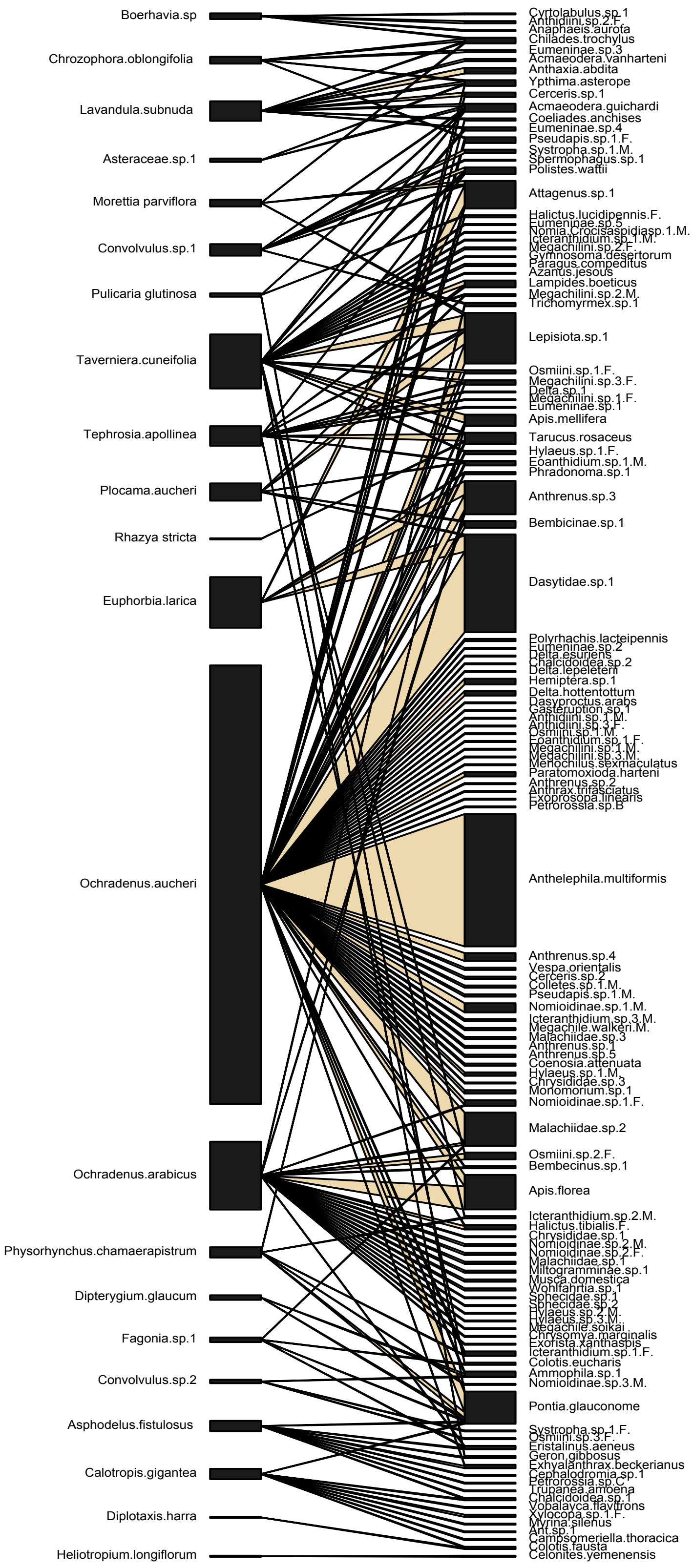
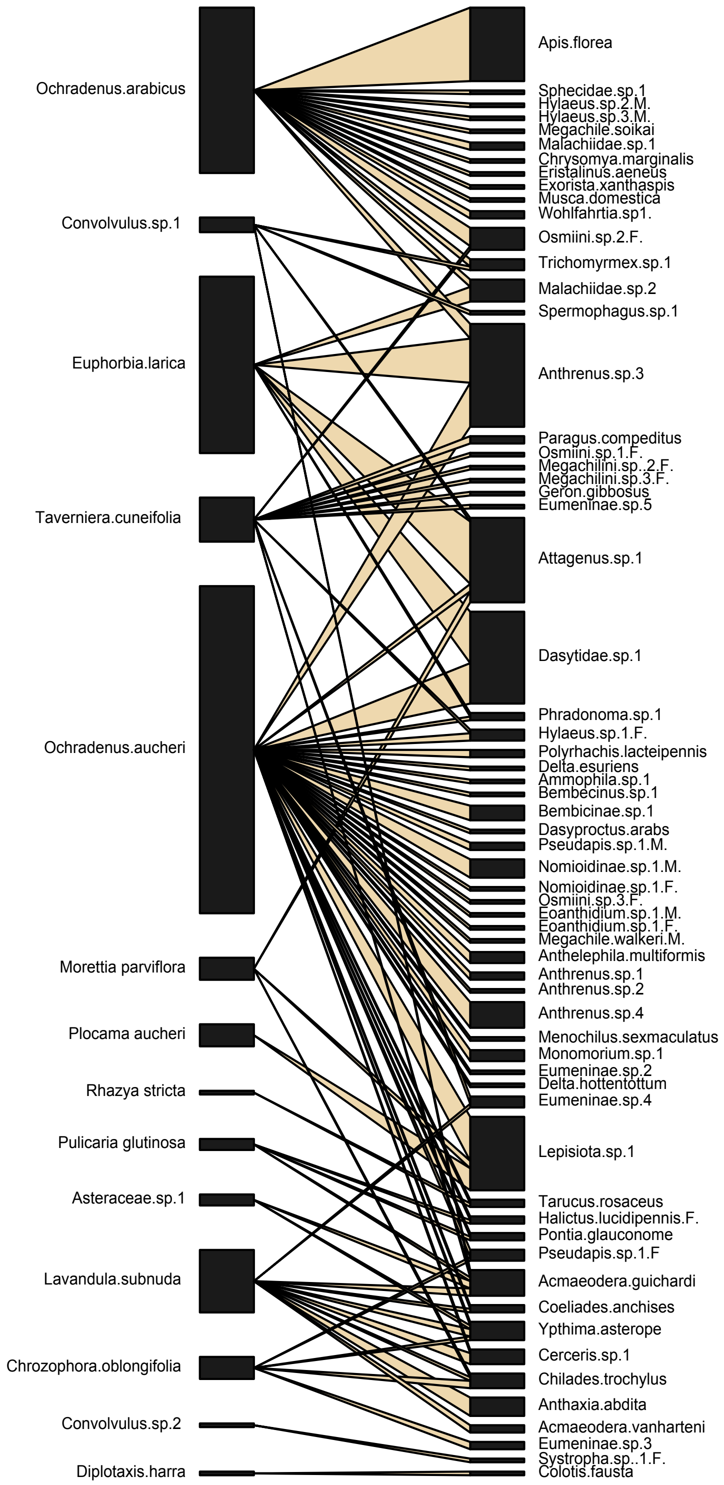

Boerhavia.sp
Chrozophora.oblongifolia
Lavandula.subnuda
Asteraceae.sp.1
Morettia parviflora
Convolvulus.sp.1
Pulicaria glutinosa
Taverniera.cuneifolia
Tephrosia.apollinea
Plocama.aucheri
Rhazya stricta
Euphorbia.larica
Ochradenus.aucheri
Ochradenus.arabicus
Physorhynchus.chamaerapistrum
Dipterygium.glaucum
Fagonia.sp.1
Convolvulus.sp.2
Asphodelus.fistulosus
Calotropis.gigantea
Diplotaxis.harra
Heliotropium.longiflorum
Cyrtolabulus.sp.1
Anthidiini.sp.2.F.
Anaphaeis.aurota
Chilades.trochylus
Eumeninae.sp.3
Acmaeodera.vanharteni
Anthaxia.abdita
Ypthima.asterope
Cerceris.sp.1
Acmaeodera.guichardi
Coeliades.anchises
Eumeninae.sp.4
Pseudapis.sp.1.F.
Systropha.sp.1.M.
Spermophagus.sp.1
Polistes.wattii
Attagenus.sp.1
Halictus.lucidipennis.F.
Eumeninae.sp.5
Nomia.Crocisaspidiasp.1.M.
Icteranthidium.sp.1.M.
Megachilini.sp.2.F.
Gymnosoma.desertorum
Paragus.compeditus
Azanus.jesous
Lampides.boeticus
Megachilini.sp.2.M.
Trichomyrmex.sp.1
Lepisiota.sp.1
Osmiini.sp.1.F.
Megachilini.sp.3.F.
Delta.sp.1
Megachilini.sp.1.F.
Eumeninae.sp.1
Apis.mellifera
Tarucus.rosaceus
Hylaeus.sp.1.F.
Eoanthidium.sp.1.M.
Phradonoma.sp.1
Anthrenus.sp.3
Bembicinae.sp.1
Dasytidae.sp.1
Polyrhachis.lacteipennis
Eumeninae.sp.2
Delta.esuriens
Chalcidoidea.sp.2
Delta.lepeleterii
Hemiptera.sp.1
Delta.hottentottum
Dasyproctus.arabs
Gasteruption.sp.1
Anthidiini.sp.1.M.
Anthidiini.sp.3.F.
Osmiini.sp.1.M.
Eoanthidium.sp.1.F.
Megachilini.sp.1.M.
Megachilini.sp.3.M.
Menochilus.sexmaculatus
Paratomoxioda.harteni
Anthrenus.sp.2
Anthrax.trifasciatus
Exoprosopa.linearis
Petrorossia.sp.B
Anthelephila.multiformis
Anthrenus.sp.4
Vespa.orientalis
Cerceris.sp.2
Colletes.sp.1.M.
Pseudapis.sp.1.M.
Nomioidinae.sp.1.M.
Icteranthidium.sp.3.M.
Megachile.walkeri.M.
Malachiidae.sp.3
Anthrenus.sp.1
Anthrenus.sp.5
Coenosia.attenuata
Hylaeus.sp.1.M.
Chrysididae.sp.3
Monomorium.sp.1
Nomioidinae.sp.1.F.
Malachiidae.sp.2
Osmiini.sp.2.F.
Bembecinus.sp.1
Apis.florea
Icteranthidium.sp.2.M.
Halictus.tibialis.F.
Chrysididae.sp.1
Nomioidinae.sp.2.M.
Nomioidinae.sp.2.F.
Malachiidae.sp.1
Miltogramminae.sp.1
Musca.domestica
Wohlfahrtia.sp.1
Sphecidae.sp.1
Sphecidae.sp.2
Hylaeus.sp.2.M.
Hylaeus.sp.3.M.
Megachile.soikai
Chrysomya.marginalis
Exorista.xanthaspis
Icteranthidium.sp.1.F.
Colotis.eucharis
Ammophila.sp.1
Nomioidinae.sp.3.M.
Pontia.glauconome
Systropha.sp.1.F.
Osmiini.sp.3.F.
Eristalinus.aeneus
Geron.gibbosus
Exhyalanthrax.beckerianus
Cephalodromia.sp.1
Petrorossia.sp.C
Trupanea.amoena
Chalcidoidea.sp.1
Vobalayca.flavifrons
Xylocopa.sp.1.F.
Myrina.silenus
Ant.sp.1
Campsomeriella.thoracica
Colotis.fausta
Celonites.yemenensis

Fig. 2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Convolvulus.sp.1
Euphorbia.larica
Taverniera.cuneifolia
Ochradenus.aucheri
Morettia parviflora
Plocama aucheri
Rhazya stricta
Pulicaria glutinosa
Asteraceae.sp.1
Lavandula.subnuda
Chrozophora.oblongifolia
Convolvulus.sp.2
Diplotaxis.harra
Apis.florea
Sphecidae.sp.1
Hylaeus.sp.2.M.
Hylaeus.sp.3.M.
Megachile.soikai
Malachiidae.sp.1
Chrysomya.marginalis
Eristalinus.aeneus
Exorista.xanthaspis
Musca.domestica
Wohlfahrtia.sp1.
Osmiini.sp.2.F.
Trichomyrmex.sp.1
Malachiidae.sp.2
Spermophagus.sp.1
Anthrenus.sp.3
Paragus.compeditus
Osmiini.sp.1.F.
Megachilini.sp..2.F.
Megachilini.sp.3.F.
Geron.gibbosus
Eumeninae.sp.5
Attagenus.sp.1
Dasytidae.sp.1
Phradonoma.sp.1
Hylaeus.sp.1.F.
Polyrhachis.lacteipennis
Delta.esuriens
Ammophila.sp.1
Bembecinus.sp.1
Bembicinae.sp.1
Dasyproctus.arabs
Pseudapis.sp.1.M.
Nomioidinae.sp.1.M.
Nomioidinae.sp.1.F.
Osmiini.sp.3.F.
Eoanthidium.sp.1.M.
Eoanthidium.sp.1.F.
Megachile.walkeri.M.
Anthelephila.multiformis
Anthrenus.sp.1
Anthrenus.sp.2
Anthrenus.sp.4
Menochilus.sexmaculatus
Monomorium.sp.1
Eumeninae.sp.2
Delta.hottentottum
Eumeninae.sp.4
Lepisiota.sp.1
Tarucus.rosaceus
Halictus.lucidipennis.F.
Pontia.glauconome
Pseudapis.sp.1.F
Acmaeodera.guichardi
Coeliades.anchises
Ypthima.asterope
Cerceris.sp.1
Chilades.trochylus
Anthaxia.abdita
Acmaeodera.vanharteni
Eumeninae.sp.3
Systropha.sp..1.F.
Colotis.fausta

Fig. 3

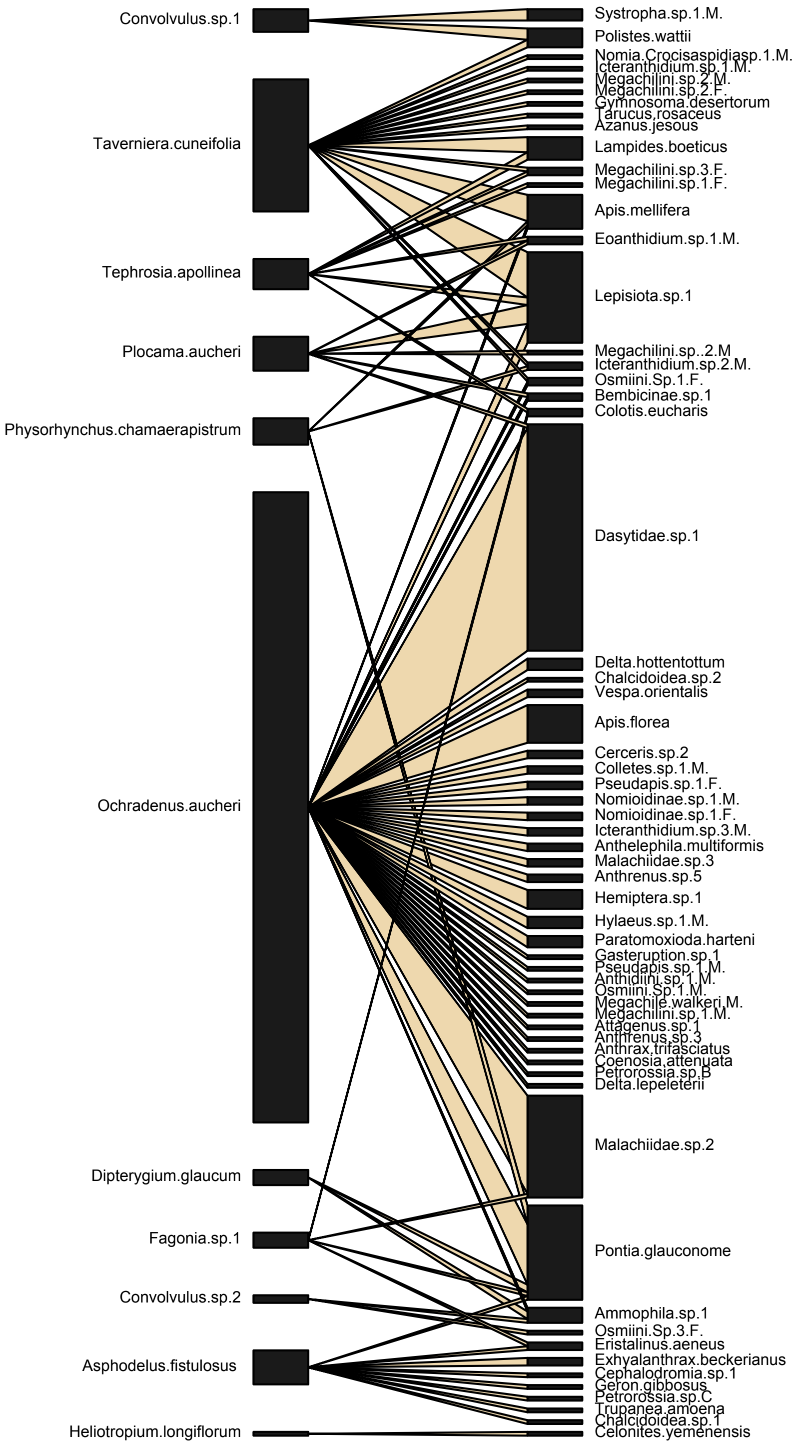

Convolvulus.sp.1
Taverniera.cuneifolia
Tephrosia.apollinea
Plocama.aucheri
Physorhynchus.chamaerapistrum
Ochradenus.aucheri
Dipterygium.glaucum
Fagonia.sp.1
Convolvulus.sp.2
Asphodelus.fistulosus
Heliotropium.longiflorum
Systropha.sp.1.M.
Polistes.wattii
Nomia.Crocisaspidiasp.1.M.
Icteranthidium.sp.1.M.
Megachilini.sp.2.M.
Megachilini.sp.2.F.
Gymnosoma.desertorum
Tarucus,rosaceus
Azanus.jesous
Lampides.boeticus
Megachilini.sp.3.F.
Megachilini.sp.1.F.
Apis.mellifera
Eoanthidium.sp.1.M.
Lepisiota.sp.1
Megachilini.sp..2.M
Icteranthidium.sp.2.M.
Osmiini.Sp.1.F.
Bembicinae.sp.1
Colotis.eucharis
Dasytidae.sp.1
Delta.hottentottum
Chalcidoidea.sp.2
Vespa.orientalis
Apis.florea
Cerceris.sp.2
Colletes.sp.1.M.
Pseudapis.sp.1.F.
Nomioidinae.sp.1.M.
Nomioidinae.sp.1.F.
Icteranthidium.sp.3.M.
Anthelephila.multiformis
Malachiidae.sp.3
Anthrenus.sp.5
Hemiptera.sp.1
Hylaeus.sp.1.M.
Paratomoxioda.harteni
Gasteruption.sp.1
Pseudapis.sp.1.M.
Anthidiini.sp.1.M.
Osmiini.Sp.1.M.
Megachile.walkeri.M.
Megachilini.sp.1.M.
Attagenus.sp.1
Anthrenus.sp.3
Anthrax.trifasciatus
Coenosia.attenuata
Petrorossia.sp.B
Delta.lepeleterii
Malachiidae.sp.2
Pontia.glauconome
Ammophila.sp.1
Osmiini.Sp.3.F.
Eristalinus.aeneus
Exhyalanthrax.beckerianus
Cephalodromia.sp.1
Geron.gibbosus
Petrorossia.sp.C
Trupanea.amoena
Chalcidoidea.sp.1
Celonites.yemenensis

Fig. 4

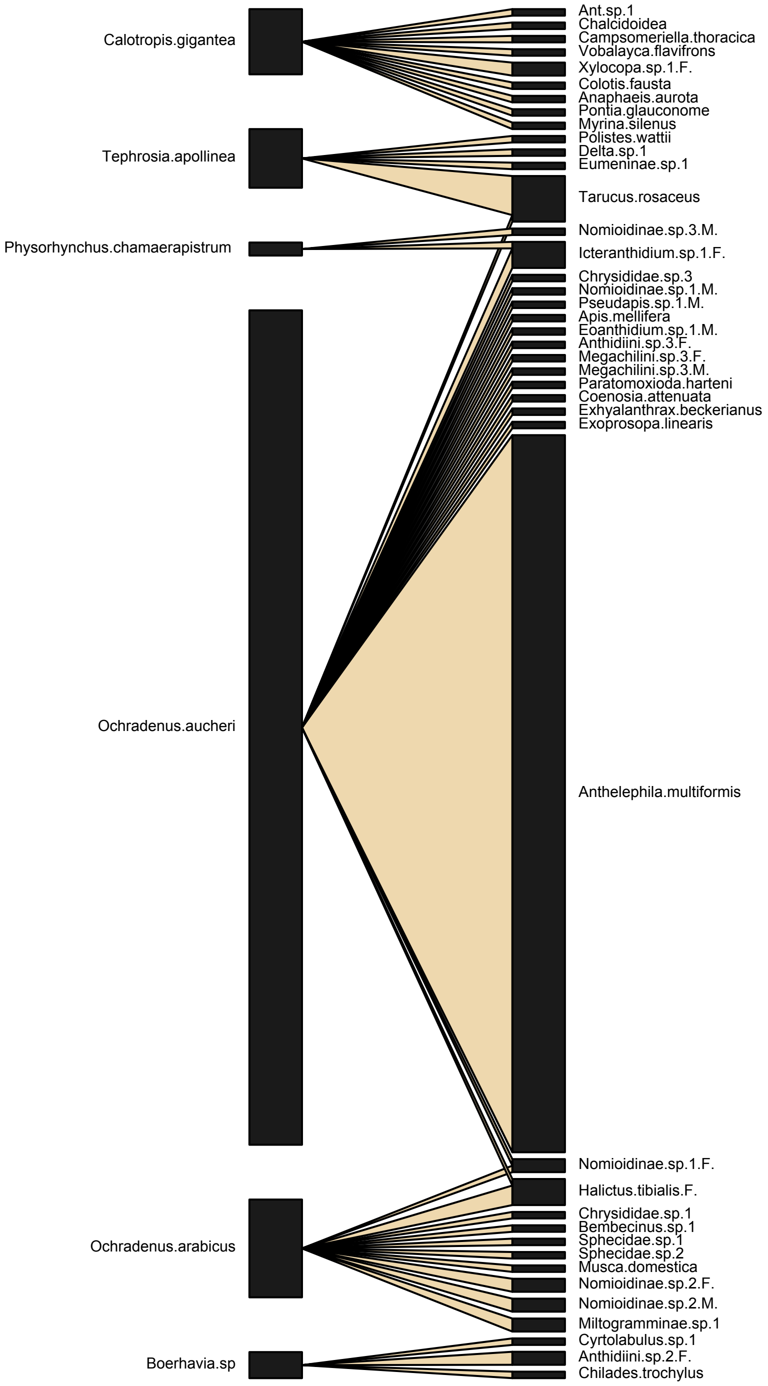

Calotropis.gigantea
Tephrosia.apollinea
Physorhynchus.chamaerapistrum
Ochradenus.aucheri
Ochradenus.arabicus
Boerhavia.sp
Ant.sp.1
Chalcidoidea
Campsomeriella.thoracica
Vobalayca.flavifrons
Xylocopa.sp.1.F.
Colotis.fausta
Anaphaeis.aurota
Pontia.glauconome
Myrina.silenus
Polistes.wattii
Delta.sp.1
Eumeninae.sp.1
Tarucus.rosaceus
Nomioidinae.sp.3.M.
Icteranthidium.sp.1.F.
Chrysididae.sp.3
Nomioidinae.sp.1.M.
Pseudapis.sp.1.M.
Apis.mellifera
Eoanthidium.sp.1.M.
Anthidiini.sp.3.F.
Megachilini.sp.3.F.
Megachilini.sp.3.M.
Paratomoxioda.harteni
Coenosia.attenuata
Exhyalanthrax.beckerianus
Exoprosopa.linearis
Anthelephila.multiformis
Nomioidinae.sp.1.F.
Halictus.tibialis.F.
Chrysididae.sp.1
Bembecinus.sp.1
Sphecidae.sp.1
Sphecidae.sp.2
Musca.domestica
Nomioidinae.sp.2.F.
Nomioidinae.sp.2.M.
Miltogramminae.sp.1
Cyrtolabulus.sp.1
Anthidiini.sp.2.F.
Chilades.trochylus

Fig. 5

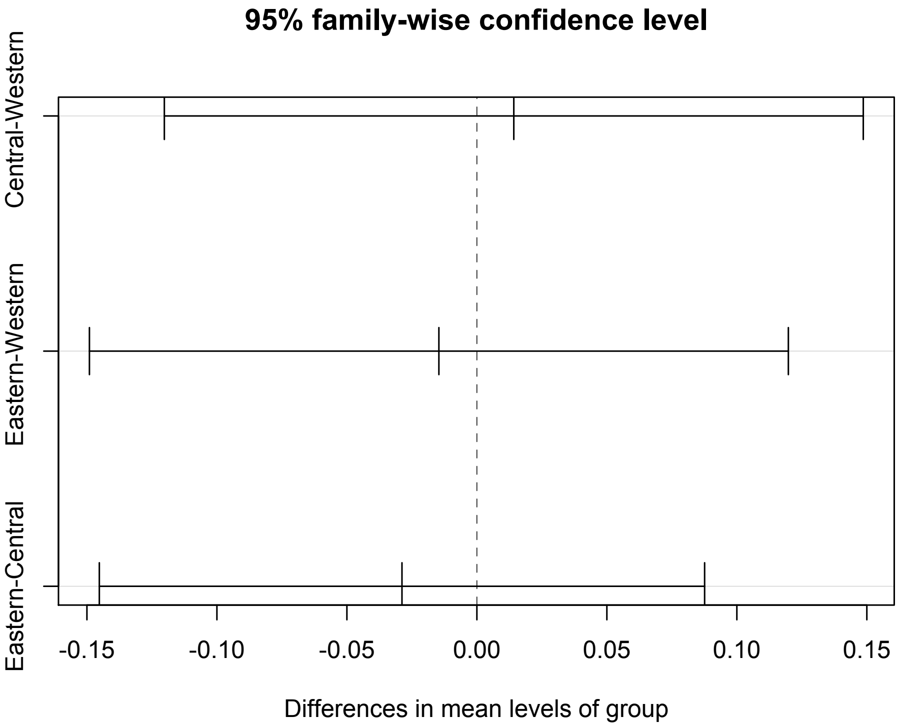

95% family-wise confidence level
Central-Western
Eastern-Western
Eastern-Central
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
Differences in mean levels of group

Fig. 6

Table 1. Plant species list with numbers of individual plants recorded at each of the thirteen survey sites (1: Yiti site 1; 2: nr. Taww Village; 3: Ghubrah Canyon; 4: Yiti site 2; 5: Oman Botanic Garden; 6: nr. Wadi Arbein; 7: Wadi Mayh; 8: nr. Bidbid Village; 9: nr. Lizugh Village; 10: Al Far Village; 11: nr. Snake Gorge; 12: Siya Village; 13: nr. Bima Village).

Family	**Species**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Asphodelaceae	*Asphodelus fistulosus*	0	5	56	0	0	17	0	0	0	0	0	1	0
Apocynaceae	*Calotropis gigantea*	0	0	0	0	0	0	0	0	0	4	0	0	0
Apocynaceae	*Rhazya stricta*	0	0	0	0	0	0	2	0	0	0	0	0	0
Asteraceae	*Pulicaria glutinosa*	0	0	0	0	0	22	0	0	0	0	0	0	0
Asteraceae	Sp. 1	0	0	0	0	0	0	0	0	0	0	0	3	0
Boraginaceae	*Heliotropium longiflorum*	0	0	0	0	0	1	0	1	0	0	0	0	0
Brassicaceae	*Diplotaxis harra*	0	2	0	1	0	0	0	0	0	0	0	4	0
Brassicaceae	*Morettia parviflora*	1	0	0	1	0	7	0	0	0	0	0	0	0
Brassicaceae	*Physorhynchus chamaerapistrum*	0	1	0	0	0	0	0	0	7	0	1	0	4

Capparaceae	*Dipterygium glaucum*	0	0	0	0	0	0	0	0	2	0	0	0	0
Convolvulaceae	*Convolvulus* sp. 1	0	0	0	1	6	0	0	0	0	0	0	0	0
Convolvulaceae	*Convolvulus* sp. 2	0	0	0	1	1	0	0	0	0	0	0	0	0
Euphorbiaceae	*Chrozophora oblongifolia*	0	0	0	0	0	0	0	0	0	0	0	3	0
Euphorbiaceae	*Euphorbia larica*	2	0	0	0	0	0	0	0	0	0	0	0	0
Fabaceae	*Taverniera cuneifolia*	2	4	0	1	1	0	0	0	0	0	0	0	0
Fabaceae	*Tephrosia apollinea*	0	3	0	0	0	0	0	5	1	11	0	0	0
Lamiaceae	*Lavandula subnuda*	1	0	0	0	0	0	0	0	0	0	0	10	0
Nyctaginaceae	*Boerhavia* sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	1
Resedaceae	*Ochradenus arabicus*	0	0	0	2	0	0	0	0	0	0	1	0	0
Resedaceae	*Ochradenus aucheri*	0	0	1	0	0	0	5	3	0	0	0	1	1
Rubiaceae	*Plocama aucheri*	0	0	0	0	0	4	0	2	0	0	0	0	0
Zygophyllaceae	*Fagonia* sp. 1	1	0	0	1	0	0	1	7	28	0	0	0	0

Table 2. Plant species with the highest numbers of links within the network as a whole

Plant Species	**Number of Links**
Ochradenus aucheri	63
Ochradenus arabicus	22
Taverniera cuneifolia	21
Tephrosia apollinea	12

Table 3. Network level indices results. The sites are separated into three blocks: in descending order (1-3) The Jebel Akhdar range, (4-8) the Jebel Nakhl range/Samail Gap area, and (9-13) the Eastern Hajar Mountains. “HL” and “LL” denote higher and lower trophic level species richness

Site	Connectance	Web asymmetry	Links per species	Compartments
Al Far	0.50	0.73	0.9	2
Bima	0.35	0.74	0.9	2
Snake Gorge	0.50	0.69	0.8	2
Bidbid	0.23	0.76	1	2
Ghubrah	0.50	0.76	0.9	2
Lizugh	0.47	0.25	0.9	1
OBG	0.38	0.40	0.8	2
Taww	0.41	0.63	1	2
Siya	0.26	0.52	1	2
Wadi Arbein	0.40	0.25	0.8	2
Wadi Mayh	0.52	0.86	1	1
Yiti 1	0.28	0.43	0.8	3
Yiti 2	0.24	0.68	1	2

Site	H2	SR (HL, LL)	Niche Overlap (HL, LL)	Total no. of interactions
Al Far	1.00	13, 2	0.54, 0.00	19
Bima	0.90	20, 3	0.73, 0.01	138
Snake Gorge	1.00	11, 2	0.82, 0.00	18
Bidbid	0.74	36, 5	0.61, 0.08	169
Ghubrah	1.00	15, 2	0.49, 0.00	44
Lizugh	0.37	5, 3	0.32, 0.62	15
OBG	0.61	7, 3	0.30, 0.17	15
Taww	0.42	13, 3	0.66, 0.24	38
Siya	0.61	16, 5	0.30, 0.10	42
Wadi Arbein	1.00	5, 3	0.32, 0.22	15
Wadi Mayh	0.60	27, 2	0.98, 0.02	91
Yiti 1	0.71	10, 4	0.40, 0.09	59
Yiti 2	0.78	26, 5	0.50, 0.09	68

Table 4. Number of *Ochradenus aucheri,* insect/plant species richness and total number of plant-insect interactions per survey site

Site	**No. of *O. aucheri***	**Insect SR**	**Plant SR**	**No. of plant-insect interactions**
Bidbid	3	36	5	169
Wadi Mayh	5	29	2	91
Yiti 2	2	28	5	136
Bima	2	21	3	138
Siya	1	18	5	42
Ghubrah	2	15	2	22
Al Far	0	13	2	19
Taww	0	13	3	38
Snake Gorge	0	12	2	18
Yiti 1	0	11	4	59
OBG	0	8	3	15
Lizugh	0	7	3	15
Wadi Arbein	0	7	4	15

Table 5. Nestedness results for the network as a whole

Weighted-interaction nestedness of dataset (WIN)	0.63
Weighted-interaction nestedness estimator (WINE)	0.62
z-score	23.26
p-value	0

Table 6. Overall network

Connectance	Web asymmetry	Links per species	Compartments	H2	SR (HL, LL)		Niche Overlap (HL, LL)	
0.07	0.70	1.3	2	0.62	124	22	0.23	0.06

Supplementary Information

Table S1. Insect species list

Order	**Family**	**Subfamily**	**Species**
Hymenoptera	Chrysididae	?	Sp. 1
Hymenoptera	Chrysididae	?	Sp. 2
Hymenoptera	Chrysididae	?	Sp. 3
Hymenoptera	Scoliidae	Scoliinae	*Campsomeriella thoracica*
Hymenoptera	Scoliidae	Scoliinae (?)	*Vobalayca flavifrons*
Hymenoptera	Formicidae	Formicinae	*Lepisiota* sp. 1
Hymenoptera	Formicidae	Formicinae	*Polyrhachis lacteipennis*
Hymenoptera	Formicidae	Myrmicinae	*Monomorium* sp. 1
Hymenoptera	Formicidae	Myrmicinae	*Trichomyrmex* sp. 1
Hymenoptera	Formicidae	?	Sp. 1
Hymenoptera	Vespidae	Eumeninae	*Cyrtolabulus* sp. 1
Hymenoptera	Vespidae	Eumeninae	*Delta* sp. 1
Hymenoptera	Vespidae	Eumeninae	*Delta esuriens*
Hymenoptera	Vespidae	Eumeninae	*Delta hottentottum*
Hymenoptera	Vespidae	Eumeninae	*Delta lepeleterii*
Hymenoptera	Vespidae	Eumeninae	Sp. 1
Hymenoptera	Vespidae	Eumeninae	Sp. 2
Hymenoptera	Vespidae	Eumeninae	Sp. 3
Hymenoptera	Vespidae	Eumeninae	Sp. 4
Hymenoptera	Vespidae	Eumeninae	Sp. 5
Hymenoptera	Vespidae	Masarinae	Sp. 1
Hymenoptera	Vespidae	Polistinae	*Polistes wattii*
Hymenoptera	Vespidae	Vespinae	*Vespa orientalis*

Hymenoptera	?	?	Chalcidoidea sp. 1
Hymenoptera	?	?	Chalcidoidea sp. 2
Hymenoptera	Gasteruptiidae	Gasteruptiinae	*Gasteruption* sp. 1
Hymenoptera	Crabronidae	Bembicinae	*Bembecinus* sp. 1
Hymenoptera	Crabronidae	Bembicinae	Sp. 1
Hymenoptera	Crabronidae	Crabroninae	*Dasyproctus arabs*
Hymenoptera	Crabronidae	Philanthinae	*Cerceris* sp. 1
Hymenoptera	Crabronidae	Philanthinae	*Cerceris* sp. 2
Hymenoptera	Sphecidae	Ammophilinae	*Ammophila* sp. 1
Hymenoptera	Sphecidae	?	Sp. 1
Hymenoptera	Sphecidae	?	Sp. 2
Hymenoptera	Colletidae	Colletinae	*Colletes* sp. 1 (M)
Hymenoptera	Colletidae	Hylaeinae	*Hylaeus* sp. 1 (F)
Hymenoptera	Colletidae	Hylaeinae	*Hylaeus* sp. 1 (M)
Hymenoptera	Colletidae	Hylaeinae	*Hylaeus* sp. 2 (M)
Hymenoptera	Colletidae	Hylaeinae	*Hylaeus* sp. 3 (M)
Hymenoptera	Halictidae	Rophitinae	*Systropha* sp. 1 (F)
Hymenoptera	Halictidae	Rophitinae	*Systropha* sp. 1 (M)
Hymenoptera	Halictidae	Nomiinae	*Nomia* sp. 1 (M)
Hymenoptera	Halictidae	Nomiinae	*Pseudapis* sp. 1(F)
Hymenoptera	Halictidae	Nomiinae	*Pseudapis* sp. 1(M)
Hymenoptera	Halictidae	Nomioidinae	Sp. 1 (F)
Hymenoptera	Halictidae	Nomioidinae	Sp. 2 (F)
Hymenoptera	Halictidae	Nomioidinae	Sp. 1 (M)
Hymenoptera	Halictidae	Nomioidinae	Sp. 2 (M)
Hymenoptera	Halictidae	Nomioidinae	Sp. 3 (M)
Hymenoptera	Halictidae	Halictinae	*Halictus*

			lucidipennis
Hymenoptera	Halictidae	Halictinae	*Halictus tibialis*
Hymenoptera	Megachilidae	Megachilinae	Osmiini sp. 1(F)
Hymenoptera	Megachilidae	Megachilinae	Osmiini sp. 2(F)
Hymenoptera	Megachilidae	Megachilinae	Osmiini sp. 3(F)
Hymenoptera	Megachilidae	Megachilinae	Osmiini sp. 1(M)
Hymenoptera	Megachilidae	Megachilinae	Anthidiini sp. 1 (M)
Hymenoptera	Megachilidae	Megachilinae	Anthidiini sp. 1 (F)
Hymenoptera	Megachilidae	Megachilinae	Anthidiini sp. 2 (F)
Hymenoptera	Megachilidae	Megachilinae	*Eoanthidium* sp. 1 (M)
Hymenoptera	Megachilidae	Megachilinae	*Eoanthidium* sp. 1 (F)
Hymenoptera	Megachilidae	Megachilinae	*Icteranthidium* sp. 1(F)
Hymenoptera	Megachilidae	Megachilinae	*Icteranthidium* sp. 1(M)
Hymenoptera	Megachilidae	Megachilinae	*Icteranthidium* sp. 2(M)
Hymenoptera	Megachilidae	Megachilinae	*Icteranthidium* sp. 3(M)
Hymenoptera	Megachilidae	Megachilinae	Megachile sp. 1(M)
Hymenoptera	Megachilidae	Megachilinae	Megachile sp. 2(M)
Hymenoptera	Megachilidae	Megachilinae	Megachile sp. 3(M)
Hymenoptera	Megachilidae	Megachilinae	Megachile sp. 1(F)
Hymenoptera	Megachilidae	Megachilinae	Megachile sp. 2(F)
Hymenoptera	Megachilidae	Megachilinae	Megachile sp.

			3(F)
Hymenoptera	Megachilidae	Megachilinae	*Megachile soikai*
Hymenoptera	Megachilidae	Megachilinae	*Megachile walkerii*
Hymenoptera	Apidae	Apinae	*Xylocopa* sp. 1 (F)
Hymenoptera	Apidae	Apinae	*Apis florea*
Hymenoptera	Apidae	Apinae	*Apis mellifera*
Lepidoptera	Hesperiidae	Coeliadinae	*Coeliades anchises*
Lepidoptera	Lycaenidae	Polyommatinae	*Azanus jesous*
Lepidoptera	Lycaenidae	Polyommatinae	*Chilades trochylus*
Lepidoptera	Lycaenidae	Polyommatinae	*Lampides boeticus*
Lepidoptera	Lycaenidae	Polyommatinae	*Tarucus rosaceus*
Lepidoptera	Lycaenidae	Theclinae	*Myrina silenus*
Lepidoptera	Nymphalidae	Satyrinae	*Ypthima asterope*
Lepidoptera	Pieridae	Pierinae	*Anaphaeis aurota*
Lepidoptera	Pieridae	Pierinae	*Colotis eucharis*
Lepidoptera	Pieridae	Pierinae	*Colotis fausta*
Lepidoptera	Pieridae	Pierinae	*Pontia glauconome*
Coleoptera	Anthicidae	Anthicinae	*Anthelephila multiformis*
Coleoptera	Buprestidae	Agrilinae	*Anthaxia abdita*
Coleoptera	Buprestidae	Polycestinae	*Acmaeodera guichardi*
Coleoptera	Buprestidae	Polycestinae	*Acmaeodera vanharteni*
Coleoptera	Chrysomelidae	Bruchinae	*Spermophagus* sp. 1
Coleoptera	Coccinellidae	Coccinellinae	*Menochilus*

			sexmaculatus
Coleoptera	Dasytidae	?	Sp. 1
Coleoptera	Dermestidae	Attageninae	*Attagenus* sp. 1
Coleoptera	Dermestidae	Megatominae	*Anthrenus* sp. 1
Coleoptera	Dermestidae	Megatominae	*Anthrenus* sp. 2
Coleoptera	Dermestidae	Megatominae	*Anthrenus* sp. 3
Coleoptera	Dermestidae	Megatominae	*Anthrenus* sp. 4
Coleoptera	Dermestidae	Megatominae	*Anthrenus* sp. 5
Coleoptera	Dermestidae	Megatominae	*Phradonoma* sp. 1
Coleoptera	Malachiidae	?	Sp. 1
Coleoptera	Malachiidae	?	Sp. 2
Coleoptera	Malachiidae	?	Sp. 3
Coleoptera	Mordellidae	Mordellinae	*Paratomoxioda harteni*
Diptera	Bombyliidae	Anthracinae	*Anthrax trifasciatus*
Diptera	Bombyliidae	Anthracinae	*Exhyalanthrax beckerianus*
Diptera	Bombyliidae	Anthracinae	*Exoprosopa linearis*
Diptera	Bombyliidae	Toxophorinae	*Geron gibbosus*
Diptera	Bombyliidae	Lomatiinae	*Petrorossia* sp. 1
Diptera	Bombyliidae	Lomatiinae	*Petrorossia* sp. 2
Diptera	Calliphoridae	Chrysomyinae	*Chrysomya marginalis*
Diptera	Muscidae	Coenosiinae	*Coenosia attenuata*
Diptera	Muscidae	Muscinae	*Musca domestica*
Diptera	Mythicomyiidae	Platypyginae	*Cephalodromia*
Diptera	Sarcophagidae	Miltogramminae	Sp. 1
Diptera	Sarcophagidae	Paramacronychiinae	*Wohlfahrtia* sp. 1
Diptera	Syrphidae	Eristalinae	*Eristalinus aeneus*
Diptera	Syrphidae	Syrphinae	*Paragus*

			compeditus
Diptera	Tachinidae	Exoristinae	*Exorista xanthaspis*
Diptera	Tachinidae	Phasiinae	*Gymnosoma desertorum/ dolycoridis*
Diptera	Tephritidae	Tephritinae	*Trupanea amoena*
Hemiptera	?	?	Sp. 1
Hemiptera	?	?	Sp. 2

Table S2. Al Far Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Ant sp.1	1	0.5	0	0.10	0.00
Chalcidoidea sp.1	1	0.5	0	0.10	0.00
Polistes wattii	1	0.5	0	0.04	0.05
Campsomeriella thoracica	1	0.5	0	0.10	0.00
Vobalayca flavifrons	1	0.5	0	0.10	0.00
Delta sp.1	1	0.5	0	0.04	0.05
Eumeninae sp.1	1	0.5	0	0.04	0.05
Xylocopa sp. 1 (F)	1	0.5	0	0.10	0.28
Colotis fausta	1	0.5	0	0.10	0.00
Anaphaeis aurota	1	0.5	0	0.10	0.00
Tarucus rosaceus	1	0.5	0	0.04	0.65
Pontia glauconome	1	0.5	0	0.10	0.00
Myrina silenus	1	0.5	0	0.10	0.00
Tephrosia apollinea	4	0.31	0	NaN	1
Calotropis gigantea	9	0.69	0	NaN	1

Table S3. Bima Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Chrysididae sp. 3	1	0.33	0	0.06	0.00
Cyrtolabulus sp. 1	1	0.33	0	0.01	0.71
Apis mellifera	1	0.33	0	0.06	0.00
Anthidiini sp. 2(F)	1	0.33	0	0.01	0.83
Anthidiini sp. 3(F)	1	0.33	0	0.06	0.00
Eoanthidium sp. 1(M)	1	0.33	0	0.06	0.00
Icteranthidium sp. 1(F)	1	0.33	0	0.06	0.19
Megachilini sp.3 (F)	1	0.33	0	0.06	0.00
Megachilini sp.3 (M)	1	0.33	0	0.06	0.00
Pseudapis sp. 1(M)	1	0.33	0	0.06	0.00
Halictus tibialis (F)	1	0.33	0	0.06	0.00
Nomioidinae sp. 1(F)	1	0.33	0	0.06	0.00
Nomioidinae sp. 1(M)	1	0.33	0	0.06	0.00
Anthelephila multiformis	1	0.33	0	0.06	0.20
Paratomoxioda harteni	1	0.33	0	0.06	0.00
Coenosia attenuata	1	0.33	0	0.06	0.00
Exhyalanthrax beckerianus	1	0.33	0	0.06	0.00
Exoprosopa linearis	1	0.33	0	0.06	0.00
Chilades trochylus	1	0.33	0	0.01	0.71
Tarucus rosaceus	1	0.33	0	0.06	0.00
Ochradenus aucheri	17	0.85	0	0.5	0.82
Boerhavia sp. 1	3	0.15	0	0.0	1.00
Physorhynchus chamaerapistrum	1	0.05	0	0.5	0.70

Table S4. Snake Gorge Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Chrysididae sp. 1	1	0.5	0	0.1	0
Bembecinus sp.1	1	0.5	0	0.1	0
Sphecidae sp. 1	1	0.5	0	0.1	0
Sphecidae sp. 2	1	0.5	0	0.1	0
Halictus tibialis (F)	1	0.5	0	0.1	0
Nomioidinae sp. 1(F)	1	0.5	0	0.1	0
Nomioidinae sp. 2(F)	1	0.5	0	0.1	0
Nomioidinae sp. 2(M)	1	0.5	0	0.1	0
Nomioidinae sp. 3(M)	1	0.5	0	0.0	1
Miltogramminae sp. 1	1	0.5	0	0.1	0
Musca domestica	1	0.5	0	0.1	0
Physorhynchus chamaerapistrum	1	0.09	0	NaN	1
Ochradenus arabicus	10	0.91	0	NaN	1

Table S5. Bidbid Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Lepisiota sp. 1	1	0.2	0.00	0.02	0.86
Chrysididae sp. 2	1	0.2	0.00	0.03	0.00
Masarinae sp. 1	1	0.2	0.00	0.00	1.00
Delta hottentottum	1	0.2	0.00	0.03	0.00
Vespa orientalis	1	0.2	0.00	0.03	0.00
Bembicinae sp. 1	1	0.2	0.00	0.03	0.00
Ammophila sp. 1	1	0.2	0.00	0.03	0.00
Gasteruption sp. 1	1	0.2	0.00	0.03	0.00
Apis florea	1	0.2	0.00	0.03	0.01
Apis mellifera	1	0.2	0.00	0.03	0.00
Colletes sp. 1 (M)	1	0.2	0.00	0.03	0.00
Hylaeus sp. 1 (M)	1	0.2	0.00	0.03	0.00
Nomioidinae sp. 1 (M)	1	0.2	0.00	0.03	0.00
Nomioidinae sp. 1 (F)	1	0.2	0.00	0.03	0.00
Anthidiini sp. 1 (M)	1	0.2	0.00	0.03	0.00

Eoanthidium sp. 1 (M)	2	0.4	0.07	0.02	0.63
Icteranthidium sp. 3 (M)	1	0.2	0.00	0.03	0.00
Osmiini sp. 1 (M)	1	0.2	0.00	0.03	0.00
Osmiini sp. 1 (F)	1	0.2	0.00	0.03	0.00
Megachilini sp. 1 (M)	1	0.2	0.00	0.03	0.00
Megachilini sp. 2 (M)	1	0.2	0.00	0.02	0.58
Megachilini sp. 1 (F)	1	0.2	0.00	0.01	0.78
Anthelephila multiformis	1	0.2	0.00	0.03	0.00
Attagenus sp. 1	1	0.2	0.00	0.03	0.00
Malachiidae sp. 2	2	0.4	0.21	0.03	0.03
Malachiidae sp. 3	1	0.2	0.00	0.03	0.00
Dasytidae sp. 1	2	0.4	0.40	0.03	0.06
Paratomoxioda harteni	1	0.2	0.00	0.03	0.00
Anthrenus sp. 3	1	0.2	0.00	0.03	0.00
Anthrenus sp. 5	1	0.2	0.00	0.03	0.00
Hemiptera sp. 1	1	0.2	0.00	0.03	0.00
Pontia glauconome	2	0.4	0.21	0.03	0.02
Colotis eucharis	2	0.4	0.11	0.02	0.69
Anthrax trifasciatus	1	0.2	0.00	0.02	0.68
Petrorossia sp. 2	1	0.2	0.00	0.02	0.68
Coenosia attenuata	1	0.2	0.00	0.03	0.00
Ochradenus aucheri	28	0.78	0.25	0.25	0.81
Fagonia sp. 1	5	0.14	0.25	0.25	0.55

Tephrosia apollinea	3	0.08	0.25	0.25	0.86
Plocama aucheri	4	0.11	0.25	0.25	0.77
Heliotropium longiflorum	1	0.03	0.00	0.00	1.00

Table S6. Ghubrah Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Lepisiota sp. 1	1	0.5	0	0.08	0.25
Chalcidoidea sp. 2	1	0.5	0	0.05	0.28
Delta lepeleterii	1	0.5	0	0.08	0.00
Cerceris sp. 2	1	0.5	0	0.08	0.13
Pseudapis sp. 1 (F)	1	0.5	0	0.08	0.13
Pseudapis sp. 1 (M)	1	0.5	0	0.08	0.00
Icteranthidium sp. 3 (M)	1	0.5	0	0.08	0.00
Osmiini sp. 1 (F)	1	0.5	0	0.08	0.00
Megachile walkeri (M)	1	0.5	0	0.08	0.00
Dasytidae sp. 1	1	0.5	0	0.08	0.00
Cephalodromia sp. 1	1	0.5	0	0.05	0.28
Eristalinus aeneus	1	0.5	0	0.05	0.28
Exhyalanthrax beckerianus	1	0.5	0	0.05	0.46
Geron gibbosus	1	0.5	0	0.05	0.28
Petrorossia sp. 1	1	0.5	0	0.05	0.28
Asphodelus fistulosus	6	0.4	0	NaN	1
Ochradenus aucheri	9	0.6	0	NaN	1

Table S7. Lizugh Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Ammophila sp. 1	1	0.33	0	0.17	0.58
Apis mellifera	1	0.33	0	0.20	0.00
Icteranthidium sp. 2 (M)	1	0.33	0	0.20	0.00
Pontia glauconome	3	1.00	1	0.27	0.01
Eristalinus aeneus	1	0.33	0	0.17	0.64
Dipterygium glaucum	2	0.4	0	0.33	0.24
Fagonia sp. 1	2	0.4	0	0.33	0.25
Physorhynchus chamaerapistrum	3	0.6	0	0.33	0.32

Table S8. Oman Botanic Garden Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Polistes wattii	2	0.67	1	0.21	0.17
Ammophila sp. 1	1	0.33	0	0.05	0.61
Systropha sp. 1 (M)	1	0.33	0	0.13	0.49
Osmiini sp. 3 (F)	1	0.33	0	0.05	0.61
Lampides boeticus	1	0.33	0	0.18	0.10
Azanus jesous	1	0.33	0	0.18	0.10
Gymnosoma desertorum/dolycoridis	1	0.33	0	0.18	0.10
Convolvulus sp.1	2	0.29	0	0.5	0.48
Convolvulus sp.2	2	0.29	0	0.0	1.00
Taverniera cuneifolia	4	0.57	0	0.5	0.37

Table S9. Taww Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Lepisiota sp. 1	2	0.67	0	0.09	0.50
Apis mellifera	1	0.33	0	0.09	0.09
Megachilini sp. 2 (F)	1	0.33	0	0.09	0.00
Megachilini sp. 3 (F)	2	0.67	0	0.09	0.08
Megachilini sp. 2 (M)	1	0.33	0	0.09	0.00
Nomia (Crocisaspidia) sp. 1	1	0.33	0	0.09	0.00
Osmiini sp. 1 (F)	1	0.33	0	0.09	0.00
Icteranthidium sp. 1 (M)	1	0.33	0	0.09	0.00
Icteranthidium sp. 2 (M)	1	0.33	0	0.09	0.00
Pontia glauconome	1	0.33	0	0.01	0.80
Tarucus rosaceus	1	0.33	0	0.09	0.00
Lampides boeticus	2	0.67	0	0.09	0.07
Trupanea amoena	1	0.33	0	0.01	0.80
Asphodelus fistulosus	2	0.15	0	0.0	1.00
Tephrosia apollinea	3	0.23	0	0.5	0.19
Taverniera cuneifolia	11	0.85	0	0.5	0.30

Table S10. Siya Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Polyrhacis lacteipennis	1	0.2	0.00	0.07	0.37
Delta esuriens	1	0.2	0.00	0.07	0.14
Delta hottentottum	1	0.2	0.00	0.07	0.14
Eumeninae sp. 2	1	0.2	0.00	0.07	0.14
Eumeninae sp. 3	1	0.2	0.00	0.06	0.47
Dasyproctus arabs	1	0.2	0.00	0.07	0.14
Pseudapis sp. 1 (F)	1	0.2	0.00	0.06	0.47
Anthrenus sp. 2	1	0.2	0.00	0.07	0.14
Menochilus sexmaculatus	1	0.2	0.00	0.07	0.14
Anthaxia abdita	1	0.2	0.00	0.07	0.47
Acmaeodera vanharteni	1	0.2	0.00	0.07	0.21
Acmaeodera guichardi	2	0.4	0.00	0.07	0.42
Chilades trochylus	2	0.4	0.07	0.07	0.24
Colotis fausta	1	0.2	0.00	0.00	1.00
Ypthima asterope	4	0.8	0.93	0.09	0.00
Coeliades anchises	1	0.2	0.00	0.07	0.00
Ochradenus aucheri	8	0.50	0	0.25	0.81
Asteraceae sp. 1	2	0.13	0	0.25	0.35
Lavandula subnuda	6	0.38	0	0.25	0.52
Diplotaxis harra	1	0.06	0	0.00	1.00
Chrozophora oblongifolia	4	0.25	0	0.25	0.69

Table S11. Wadi Arbein Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Lepisiota sp. 1	2	0.67	0	0.13	0.78
Halictus lucidipennis (F)	1	0.33	0	0.25	0.39
Acmaeodera guichardi	1	0.33	0	0.25	0.39
Chilades trochylus	1	0.33	0	0.13	0.61
Pontia glauconome	1	0.33	0	0.25	0.37
Plocama aucheri	1	0.2	0	0.5	0.64
Morettia parviflora	2	0.4	0	0.5	0.22
Pulicaria glutinosa	3	0.6	0	0.00	1.00

Table S12. Wadi Mayh Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Lepisiota sp. 1	1	0.5	0	0.04	0.00
Monomorium sp.1	1	0.5	0	0.04	0.00
Cerceris sp. 1	1	0.5	0	0.04	0.00
Bembecinus sp. 1	1	0.5	0	0.04	0.00
Bembicinae sp. 1	1	0.5	0	0.04	0.00
Ammophila sp. 1	1	0.5	0	0.04	0.00
Hylaeus sp. 1 (F)	1	0.5	0	0.04	0.00
Halictus lucidipennis (F)	1	0.5	0	0.04	0.00
Nomioidinae sp.1 (M)	1	0.5	0	0.04	0.00
Nomioidinae sp.1 (F)	1	0.5	0	0.04	0.00
Osmiini sp. 3 (F)	1	0.5	0	0.04	0.00
Pseudapis sp. 1 (F)	1	0.5	0	0.04	0.00
Pseudapis sp. 1 (M)	1	0.5	0	0.04	0.00
Megachile walkeri (M)	1	0.5	0	0.04	0.00
Eoanthidium sp. 1 (M)	1	0.5	0	0.04	0.00
Eoanthidium sp. 1 (F)	1	0.5	0	0.04	0.00
Anthelephila multiformis	1	0.5	0	0.04	0.00
Attagenus sp.1	1	0.5	0	0.04	0.00
Dasytidae sp.1	1	0.5	0	0.04	0.00
Anthrenus sp. 1	1	0.5	0	0.04	0.00
Anthrenus sp. 3	1	0.5	0	0.04	0.00
Anthrenus sp. 4	1	0.5	0	0.04	0.00
Phradonoma sp. 1	1	0.5	0	0.04	0.00
Tarucus rosaceus	2	1.0	0	0.04	0.41
Pontia glauconome	1	0.5	0	0.04	0.00
Coeliades anchises	1	0.5	0	0.04	0.00
Hemiptera sp. 2	1	0.5	0	0.04	0.00
Ochradenus aucheri	27	1.00	0	0.5	0.28
Rhazya stricta	1	0.04	0	0.5	0.72

Table S13. Yiti 1 Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Attagenus sp. 1	2	0.50	0	0.14	0.09
Malachiidae sp. 2	1	0.25	0	0.14	0.00
Dasytidae sp. 1	1	0.25	0	0.14	0.06
Anthrenus sp. 3	1	0.25	0	0.14	0.04
Phradonoma sp. 1	1	0.25	0	0.14	0.00
Eumeninae sp. 4	1	0.25	0	0.00	1.00
Cerceris sp. 1	1	0.25	0	0.14	0.00
Megachilini sp. 3 (F)	1	0.25	0	0.06	0.72
Osmiini sp. 1 (F)	1	0.25	0	0.06	0.72
Paragus compeditus	1	0.25	0	0.06	0.72
Lavandula subnuda	1	0.1	0	0.0	1.00
Taverniera cuneifolia	3	0.3	0	0.0	1.00
Euphorbia larica	6	0.6	0	0.5	0.66
Morettia parviflora	1	0.1	0	0.5	0.19

Table S14. Yiti 2 Network Results

Species	Degree	ND	Betweeness	Closeness	d’
Lepisiota sp.1	2	0.4	0.02	0.04	0.54
Trichomyrmex sp.1	2	0.4	0.22	0.06	0.13
Sphecidae sp. 1	1	0.2	0.00	0.04	0.00
Eumeninae sp. 4	1	0.2	0.00	0.04	0.43
Eumeninae sp. 5	1	0.2	0.00	0.04	0.35
Apis florea	1	0.2	0.00	0.04	0.29
Hylaeus sp. 1 (F)	1	0.2	0.00	0.04	0.35
Hylaeus sp. 2 (M)	1	0.2	0.00	0.04	0.00
Hylaeus sp. 3 (M)	1	0.2	0.00	0.04	0.00
Megachilini sp. 2 (F)	1	0.2	0.00	0.04	0.35
Megachile soikai	1	0.2	0.00	0.04	0.00
Osmiini sp. 2 (F)	2	0.4	0.66	0.05	0.01
Systropha sp. 1 (F)	1	0.2	0.00	0.00	1.00
Attagenus sp. 1	2	0.4	0.01	0.03	0.67
Malachiidae sp. 1	1	0.2	0.00	0.04	0.01
Malachiidae sp. 2	1	0.2	0.00	0.04	0.01
Anthrenus sp. 3	1	0.2	0.00	0.04	0.09
Acmaeodera guichardi	2	0.4	0.09	0.04	0.38
Spermophagus sp. 1	1	0.2	0.00	0.03	0.64
Chrysomya marginalis	1	0.2	0.00	0.04	0.00
Eristalinus aeneus	1	0.2	0.00	0.04	0.00
Exorista xanthaspis	1	0.2	0.00	0.04	0.00
Geron gibbosus	1	0.2	0.00	0.04	0.35
Musca domestica	1	0.2	0.00	0.04	0.00
Paragus compeditus	1	0.2	0.00	0.04	0.35
Wohlfahrtia sp. 1	1	0.2	0.00	0.04	0.01
Ochradenus arabicus	15	0.58	0.0	0.23	0.88
Morettia parviflora	2	0.08	0.0	0.23	0.57
Convolvulus sp. 1	4	0.15	0.5	0.23	0.68
Convolvulus sp. 2	1	0.04	0.0	0.00	1.00
Taverniera cuneifolia	9	0.35	0.5	0.27	0.77

Table S15. List of indices from the bipartite package (Dormann et al., 2009) used to analyse different properties of the network.

Index	Formulae	Range of values
Connectance	$C = L/(IJ)$	-Realised proportion of possible links within the network.
Web Asymmetry	$W = (I-J)/(I+J)$	-Rescaled to [-1, 1] -Positive numbers= more lower-trophic level spp. -Negative numbers= more higher-trophic level spp.
Links per species	$\bar{L}_x = L/(I+J)$	-Mean number of links per spp.
H_2'	n/a	-At the level of the network -0: no specialisation -1: perfect specialisation
d'	n/a	-At the level of the individual species -0: no specialisation -1: perfect specialisation
Niche Overlap	n/a	-0: no common use of niches -1: perfect niche overlap

L: number of realised links in the network.

I: total number of plant species

J: total number of insect species

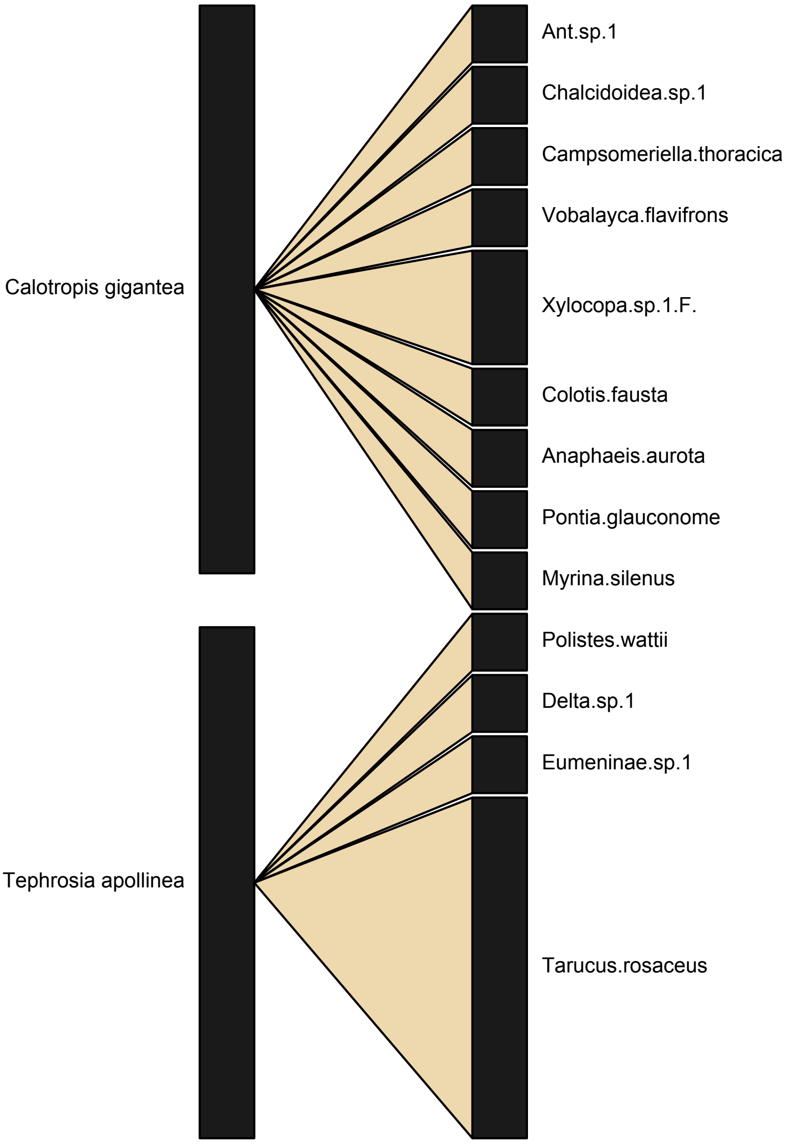


Figure S1. Bipartite graph of the Al Far network

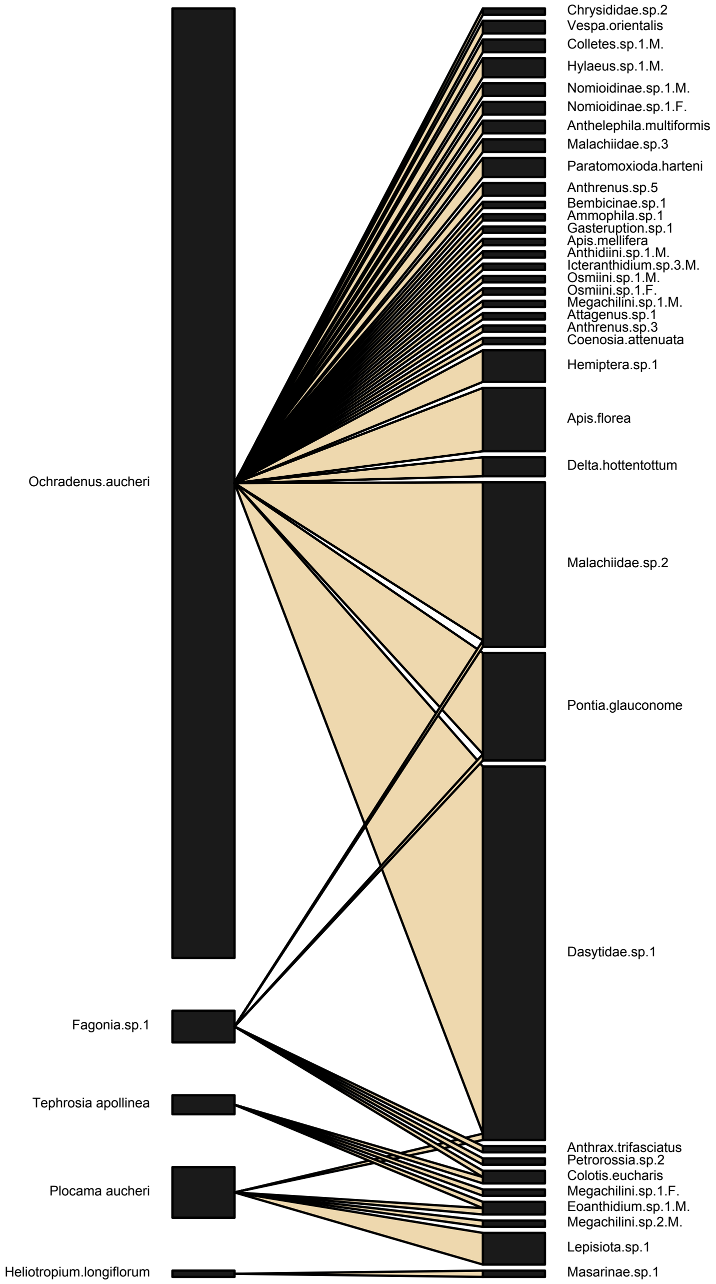


Figure S2. Bipartite graph of the Bima network

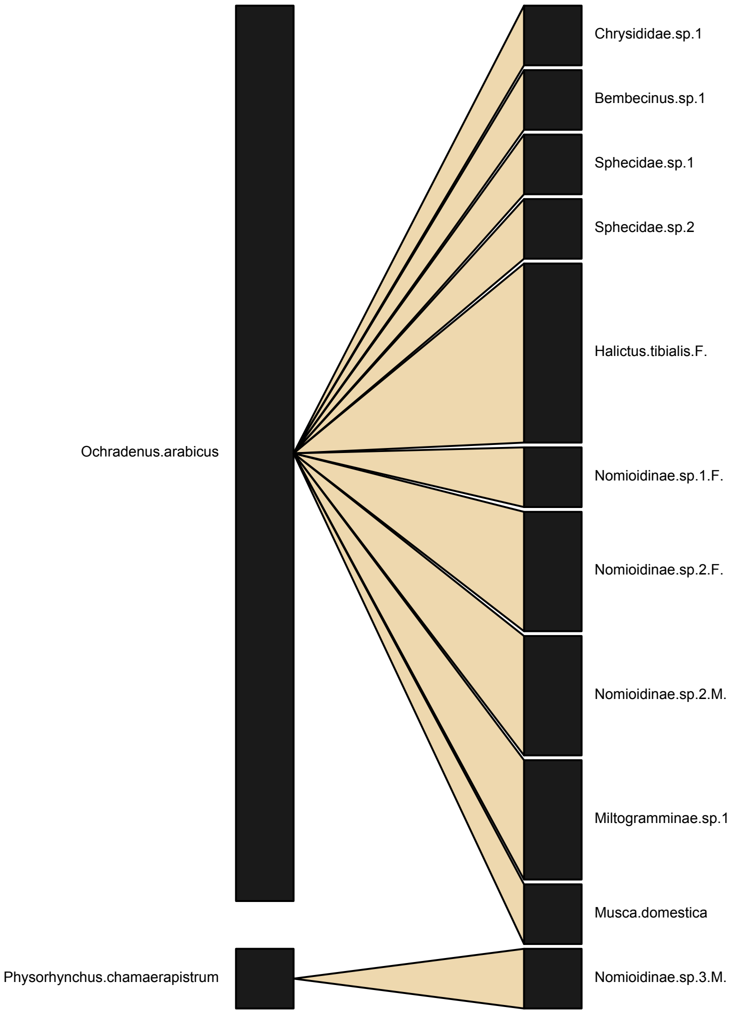


Figure S3. Bipartite graph of the Snake Gorge network

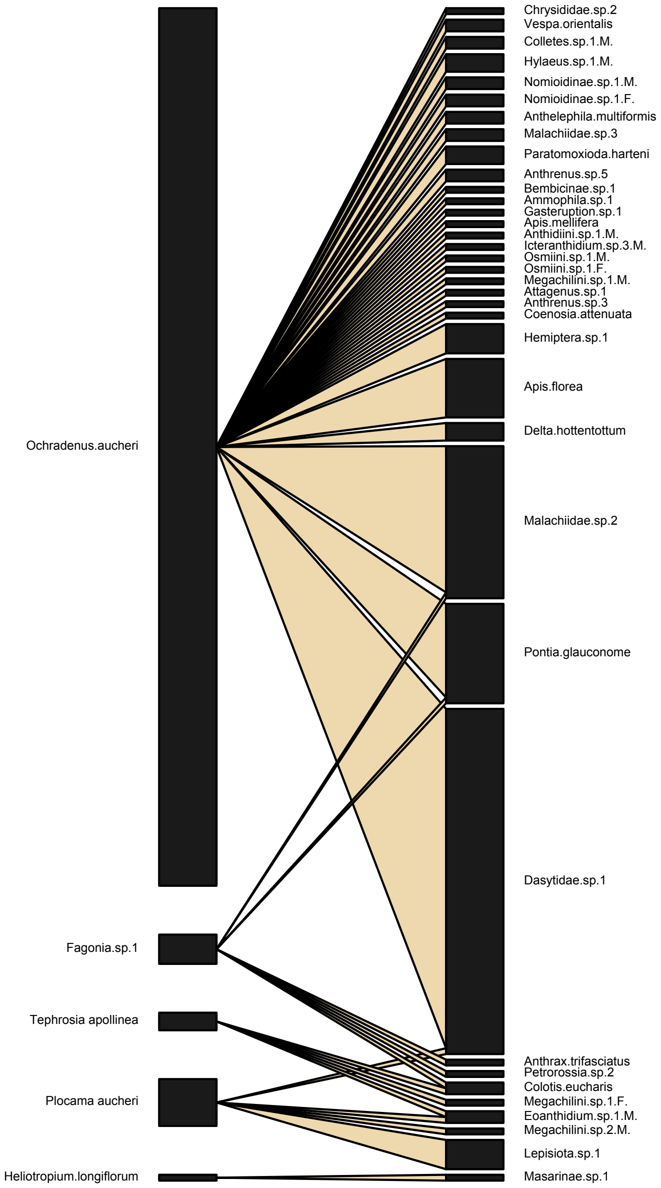


Figure S4. Bipartite graph of the Bidbid network

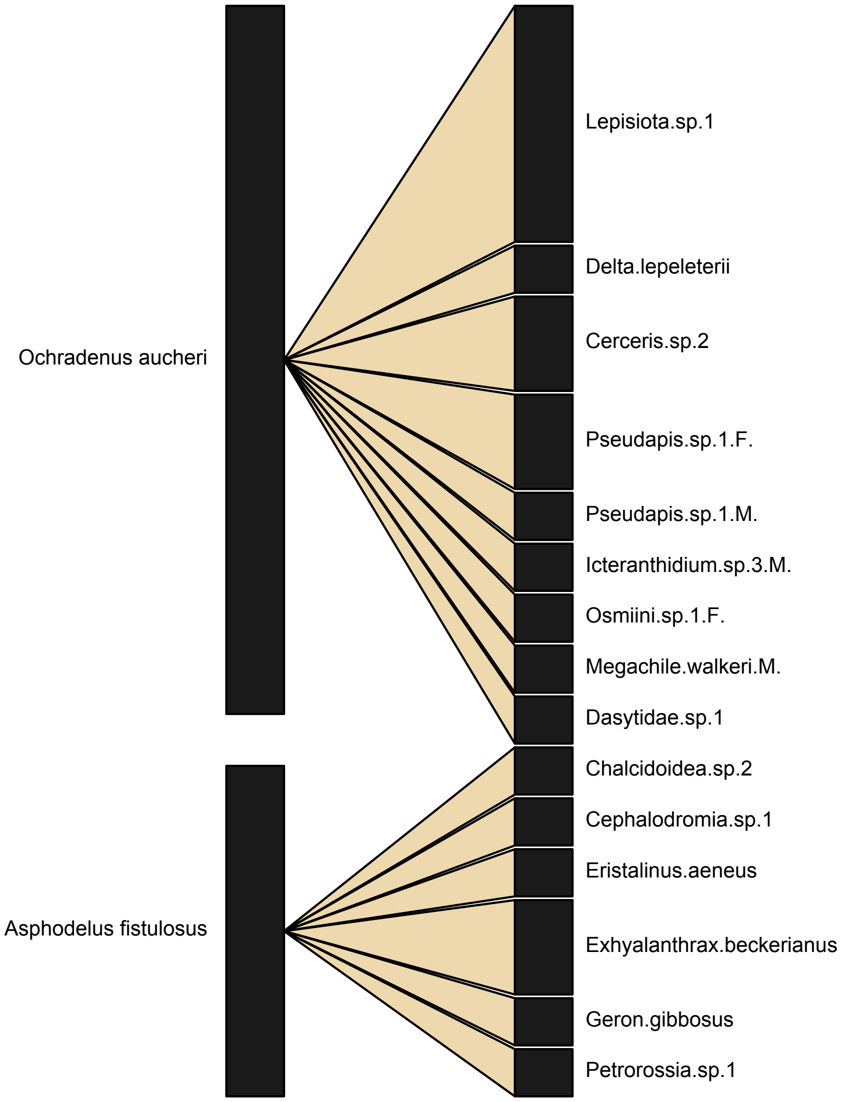


Figure S5. Bipartite graph of the Ghubrah network

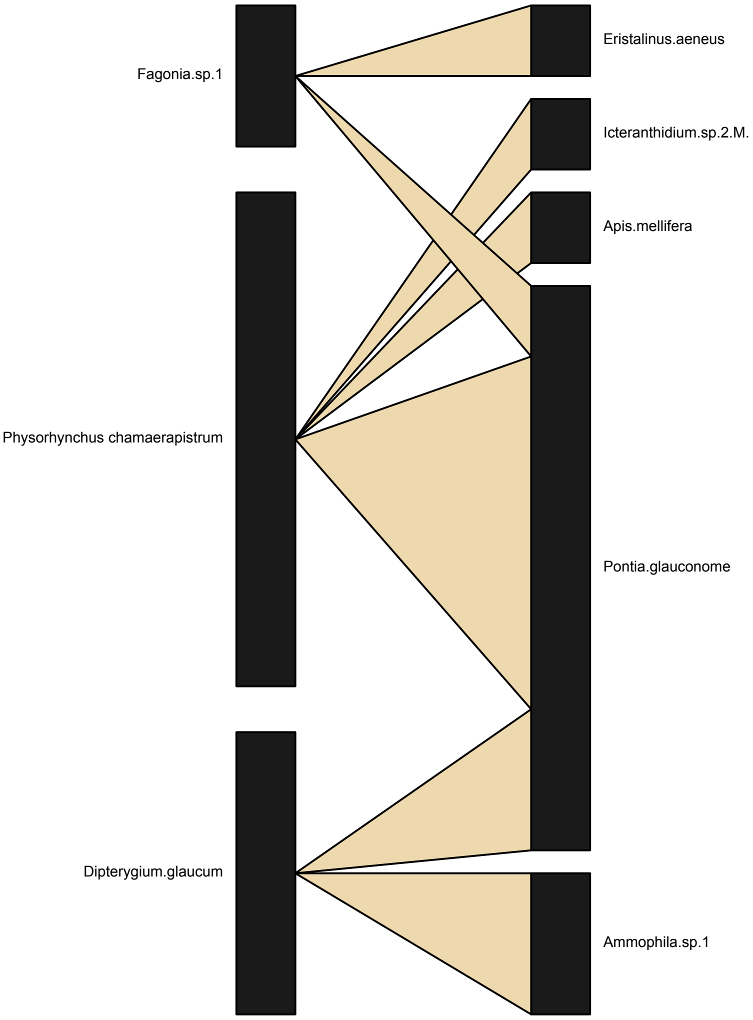


Figure S6. Bipartite graph of the Lizugh network

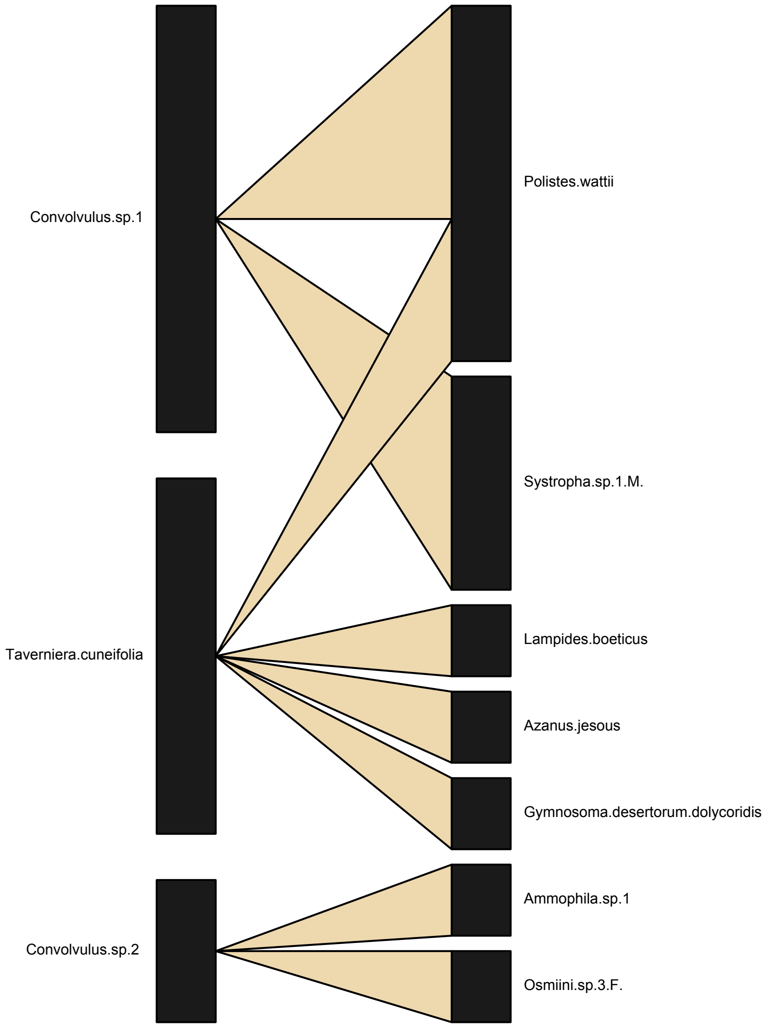


Figure S7. Bipartite graph of the Oman Botanic Garden network

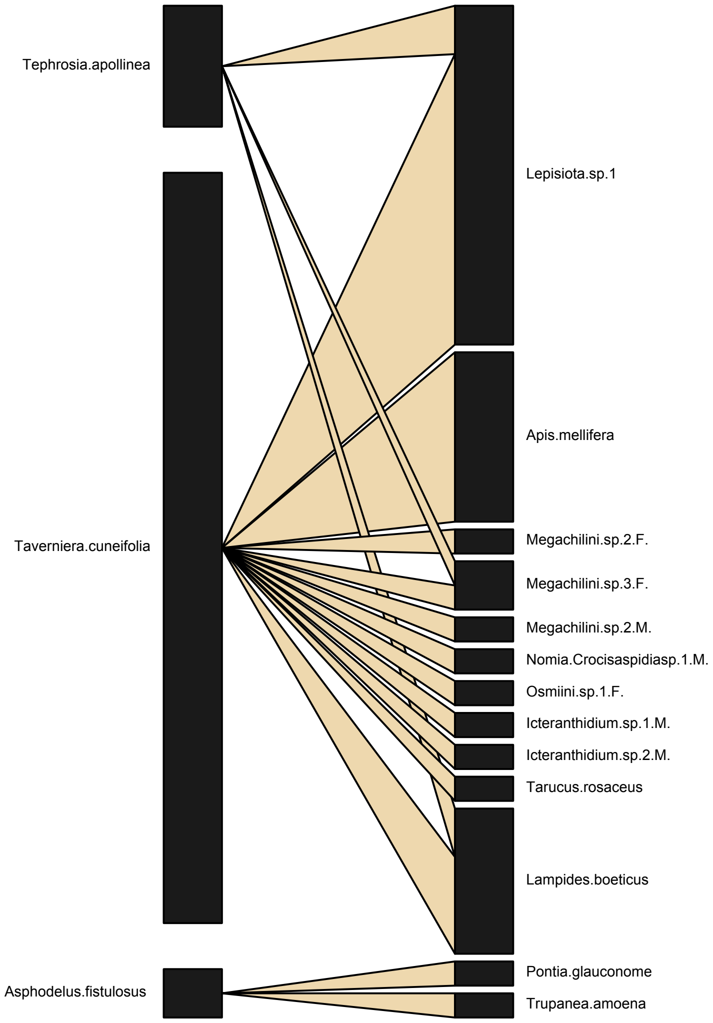


Figure S8. Bipartite graph of the Taww network

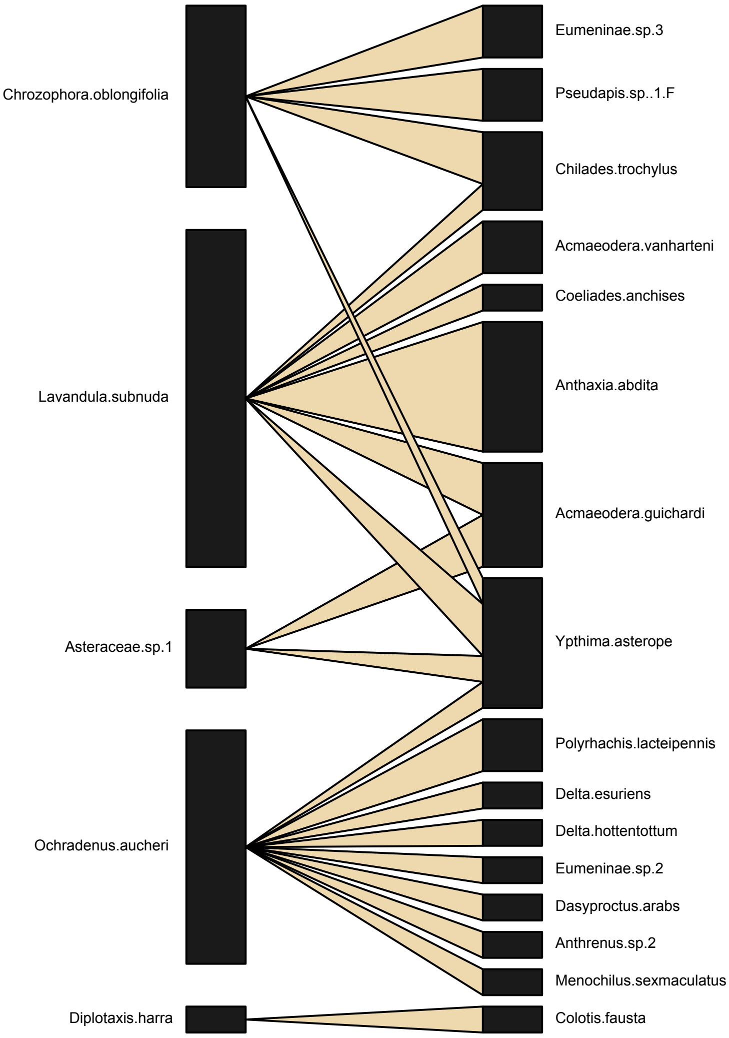


Figure S9. Bipartite graph of the Siya network

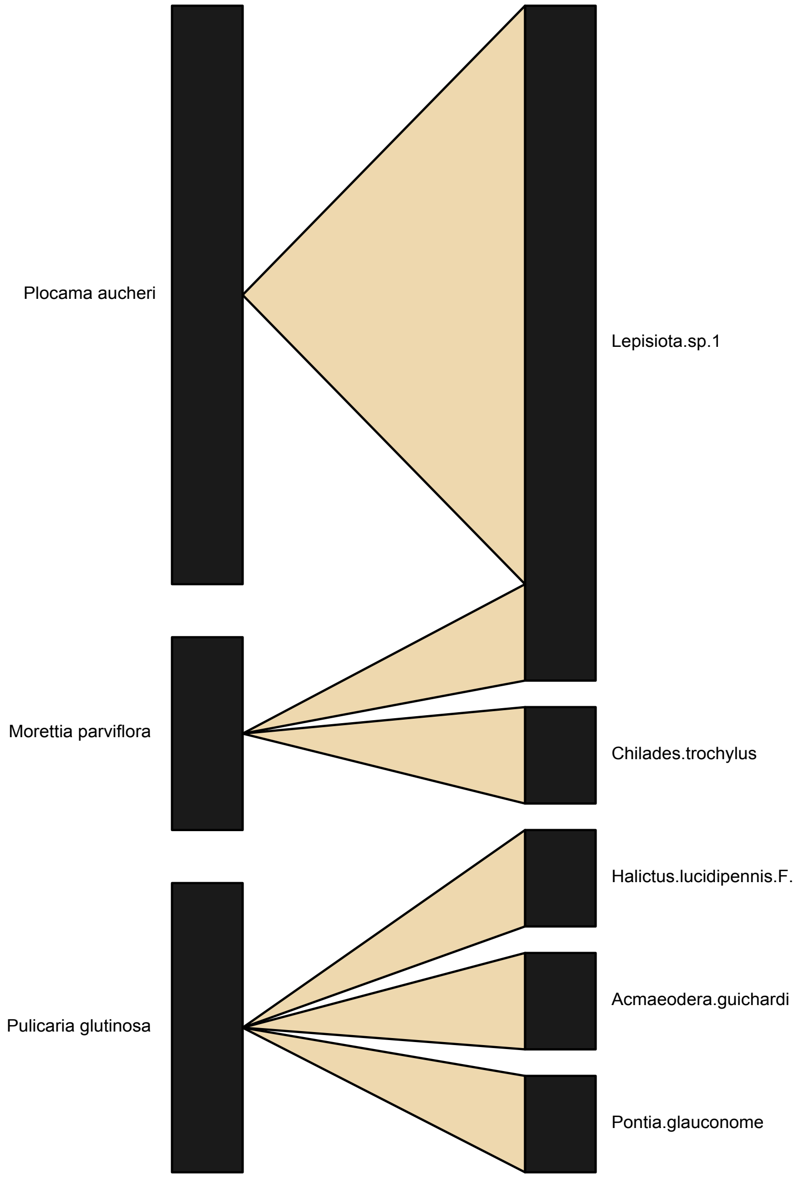


Figure S10. Bipartite graph of the Wadi Arbein network

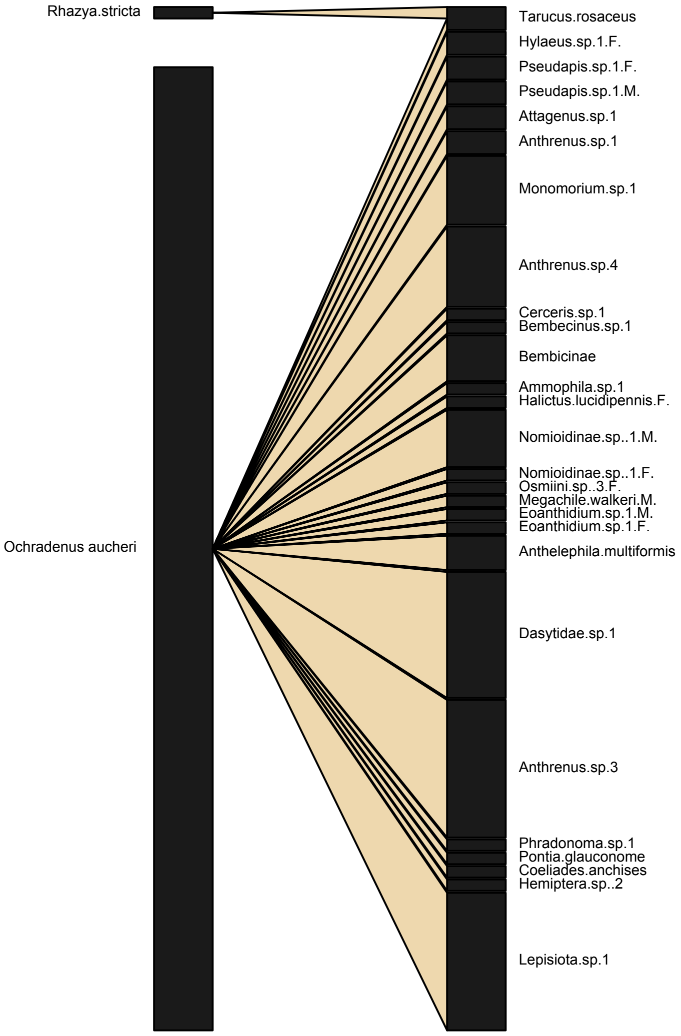


Figure S11. Bipartite graph of the Wadi Mayh network

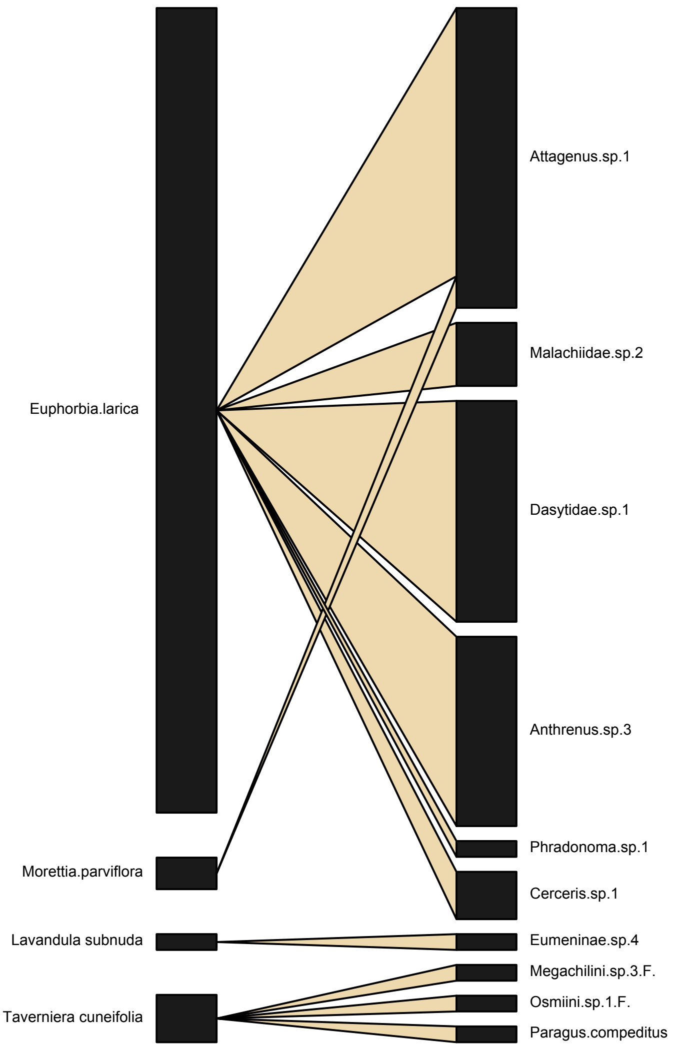


Figure S12. Bipartite graph of the Yiti 1 network

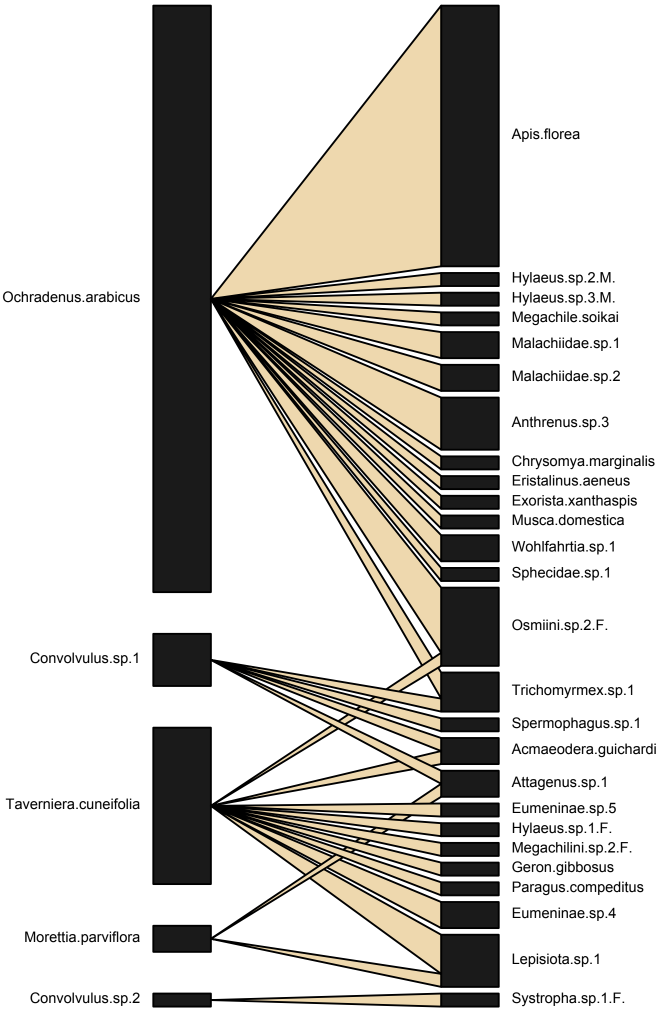


Figure S13. Bipartite graph of the Yiti 2 network

Chapter 3.

Species turnover amongst insect visitors to *Euphorbia larica* along an altitudinal and temporal gradient

Species turnover amongst insect visitors to *Euphorbia larica* along an altitudinal and temporal gradient

Abstract

Interactions within networks have traditionally been viewed as being static. However, studying them through time has shown that turnover is often high and network structure varies among seasons and years. In this study, I look at whether patterns of functional traits and taxonomic distinctness change temporally and spatially for visitors to *Euphorbia larica.* The results suggest a constant loss and gain of species, with no altitudinal replacement of bees by Diptera, as is common in other altitudinal studies. *E. larica* appears to be a generalist, and its visitor community reflects the asymmetrical pattern typical of such networks. This suggests an important role for secondary pollinators because the core of the network is composed of species not generally considered primary pollinators outside of specialised scenarios.

Introduction

While studying pollinators at a community level has become increasingly common over the last few decades (Memmott, 1999; Dupont et al., 2003; Lucas et al., 2018), studies of changes in pollinator interactions through time remain rare (Olesen et al., 2008; Dorchin et al., 2017), with most studies taking place during a single season or year. This static approach makes it difficult to understand the strength of an interaction through time between an insect and the plants they visit. Hence this gives no information regarding their potential coevolutionary relationship or selection pressures. Temporal changes to the abundance of individual visitor or plant species can affect the overall species assemblage and stability at a local level, and the degree of specialisation a species experiences (Souza et al., 2018). Biotic interactions on a broader scale are believed to influence species ranges at the regional to continental level (Araújo & Luoto, 2007; Morales-Castilla et al., 2015), and therefore partially determine geographic ranges. Insects are the primary pollinators of angiosperms (Zurbuchen et al., 2010) and are coming under increasing threat due to factors such as climate change (Singer & Parmesan, 2010). Consequently, understanding the structure of pollination networks and how insects respond to time and space is fundamental to implementing conservation policies that maintain these vital links.

For reciprocal evolution between a host plant and one or more visitors to occur, a relationship must be consistent with some degree of specialisation. Thompson, (1994) highlights that mutual selection can occur between a plant and its pollinator even if specialisation is not constant during the whole of an insect's lifetime. For instance, a bee species may alter how often it forages at a particular plant once other pollen sources become available. Thompson does imply this relationship is temporally consistent at least sometimes, allowing reciprocal coevolution to occur. However, Thompson (2005) also emphasises that selection for coevolution between two species may not be consistent throughout the whole of their ranges, with different populations experiencing differing levels of selection between coevolving partners. A possible cause for this scenario is when pairs of species do not have completely overlapping ranges. Therefore the interaction is not spatially consistent, or indeed necessarily temporally consistent. Within populations at a more local level, several studies have found strong year-to-year temporal turnover in pollinator species (Petanidou & Potts, 2006; Olesen et al., 2008), suggesting that interactions between certain plant and insect species are unreliable, thus obviating the possibility for a coevolutionary relationship to develop.

Unpredictability in visitation rates may be increased further in montane habitats where, for example, Lefebvre et al. (2014) have shown how even the Orders of pollinating insects change over an altitudinal gradient. This was first documented as early as the 1870s, when Müller recognised that at high altitudes in the Alps, butterflies replace bees as the primary pollinators (Thompson, 1994). Habitat filtering can prevent certain insect species entering an environment, for example due to their inability to cope with changing temperatures, wind speeds, and precipitation (Sargent & Ackerly, 2008). In the Andes, bees are replaced by Diptera as the dominant pollinators at higher altitudes (Arroyo et al., 1982; Hodkinson, 2005), and one hypothesis suggests that this is due to the decrease in temperature as well as the environmental conditions (such as damp soils and riverine habitats) being more favourable to the larvae of Diptera (Lefebvre et al., 2018). However, although the replacement of bees by other pollinating insects at high altitudes is commonly recognised (Hodkinson, 2005), apart from air temperature, other climatic variables such as wind speed or precipitation do not share the same global patterns along altitudinal gradients (Körner, 2007). Therefore, when discussing variations in the abundance of different taxa along altitudinal gradients, climatic variables must be considered locally and cannot be applied to mountain ranges broadly. Furthermore, many taxa do not necessarily show linear declines in abundance with altitude, and instead mid-elevation peaks in abundance are a common phenomenon. This observation has been recorded in a wide range of taxa such as in ant species (Sanders, 2002; Szewczyk & McCain, 2019), beetles of the subfamily Steninae (Betz et al., 2020), and the Dipteran family Empididae (Plant et al., 2012). For plant species that grow from sea level to high altitudes, these factors create a mosaic of shifting pollinators that vary in their abilities to transfer pollen successfully. This type of situation is seen in the community of pollinators that visit *Cytisus scoparius* (Fabaceae) in the mountains in Spain (Malo & Baonza, 2002). Here there is a transition from small bee species to larger species, such as *Bombus* spp. with increasing altitude. Pollination success varied with flower size, with seed set higher at lower altitudes where plants were recorded with higher numbers of small flowers. There appears to be a selective pressure for smaller flowers at lower altitudes where smaller bee species were more common. At higher altitudes climatic conditions are unsuitable for small bees. The authors hypothesise that as smaller bees cannot easily access larger flowers, they favour small flowers hence increased pollination success in plants with smaller flowers. This variation in pollination success is as a result of a mosaic of pollinator types.

Nevertheless, while individual visitors to a plant can vary, if functional-group specialisation (based on phylogenetic or morphological similarities: Fenster et al., 2004) is consistent throughout a plant species range, selection may still occur for floral types attractive to certain insect groups. For instance, flowers may evolve traits attractive to both long-tongued bees and Diptera, thus creating a pollination syndrome based around this tongue type (Faegri & van der Pijl, 1966). The idea of floral syndromes has been challenged because pollinators often visit multiple plant species differing in their apparent floral syndrome (Rodríguez-Gironés & Santamaría, 2010). The pollination effectiveness of different functional groups is related to visitation rates, a measure of interaction strength (Bascompte et al., 2006), as well as how efficient each group is in actually delivering the correct pollen to the stigmas (Traveset & Saez, 1997). Therefore when comparing community structure between seasons and years, it is appropriate to use indices that examine phylogenetic and functional diversity rather than simply species richness (Clarke & Warwick, 1998, 1999, 2001). This allows greater insight into whether certain groups of insects drive the evolution of particular floral shapes, colours, scents etc.

When comparing changes to communities in response to space and time, Baselga (2010, 2012) highlighted how beta diversity is composed of two different phenomena, species replacement and nestedness. Species replacement (spatial turnover) records spatial losses and gains in species, as well as different compositions of species (as, for example, where a similar number of Dipteran species replace bee species along an altitudinal gradient). In contrast, nestedness implies that a site can contain a subset of the taxa found in a more species-rich site without replacement having occurred. Thus it is important to separate beta diversity into its two components to understand the processes that underlie the observed patterns and how these may affect plant-pollinator relationships.

While the environmental gradients that occur in mountains can physically partition pollinators by their ability to respond to changing abiotic factors, pollination networks can also be partitioned through time/seasons (Basilio et al., 2006; Baldock et al., 2011). Sampling networks at multiple time periods can reveal “forbidden links” (Jordano et al., 2003), insects and plants within the same habitat that are unable to form links due to different phenologies, or morphologies that physically prevent interactions (Baldock et al., 2011). More recent work investigates species interaction turnover (Poisot et al., 2012; Poisot et al., 2015; CaraDonna et al., 2017), the case where pollinators do not disappear from a habitat, but alter the plant species from which they feed. This means at a single location a plant can be visited by a series of separate communities of pollinating insects that overlap and interact to varying degrees as the season progresses (Basilio et al., 2006).

In terms of consistent densities and temporal visitation rates related to pollinator effectiveness, several studies have shown that the stability of pollinator communities increases with plant species richness (Ghazoul, 2006; Ebeling et al., 2008). In the study site of the Hajar Mountains of Oman, where the main flowering season is limited to January-March, this suggests that pollinator species richness and abundance should be low outside these three months and perhaps show greater fluctuations in composition. This would mean increased instability for insect-pollinated plants that flower outside of the spring months. The results from trapping over two years using yellow pan traps (chapter four) support this supposition, at least for the bees. For example, between May 2017 and January 2018, no more than one bee was collected in each 24-hr trapping period, while between April and November 2018, a total of 8 bees were collected. This contrasts with the results from trapping events during the early spring. Between February and April 2017 a total of 211 individuals were collected, while during February and March 2018, 23 individuals were collected. While abundance was clearly considerably lower in the spring of 2018, due to only 8 bees being collected during the rest of the year abundance still peaked in the early spring months.

Within this chapter I explore the functional and taxonomic diversity of insects visiting *Euphorbia larica* Boiss. (Euphorbiaceae), a plant that flowers both within and outside the main flowering season in the Hajar Mountains, and ask how these change temporally and spatially along an altitudinal gradient. This provides an opportunity to investigate turnover of visitor species both along an altitudinal gradient and during different seasons. From such data I study how turnover patterns influence the stability of the network around *E. larica*, and whether patterns of functional traits of visitors vary through time and space.

I predict insect species richness will increase during the January surveys compared to out-of-season surveys in response to the increased flowering diversity in the environment as a whole. As Diptera are important pollinators of early season flowering plants (Motten 1986; Goldblatt et al., 2004; Ssymank et al., 2008), I expect flies to dominate the species assemblage during the October surveys, with a higher turnover than other pollinators when the surveys are repeated in January. I would expect a higher turnover as Diptera are generally considered generalists in the flowers they will visit. If there is sufficient rainfall, the flowering season starts in January in the Hajar Mountains. Therefore, an increase in the floral options means specialism by Dipteran species to *E. larica* may decline as they're not confined to this one species of plant. Likewise I expect bees to be replaced by Diptera with increasing altitude. As the nectaries on the cyathia of *E. larica* are easily accessible, I expect to see visiting species exhibit a wide range of functional traits.

Specifically I ask the following:

1. Do the visitors to *E. larica* show evidence of functional-group specialisation?
2. Do different orders of pollinators replace each other along an altitudinal gradient?
3. What type of turnover exists and does this vary spatially or temporally?
4. Are there discrete communities of visitors to *E. larica* at different periods of time, indicative of seasonal partitioning of pollinators?

Methods

Study species

Euphorbia larica (Boiss.) (Euphorbiaceae), like many Euphorbiaceae (Raju & Ezradanam, 2002) is a monoecious spurge (Fig 1 & 2), common throughout southern Arabia and Iran. *E. larica* is one of 21 species of *Euphorbia* found in Oman (Ghazanfar & Patzelt, 2005). Of these 21 species, nine are found in the Hajar Mountains of northern Oman, all of which are recorded as flowering and fruiting during February-April (Ghazanfar & Patzelt, 2005) (Table S1). In the Hajar Mountains the plant is abundant below 1500 m, where it is a dominant component of the plant community (Patzelt, 2015).

Flowering of the cyathia and fruiting is recorded in Ghazanfar & Patzelt (2005) from September in Dhofar in southern Oman, and March-April in northern Oman. However, my observations in the Hajar have shown that flowering and fruiting is continuous from October until the end of May, and flowering may ensue whenever rainfall occurs (S. Ghazanfar, pers. comm., April 2019). Whether flowering continues during the summer months is unknown.

The involucre is 1-2 mm long, 4-6 mm in diameter, forming a cup shape that acts as a platform for insects feeding from the nectaries (Ghazanfar & Patzelt, 2005). Nectaries are located on the tips of the bracts (Ghazanfar & Patzelt, 2005). Pollination of almost all species of *Euphorbia* is predominately recorded as zoophilous (Narbona et al., 2002).

Data collection

The study was carried out in the Hajar Mountains, which run across northern Oman: the xeric habitats are composed of plant communities that are predominately animal-pollinated (Regal, 1982). Surveys were conducted across three seasons: October/November 2016, January 2017, and November 2018. During each season seven fieldsites were visited and at each field site, five individual *E. larica* plants were surveyed for their insect visitors.

As one of the aims of the study was to record whether different orders of insect replaced each along an altitudinal gradient, field sites were separated into three altitudinal bands: lowland (0-300 m a.s.l.), mid-level (300-800 m a.s.l.) and highland (800-1400 m a.s.l.) The highest point of the Hajar mountains is ~3000 m a.s.l. on Jebel Shams (Dickhoefer et al., 2010), so the terms low, mid, and high are in relation to the distribution of *E. larica* and not to the mountains themselves. Table S2 lists the location and altitude of each field site (Fig 2 & 3 show the location of all field sites). On arrival at a chosen site (chosen due to its altitude) an *E. larica* plant was selected as one of the survey plants, purely based on whether it was flowering or not.

Prior to the start of the fieldwork the aim was to repeat surveys at the same seven sites during each of the three seasons. However, unforeseen logistical issues prevented the same mid-level and highland sites being visited during each of the three seasons. Only the three lowland sites, Yiti, Taww and Buwah were visited in all three seasons. Nevertheless, if an individual site was changed, a new site was selected at the same altitudinal level as the original site. This was done to try to control for variation in insect species that may be influenced by factors relating to altitude. Consequently, the same number of sites in the same altitudinal band was surveyed at in each of the three seasons.

At each plant, 10 minutes was first spent collecting beetles feeding on nectar within the involucre. Immediately after, a further 10 minutes was then spent at each plant to collect any other insects seen landing on the cyathia. Beetles drop from the involucre if disturbed, and hence were collected first in order not to be lost when collecting other insects with a hand net.

Baldock et al (2011) suggest the rate of network interactions observed is highly dependent on the time of day. My observations showed insect activity was greatest in the morning and declined by midday with rising temperatures, a common observation with the flight activity of bees (Kastinger & Weber, 2001). While some species may have been more active later in the afternoon, particularly at higher altitudes where temperatures are lower, as well as at night, in order to standardise the surveys, all data collection started at 08.00 am.

Because a single *E. larica* can contain several hundred open cyathia at any given time, each plant was ranked on an ordinal scale of 1-5 based on the estimated number of cyathia. This was scored as follows: 1 = extremely few (<10 cyathia), 2 = few (~10-50), 3 = moderate (~50-100), 4 = abundant (~100-200), and 5 = very abundant numbers of open cyathia (>200). Figures S1-3 give the cyathia scores for the three survey periods.

All insects were collected for identification. Staff at the National Museum, Cardiff, identified the Coleoptera and Diptera specimens, while staff at the Royal Belgian Institute of Natural Sciences identified the bees. Butterflies and other Hymenoptera were identified using Larsen & Larsen (1980), as well as the Arthropod Fauna of the UAE book series (van Harten, 2010; 2011; 2014) and the collection in the Natural History Museum, London (NHM). Dr Polaszek at the NHM reviewed the Hymenoptera identifications.

Data Analysis

To consider which factors influence insect abundance on *E. larica,* a generalised linear model (GLM) with negative binomial errors was used (GLM-nb). Three factors, estimated numbers of cyathia per plant (5 levels: 1-5), elevational band (three levels: lowland, mid-level and highland), and season (three levels: October, January and November) were selected as independent variables. Insect abundance (count variable) was the response variable:

Model 1: Insect abundance~ No. of Cyathia per plant + Elevation + Season

Insect abundance was over-dispersed. The variance ratio was 13.6, while the variance-to-mean ratio was 6.51 vs. 88.89. Hence the decision to use a negative binomial error was appropriate. Table 1 shows the mean number of insects by cyathia level, elevational level, and seasonal level. These variables appeared to be suitable candidates for predicting the outcome variable, insect abundance, as the mean values of the levels varied within the three factors.

Likelihood-ratio tests were used to test if the three factors when included within the model were significant or whether insect abundance could be better explained by a simplified model. The analysis was carried out using the MASS package in R. Pairwise comparisons between the different levels in each of the three factors using Tukey’s HSD (honestly significant difference) test was done using the function glht in the multcomp package in R.

To test for insect turnover along the altitudinal gradient and between seasons, the Sørensen dissimilarity amongst sites was calculated. Beta diversity (β), change in species assemblage between different sites, was originally introduced by Whittaker (1960) and describes the number of different communities within a region. To quantify β the ratio between the regional diversity (gamma) and the local diversity (alpha) is described. Baselga describes this type of β as multiplicative β diversity, as gamma diversity is the multiplication of alpha diversity by the total number of sites (N) that is recorded during a study. β quantifies the number of different communities in the different sites. However, unless two communities are identical, β is always composed of two/a combination of two antithetic components, nestedness and species loss. The schema below, with letters signifying species as present and ‘*’ where a species is missing, represents the different patterns that can emerge between sites.

Nestedness:

Site 1: A B C D E F G H I J K L

Site 2: A B C D * * * * * * * *

Site 3: A B * * * * * * * * * *

Spatial turnover

Site 1: A B C D E F * * * * * *

Site 2: A B C * * * G H I * *

Site 3: A B C * * * ** * * J K L

Turnover & Nestedness

Site 1: A B C D E F G H I J K L

Site 2: A B C D E F * * * * * *

Site 3: A B C * * * G H I * * *

(Based on Baselga (2010))

Here in the schema above Sørensen dissimilarity will be the same in all sites as gamma diversity equals 12 species and the alpha diversity is 6 (mean site diversity). As β equals 2 in the examples above, Sørensen dissimilarity is 0.5 for all sites. This problematic as while the Sørensen dissimilarity is the same, clearly different processes are occurring in the three scenarios.

Therefore an approach that differentiates between these processes was taken. To investigate how insect β changed spatially between sites during the three seasons, the function *beta.multi* contained within the R package *betapart* was used (Baselga et al., 2013). This is broken down into two components, spatial species turnover, measured as Simpson dissimilarity (β_{SIM}) and nestedness, measured as nestedness-resultant fraction of Sørensen dissimilarity (β_{SNE}) (Baselga, 2010; Baselga et al., 2013). The function uses presence-absence data to calculate the overall Sørensen dissimilarity (β_{SOR}) between sites. The Sørensen dissimilarity is a monotonic transformation of multiplicative β (gamma/alpha), which can range from 1 to N (number of sites in a region). Sørensen dissimilarity is independent of the total number of sites as it is beta-1 divided by N-1. This gives a value of 0-1. Simpson dissimilarity is the component within *beta.multi* used to calculate the turnover component as it deems nested assemblages to be wholly similar (Baselga, 2010; 2012). Like Sørensen dissimilarity, Simpson dissimilarity is standardised giving a score of 0-1. In both cases zero values indicates no nestedness or species turnover, while a score of one shows total nestedness or species turnover between sites.

To measure turnover between seasons, a second function in the *betapart* package, *beta.temp*, was used. As highlighted in the methods, while the number of sites surveyed in each of the altitudinal bands (lowland, mid-elevation and highland) was the same in each season, the location of individual sites varied. Therefore, it was therefore not possible to make direct comparisons of turnover between each of the seven field sites surveyed in the different seasons. Consequently, all species recorded at individual sites within the same season were grouped together to make an overall comparison of turnover between the three survey periods. Hence a comparison was made between the overall dissimilarity of October/November 2016 vs. January 2017, January 2017 vs. November 2018, and October/November 2016 vs. November 2018 rather than between individual sites.

To look for patterns of relatedness between species visiting *E. larica*, the function *taxondive* in the R package *vegan* (Dixon, 2003) was used. Taxonomic indices can reveal important information that simple diversity indices may not e.g. by providing information on the 'relatedness' of species rather than just their identify and individual abundances (Oksanen, 2019). Certain related species may provide important pollination services to a plant that other non-related species fail to do e.g. male *Eucera* spp. are recorded as spending the night in Oncocyclus *Iris* spp. and hence are important pollinators of this genus (Monty et al., 2006). While other taxa visit these plants they do not play the same role as pollinators that *Eucera* spp. do. Measuring the taxonomic distinctness of visitors to *Iris* would reveal that a relationship exists between these plants and several closely related bee species. Therefore the indices have the potential to indicate that if a number of related species visit a plant this may not be a random event and could indicate some type of behavioural or morphological specialisation.

Clarke & Warwick (1998, 2001) developed taxonomic distinctness indices, the average taxonomic distances between species in a community, in order to provide this type of information. These distances can be visualised as the length of a path that join two taxa, when drawn through a Linnean or phylogenetic classification of the set of species recorded at a site (Clarke & Warwick, 2001).

The equation that describes the taxonomic distinctness index is given in Clarke & Warwick (1998):

$$\Delta^{+} = [\Sigma\Sigma_{i<j}\omega_{ij}]/[s(s-1)/2]$$

This equation gives the "index value (*taxonomic relatedness of species under consideration*) for a single site, and summation goes over species *i* and *j*. Here *ω* are taxonomic distances among taxa" (Dixon, 2003) and *s* is the number of species present at the site.

This function provides indices that test for taxonomic diversity and distinctness within a community (Clarke & Warwick, 1998, 1999, 2001). It was used to test for patterns of phylogenetic diversity, which could imply functional-group specialisation and a floral syndrome around *E. larica*.

The R package *FD* (Laliberté et al., 2014) was used to measure how species traits reveal functional diversity within the seasons and over the altitudinal distribution. The following binary and nominal traits were explored: presence of a scopa (yes/no), lifestyle ("pollinator", "parasitoid" and “secondary pollinators”), and body form (“hairy”, “smooth” and “scales”).

Species were assigned to a lifestyle trait based on presumed effectiveness as a pollinator. For instance while I could not definitely say the bee species *Icteranthidium* sp. 1 pollinates *E. larica,* based on a bees behaviour it is relatively safe to assign it to the pollinator category. Conversely a species of ant is presumed to be generally more likely to act as a secondary pollinator due to the fact their smooth, mainly hairless bodies mean they rarely act as successful carriers of pollen. This term does not imply a species is not potentially a pollinator. Instead it is used to differentiate taxa from other species that are known to be important pollinators, such as bees or hoverflies. The category ‘scales’ for body form describes the setae of the dermestid beetles.

Results

Composition of the species assemblage visiting E. larica

Over the course of the three survey periods, a total of 91 species (Table S3-S5) were recorded with 688 interactions between visitors and *E. larica*. Interactions between an insect and *E. larica* were lowest in January 2017 (394 in October/November 2016, 136 in January 2017, and 152 in November 2018). Insect species were noted from the following orders: Coleoptera, Diptera, Hymenoptera and Lepidoptera. Thysanoptera were observed in the cyathia, but were not included within this study. Species richness (Table 2) was greatest in the October/November 2016 surveys (48 species) and then declined over the next two survey periods January 2017 (44 species) and November 2018 (35 species). Plant species richness at the survey sites was low in the October/November 2016 and November 2018 survey periods. *Achyranthes aspera* (Amaranthaceae), *Aerva javanica* (Amaranthaceae), *Amaranthus graecizans* (Amaranthaceae), *Polygalea erioptera* (Polygalaceae), and *Solanum incanum* (Solanaceae) were all recorded flowering, although their abundance was low at all sites. The plant community recorded in Chapter 2. was typical of the plant diversity seen during the January 2017 surveys.

In the two autumn surveys, Coleoptera and ants dominated the visitor network in terms of abundance of individual species. While beetle abundance was low in January, ants were again the most abundant visitors (Figs 5-7). The beetle *Spermophagus* sp. 1 (Chrysomelidae) was the single most abundant species recorded during the study, with 84 specimens alone noted during the October/November 2016 surveys.

The Diptera (38 spp) and Hymenoptera (37 spp) were the most species-rich taxa. Amongst the Diptera, the Bombyliidae was the most species-rich group with 21 species recorded. Whilst an almost equal number of Hymenoptera and Diptera were recorded visiting *E. larica*, the majority of the Hymenoptera were taxa not normally associated with pollination, such as Formicidae and Chalcidoidea. Consequently, due to the low species richness and abundance of bees, these data suggest that Diptera are likely to be key pollinators of *E. larica* unless other taxa play an unexpectedly large role. Of the five bee species recorded, only the megachilid *Icteranthidium* sp.1 was noted outside of the spring period. Bees and Lepidoptera showed both low species richness and abundance, suggesting they play little role in pollination of *E. larica* (see Tables S3-5 for a full list of species during each survey period).

The factors cyathia, season and elevation were tested using likelihood-ratio tests. All three factors were individually significant and had a positive effect on insect abundance (Cyathia: $\chi^2(4)=43.79$, $p < .001$; Elevation: $\chi^2(2)=16.23$, $p < .001$; Season: $\chi^2(2)=12.13$, $p < .001$). Hence they were retained as predictors in the model in order to explain the response variable, insect abundance on *E. larica.*

After running the model, all coefficients for the cyathia levels (Table 3) were positive and had significant ($p < .001$) relationship with insect abundance when compared to the reference group, cyathia level 1 (Figure 8). The expected log count for cyathia level 2 was 1.78 higher than the expected log count for cyathia level 1, cyathia level 3 was 2.06 higher, cyathia level 4 was 2.71 higher, and cyathia level 5 was 3.78 higher. The results of the pairwise comparisons of cyathia levels (Table 4) repeated the observation from the analysis of deviance table that all comparisons of cyathia levels 2-5 with level 1 returned a significant result ($p < .001$). Additionally the comparison of the level 4-2 means also returned a significant result (*p* < .001). However, this result may be due to one outlier on a plant that was given an estimated cyathia score of 4, which was recorded as having 73 insects visiting it (of which 36 visitors were the ant species *Lepisiota gracilicornis*). Otherwise all other pairwise comparisons between cyathia levels were non-significant (*p* > 0.05). This suggests insect abundance does not keep increasing on *E. larica* as the number of cyathia increases i.e. insect abundance was not greater on a plant that was given a score of 3 for its estimated number of cyathia compared to a plant scored 2.

Insect abundance declined significantly on *E. larica* from the lowlands to the midlevel (Figure 9 & Table 5). The expected log count for the lowland surveys was 0.94 higher than the reference group, highlands (Table 3). This was statistically significant (*p* < .001). However, there was not a further significant decline in abundance from the mid-levels compared to the highlands. While the expected log count for the mid-level was positive (0.26), suggesting insect abundance was higher at this mid-level elevation than in the highlands, this coefficient was not statistically significant. Unlike in other systems, which show a mid-elevation increase in insect abundance, on *E. larica* insect abundance was greatest in the lowlands and then declined sharply at mid-elevations before continuing to slowly decline in the highlands. This second decline (mid-level to highlands) was at a much lesser extent compared to the initial lowland-mid-level decline in abundance. Therefore insect abundance on *E. larica* is clustered in the lowland Hajar Mountains.

The expected log count for the October surveys was 0.59 higher than the reference group, January (Figure 10 & Table 3). This was statistically significant ($p < .001$) reflecting the much higher abundance of insects in October compared to January. Insect abundance declined in November compared to January (expected log count for the November surveys was 0.17 lower than the reference group, January), although this result was not significant. Consequently, insect abundance was greatest in October 2016 (Table 6). However, the results suggest this high level of abundance is temporally fluid as in November 2018, although not statistically significant, insect abundance was slightly lower compared to January 2017. This suggests insect abundance does not show a straightforward scenario from high abundance in the autumn to low abundance in the spring. Instead the results of this study suggest abundance fluctuates temporally and may be a result of another factor for instance rainfall. The amount of precipitation could influence the number of open cyathia and therefore attractiveness of insects to *E. larica*.

Species turnover

Beta diversity among sites within the three survey periods all showed the same pattern of high species replacement (β_{SIM}, Simpson dissimilarity) and extremely low levels of nestedness (β_{SNE}, nestedness-resultant fraction of Sørensen dissimilarity)(Table 7). While taxa were replaced along the altitudinal gradient, Diptera appeared at all altitudes, and therefore there was no evidence of replacement of bees by Diptera at higher altitudes. Butterfly and bee species richness was so low that there were no examples of replacement with altitude of these taxa.

Overall turnover among the three survey periods showed a similar pattern of low nestedness and high species replacement as the dominant component of beta diversity (Tables 8, 9 & 10). However, species replacement among seasons was not as intense as along the altitudinal gradient within seasons, due to a small core of species reappearing in the different seasons (Table S6). The greatest change in nestedness, and therefore species loss, was recorded between the October 2016 and November 2018 surveys (β_{SNE} 0.06), indicating a gradual loss of species over longer periods of time. As for the overall results, there was no dramatic loss of total species richness and the assemblage of insect visitors, although dynamic, appeared to be relatively stable among seasons.

Taxonomic Diversity

Taxonomic distinctness (Δ^+) showed high diversity levels for all sites (mean ± SD= 85.8 ± 4.6) throughout the study (Tables 11, 12 & 13), while the range of values was relatively narrow, especially when an outlier (72.1 Δ^+ Jebel Shams 2, from October 2016) was removed. Though species richness showed a linear decline with altitude during all three-survey periods (Figure 11), there was no linear increase or decrease of Δ^+ with altitude in any of the seasons. For instance in the October/November 2016 surveys, the site Jebel Shams 2 (altitudinal band 1300-1400m) had the lowest Δ^+ score (72.1), while the other high altitude site, Jebel Shams 1 (altitudinal band 1200-1300m) had the highest Δ^+ (90.8) recorded during that season. Likewise during the other two sampling periods, Δ^+ showed mixed results at different altitudes. This implies altitude played little role in taxonomic distinctness, which was instead site-specific. Therefore distinctness did not coalesce around a particular taxon as altitude increased.

Only the site Yiti (altitudinal band 0-100m), in the January 2017 surveys (Table 11), showed a significantly lower taxonomic distinctness, when compared with all sites in January as a whole ($P < 0.01$). Whilst the Yiti site had the highest species richness (15 species) for the January sites, the species recorded were taxonomically closely related. This result suggests taxonomic diversity, apart from that recorded at Yiti, was high amongst all sites and therefore no single group dominated particular altitudinal bands.

Functional Diversity

The community-level weighted means (CWM) of trait values showed species considered as 'secondary pollinators' dominated in all but two sites, Buwah (January 2017) and Salma Plateau (November 2018) (Tables 14-16). The lack of bee species visiting *E. larica* meant individuals showing the ‘scopa’ trait failed to dominate any of the sites. Only the November 2018 surveys showed a linear change of body form with altitude. The ‘Smooth’/’scales’ trait reflected the abundance of ants and Dermestid species in the lowland sites, changing to ‘hairy’, meaning a dominance by Diptera, Lepidoptera and non-bee hymenopterans at higher altitudes.

Temperature at survey sites

Mean air temperatures for the three survey periods followed the expected pattern (Tables S7-9), warmer in the autumn surveys (30.9 ^{o}C ± 4.0 mean ± standard deviation October/November 2016; 29.2 ^{o}C ± 3.0 mean ± standard deviation November 2018) and cooler in the winter survey (25 ^{o}C ± 2.7 mean ± standard deviation January 2017). The maximum (35 ^{o}C) and minimum temperatures (22.1 ^{o}C) were both recorded from the nr. Taww Vilage site in October/November 2016 and January 2017 surveys respectively.

The range of temperatures between sites (11.2 ^{o}C October/November 2016; 8.1 ^{o}C January 2017; 9 ^{o}C November 2018) was similar across all survey periods, although this was slightly greater in the two autumn survey periods. There was no observed linear decline of temperatures with altitude during any survey period (Figures S4-6). However, this is likely due to the surveys taking place slightly later in the mornings at the higher altitude sites when daily air temperatures had risen. Therefore, this is not an indication that higher altitude sites were warmer than lower altitude survey sites.

Discussion

As CaraDonna et al (2017) emphasised, while communities and populations are recognised as experiencing temporal turnover (Chesson & Huntly, 1989), interaction networks have generally been considered to be static bodies (Poisot et al., 2015). In the case of the insect assemblage visiting *Euphorbia larica* this view is unfounded. The results agree not only with the findings of CaraDonna et al (2017), i.e. that species interactions are fluid through time, but in my case they vary spatially as well. When the turnover of visitors was considered along the full altitudinal gradient, species replacement was the dominant process-structuring turnover within the insect community, with little nestedness. This suggests a series of different communities at each of the sites I surveyed *E. larica*.

Based on the frequency of visits (Morales-Castilla et al., 2015), the interaction varied from strong to weak, although about half of all taxa in each survey season were recorded visiting *E. larica* only once. Of the 14 species recorded more than five times (and hence in the context of this study, strong interactors), 11 were beetles or ants. As a consequence, the relationship between most insect species and *E. larica* could be classified as weak, and the network showed the typical asymmetrical pattern of many community-level networks, exemplified by a few abundant species and a long train of rare, transient species (Bascompte et al, 2003; Fang & Huang, 2012). The visitation network of *E. larica* has a core of beetle and ant species with multiple other taxa (bombyliids, butterflies and bees) on the periphery of the network.

While ants are typically considered poor pollinators, beetles can play an underappreciated role in pollination. This disregard of the importance of beetles as pollinators may be due to a geographical bias in pollination studies as within Europe and North America, beetles have a less conspicuous role. In the Southern Hemisphere, and particularly in arid or tropical environments, beetles have a more prominent role in pollination networks (Momose et al., 1998; Willmer, 2011). Important Coleoptera families in relation to pollination, include the Cantharidae (soldier beetles) and Cerambycidae (longhorn beetles) (Willmer, 2011). Euphorbids have been noted as attracting beetles as their cyathia form a platform that allows beetles to walk or settle on while feeding (Willmer, 2011).

The extremely high rate of turnover (with only 7% of species recorded in all three surveys: Table S6), agreed with other network studies that have investigated temporal variation in network structure. In a scrub community in Greece, for example, only 5% of species were recorded in all four years of the study (Petanidou et al., 2008; Fang & Huang, 2012). This constant loss and gain of species appears to be typical of most networks when studied over time.

After bees, Diptera are thought to constitute the most important element of most pollinator communities (Ssymank et al., 2008). However, to date, most studies on pollination and Diptera have focused on the role of hoverflies (Syrphidae) and have underappreciated the potential importance of other families (Orford et al., 2016). For instance, at high altitudes in the French Alps, Empidinae flies represented 54% of all visitors to plants (Lefebvre et al., 2014). In my study, the Diptera formed a taxonomically rich part of the visitation network, with 12 families (Tables S6-8) and 40% of all species in both the October 2016 and November 2018 surveys. As predicted therefore, they constitute a major part of the pollinator community in the early blooming period in the Hajar Mountains.

During January 2017, Diptera species richness decreased to 30% of the total. The makeup of the Dipteran community was fluid, like all other elements within this visitation network. In January 2017, levels of species replacement were particularly evident in the Bombyliidae, known to be both important pollinators (Kearns, 2001) and particularly species-rich in arid environments (Kastinger & Weber, 2001). Of the 16-bombyliid species from the earlier surveys, only three *Petrorossia* spp were recorded again three months later. The March 2018 surveys (chapter two) that investigated the lowland visitation network found only two species of bombyliid in common with the October 2016 surveys. This could merely be a phenological issue. Although Diptera and particularly the Bombyliidae formed a sizeable component of the visitor assemblage, their low abundance and interaction levels suggest that they play only a secondary role in the pollination of *E. larica.* This conclusion is supported by the CWMs of the analysis of functional diversity, which showed beetles, ants and other non-typcial pollinating Hymenoptera, such as Chalcidoidea were dominant at nearly all sites (Tables 14-16).

While overall species replacement was high throughout the study, there was little evidence for specific taxonomic groups replacing each other with altitude, a common observation in pollinator communities of montane environments (Arroyo et al., 1982; Devoto et al., 2005; Lázaro et al., 2008; Pellissier et al., 2010; Lefebvre et al., 2014). This was shown by the taxonomic distinctness, which was high at all sites throughout the study (ignoring Yiti, Table 11-13). A transition from dominance of one Order to another would have led to a decline in taxonomic distinctness, but there was no such decline. Whilst beetles tended to be present at higher abundances in lowland sites, there was no clear transition to dominance of any other Order at higher altitudes. Instead a miscellany of taxa was seen at all altitudes e.g. among braconids, *Glyptomorpha* sp. was recorded in the lowlands, *Cardiochiles* sp. 1 at mid-elevation, and *Glyptomorpha irreptor* at high elevations. This type of pattern was seen across multiple taxa.

Different types of pollinator are known to show varied response to floral traits such as floral display size (Thompson, 2001). An increase in floral display and the density of conspecific plants in a patch is generally expected to increase pollinator visitation rates (Ohashi & Yahara, 2001;Elliot & Irwin, 2009) because pollinators become more constant. This is advantageous to a plant because there is a greater chance that it will receive conspecific pollen (Feldman, 2006). However, after a certain threshold in abundance is reached, larger patches with profuse displays per plant may experience pollen limitation as pollinator service becomes insufficient for all flowers.

In this study floral display did not have a significant effect on the abundance of insects visiting *E. larica.* While the GLM-nb showed a positive, significant effect when comparing *E. larica* plants given a score of 1 with all other *E. larica* scored 2-5, as numbers of cyathia increased, the average number of insect visitors did not. This was shown by comparing the Tukey HSD results, which made comparisons between the mean numbers of insects on the different cyathia levels. It is not surprising that plants with an estimated cyathia score greater than 1 (<10 cyathia) had a greater abundance of insects on them. However, it was unexpected that while insect abundance was greater on plants with a higher estimated number of cyathia (Figures 8-10), there was no significant difference between their means. For instance, there were not significant differences between a means of plants scored 5 (>200 cyathia) compared to a plant scored 2(~10-50 cyathia). This suggests that after an initial increase in insect abundance in correlation with increased cyathia abundance, an asymptote was reached. This may be due to pollinator limitation, which has been recorded in other studies. In *Orchis militaris*, visitation rates by bees did not increase with greater floral display (Henneresse et al., 2019), attributed to low bee abundance. In the case of this study, pollination limitation may possibly occur as a result of the physical conditions occurring within the Hajar Mountains. Most of the plants of the Hajar

Mountains occur in isolated wadis (deep dry river canyons), with strong winds along ridge tops preventing easy movement of pollinators between different areas, which may explain the limitation observed in this study.

Another possible observation supporting this idea of pollinator limitation was the fact out of 105 plants surveyed at, only one plant was given an estimated cyathia score of 5. While this may be due to water limitation preventing plants supporting a copious floral display, it could also suggest that as pollinators are at relatively low levels throughout the mountains, it is not advantageous for plants to produce huge displays of flowers. Further studies should be conducted in seasons when precipitation is high to try to investigate whether cyathia abundance is a reaction to water availability or an evolutionary response to low pollinator abundance making large displays damaging to plant fitness.

The species richness and abundance of bees visiting *E. larica* was conspicuously low in this study. This was surprising; especially since bee diversity is high during January (personal observation) when the main blooming period begins. In a survey of bees in Isfahan province (Iran: Ghahnavieh & Monfared, 2019), three species of *Andrena* and two of *Lasioglossum* visited *Euphorbia* spp, indicating this genus does attract bees. A possible explanation of the lack of recorded bees in Oman may be due to the fact that the cyathia of *E. larica* are small and the nectaries may not produce enough nectar to meet the high-energy requirements of bees. Faegri (1978) suggested that small flowers exclude large pollinators on energy grounds, and mentioned ants as an example of a visitor with a low energy budget where their requirements would be met from small flowers. Ants and small beetles were the most abundant visitors to *E. larica*, which may add support to this proposition.

While several studies have shown that along altitudinal gradients replacement occurs between different orders of insect, in the case of a single plant, *E. larica,* this does not appear to be the case. At certain times of the year *E. larica* appears to be an important floral resource for a wide variety of insects in the Hajar Mountains. This was particularly true in October 2016. However, the decrease in insect species richness and abundance in the November 2018 surveys reflect that this is not always the case at the same times of the year. Further studies should include data on precipitation to see whether the species replacement observed in this study is a response to a general increase in plant species richness due to water availability. This may explain the loss in insect abundance through time.

Conclusion

Euphorbia larica appears to be a generalist as it’s nectaries are easily accessed and a wide range of potential pollinators visit the plant. From the variety of species visiting, there was no evidence of a single dominant "most effective" visitor (Stebbins 1970), and it appears that pollination is achieved by a wide range of opportunistic visitors. The fact that the nectar of *E. larica* is so easily accessed suggests it has evolved to attract a variety of visitors with no specific specialism*.* Turnover was high amongst visitors; while bombyliids dominated October surveys, by January this group had been almost completely replaced by a range of different Diptera genera. No single functional group was present throughout the surveys; "secondary pollinators" was the most common behavioural trait of visitors, which did not constitute a single functional type. No single taxon dominated either, and no evidence was found of Orders replacing each other along the altitudinal gradient. Instead, a series of different visitor communities existed both spatially and temporally.

Figures and Tables

Figure 1. Cyathium, *Euphorbia larica*

Figure 2. *Euphorbia larica*

Figure 3. Section of the Hajar Mountains where the *E. larica* survey sites were located

Figure 4. *E. larica* survey site localities

Figure 5. October/November 2016 bipartite graph of the *E. larica*-visitor community

Figure 6. January 2017 bipartite graph of the *E. larica*-visitor community

Figure 7. November 2018 bipartite graph of the *E. larica*-visitor community

Figure 8. Boxplot showing the insect abundance at the three elevational bands: Highland, Mid-level & Lowland.

Figure 9. Boxplot showing the insect abundance on the five estimated cyathia ranks.

Figure 10. Boxplot showing the insect abundance during the three survey periods: October/November 2016, January 2017 & November 2018

Figure 11. Species richness patterns during the three survey periods. All three-survey periods saw linear declines of species richness with increasing altitude.

Fig. 1

Fig. 2

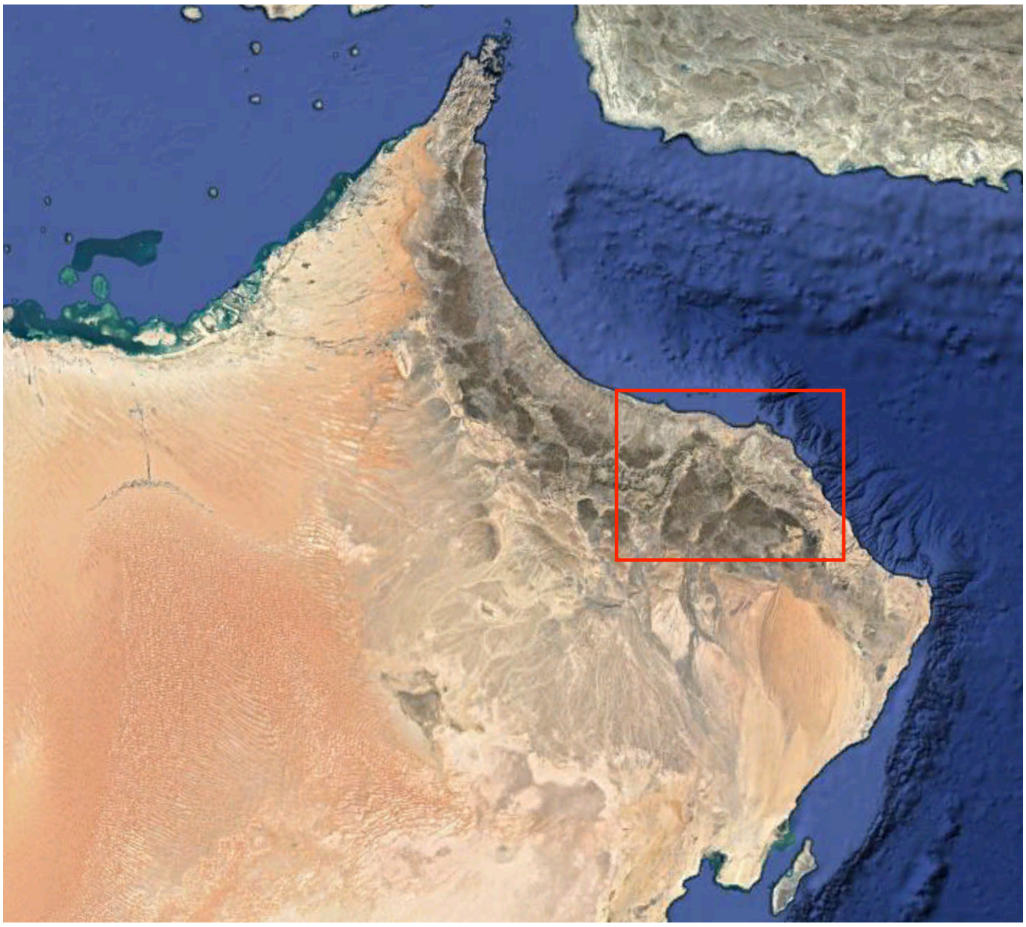


Fig. 3


Taww
Yiti
Ghubrah Canyon
Buwah
A'Tekhah
Jebel Shams 2
Jebel Shams 1
Al Hodinia
Old Road to Sur
Birkat Al Mouz 1
Birkat Al Mouz 2
Salma Plateau

Fig. 4

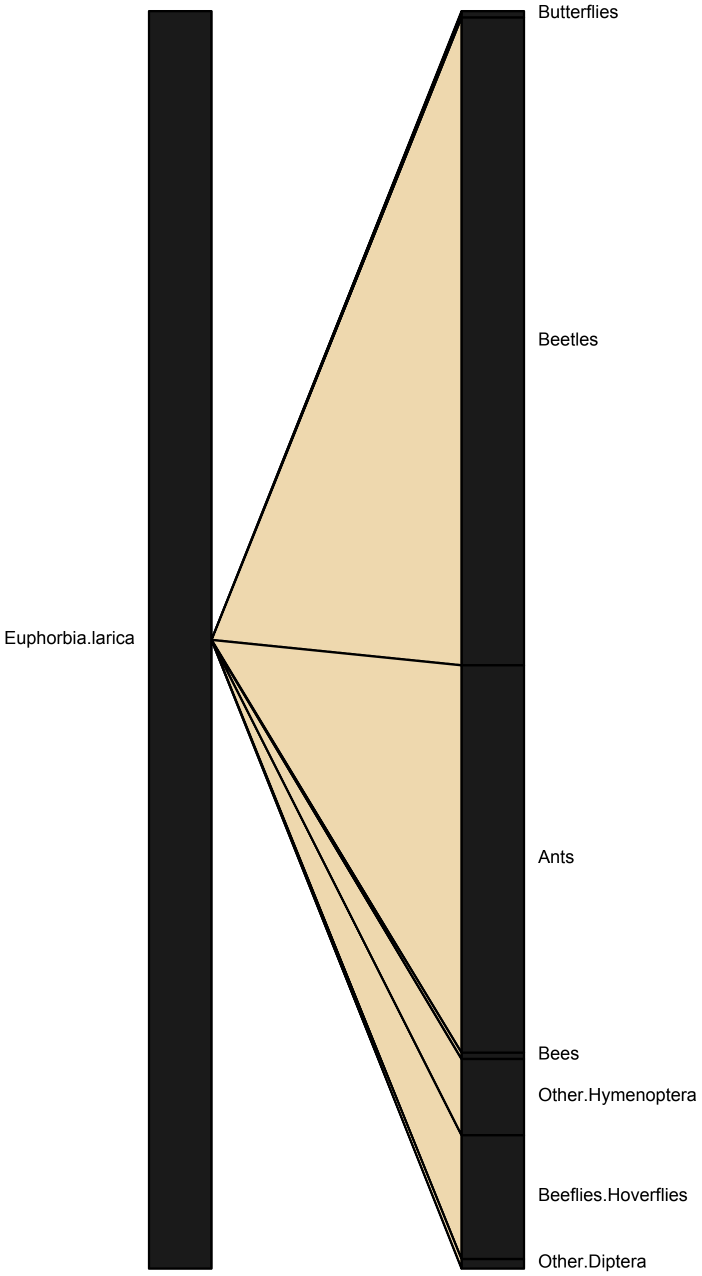

Euphorbia.larica
Butterflies
Beetles
Ants
Bees
Other.Hymenoptera
Beeflies.Hoverflies
Other.Diptera

Fig. 5

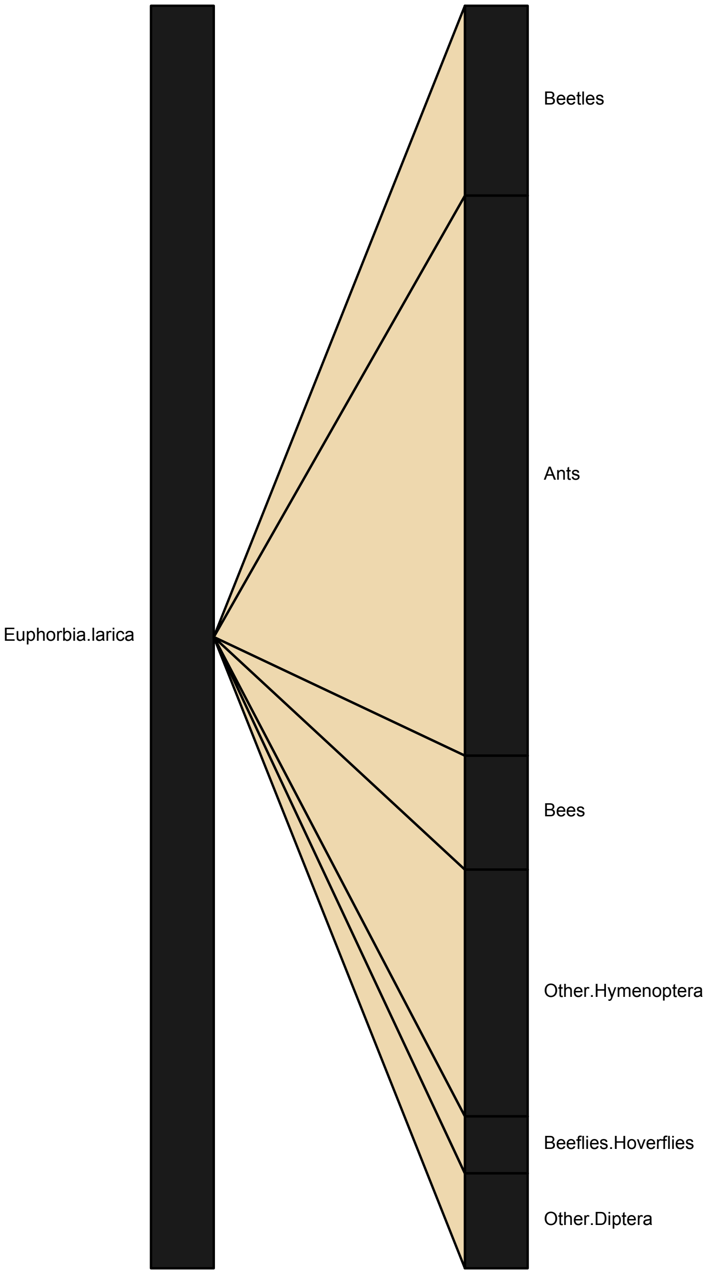

Euphorbia.larica
Beetles
Ants
Bees
Other.Hymenoptera
Beeflies.Hoverflies
Other.Diptera

Fig. 6

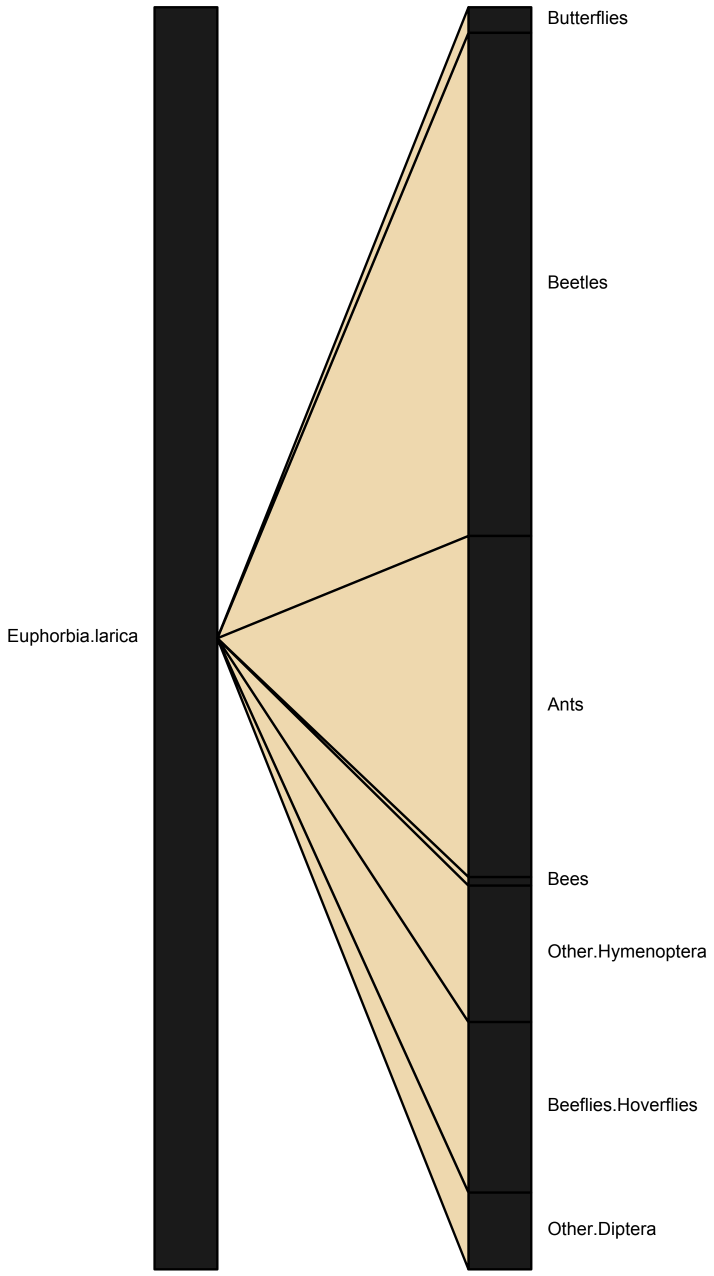

Euphorbia.larica
Butterflies
Beetles
Ants
Bees
Other.Hymenoptera
Beeflies.Hoverflies
Other.Diptera

Fig. 7

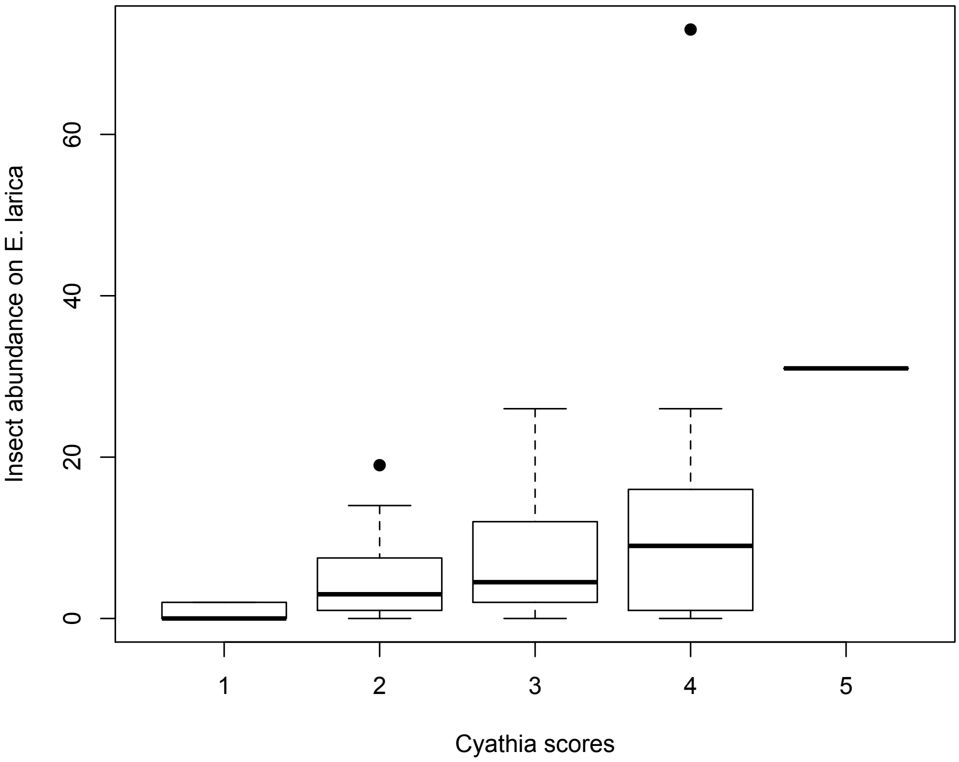


Fig. 8

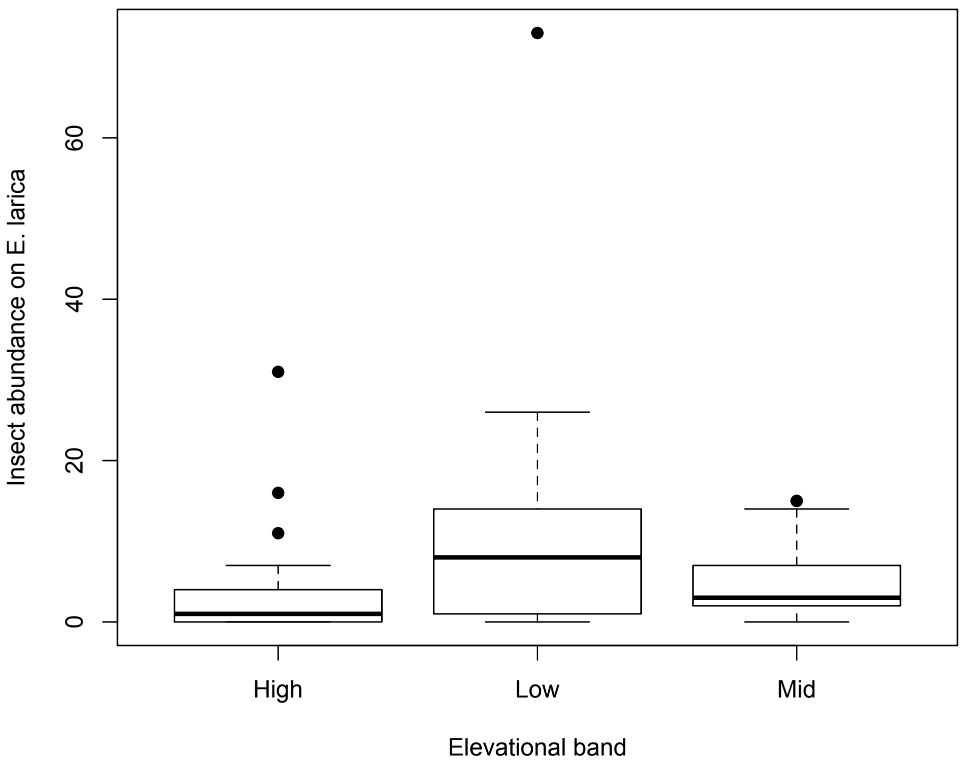

Insect abundance on E. larica
0
20
40
60
High
Low
Mid
Elevational band

Fig. 9

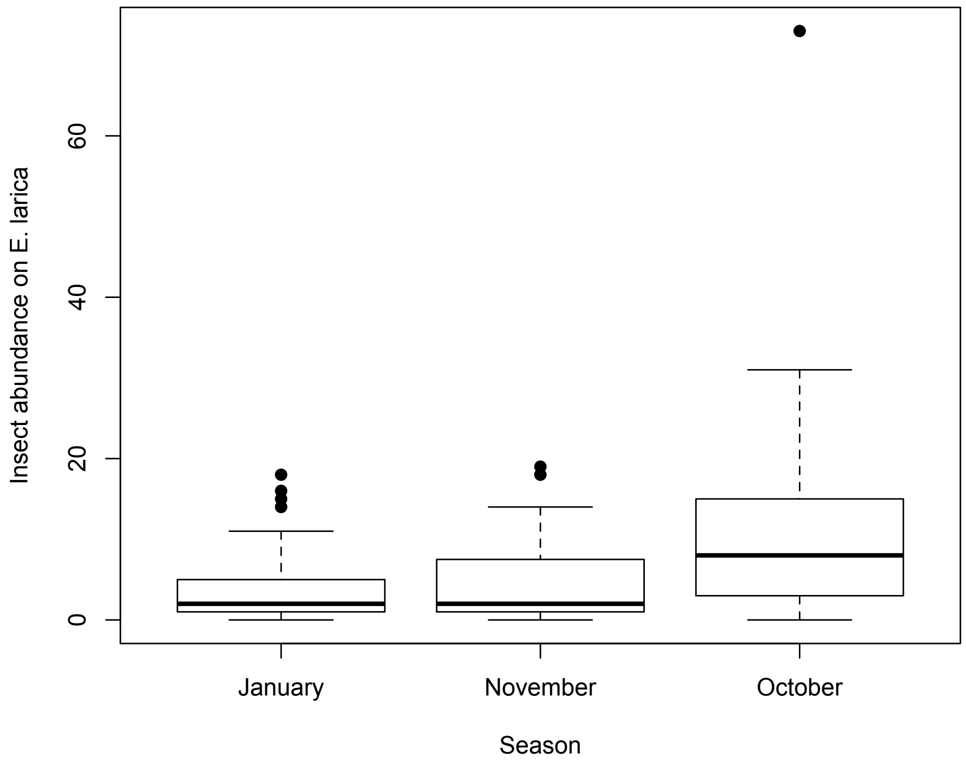

Insect abundance on E. larica
0
20
40
60
January
November
October
Season

Fig. 10

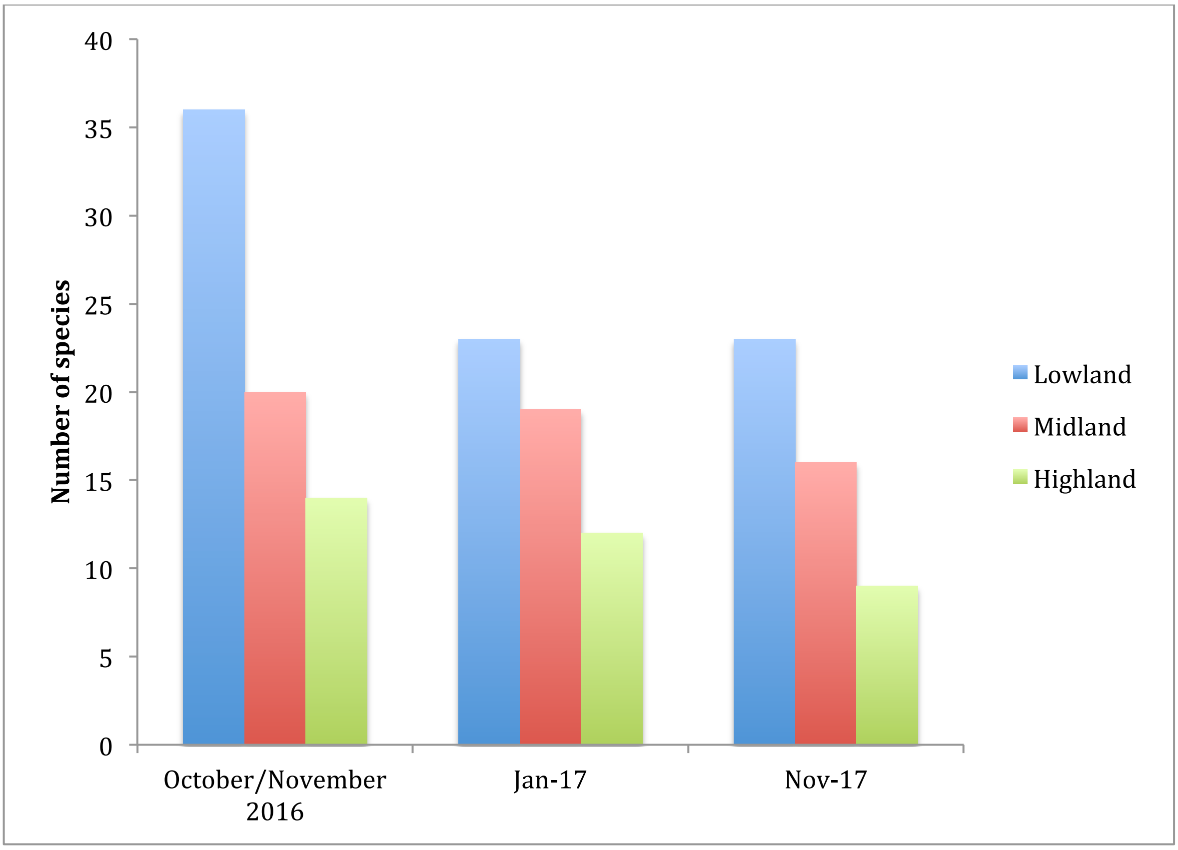

Number of species
40
35
30
25
20
15
10
5
0
October/November 2016
Jan-17
Nov-17
Lowland
Midland
Highland

Fig 11.

Table 1. Mean and SD for the levels in three factors (Cyathia, Season & Elevation) included in the GLM-nb

Factor levels	**Mean ± SD**
Cyathia rank 1	0.7 ± 0.9
Cyathia rank 2	4.8 ± 5.1
Cyathia rank 3	7.4 ± 6.8
Cyathia rank 4	13.9 ± 18.7
Cyathia rank 5	31 ± NA
October	11.3 ± 13.5
January	3.9 ± 5
November	4.4 ± 5.3
Lowland	9.5 ± 12.3
Midlevel	4.9 ± 4.6
Highlands	3.6 ± 6.3

Table 2. Species richness and number of interactions during the three survey periods

Survey Date	**Species richness**	**Total no. of interactions**	**Mean ± SD of interactions**
October/November 2016	48	396	8.3 ± 15.7
January 2017	43	140	3.2 ± 5.7
November 2018	34	192	5.2 ± 13.2

Table 3. Negative binomial GLM results

	Estimate	SE	Z-value	P-value
Intercept	-0.93	0.40	-2.32	P= 0.02
Cyathia 2	1.78	0.40	4.55	P= <0.001
Cyathia 3	2.06	0.39	5.26	P= <0.001
Cyathia 4	2.71	0.43	6.37	P= <0.001
Cyathia 5	3.77	0.91	4.16	P= <0.001
Low elevation	0.94	0.24	3.90	P= <0.001
Mid elevation	0.26	0.27	0.99	0.32
November 2018	-0.17	0.24	-0.73	0.47
October 2016	0.59	0.23	2.57	0.01

Table 4 Multipe comparisons of cyathia means: Tukey Contrasts

Cyathia pairwise comparison	Estimate	SE	Z value	P-value
Cy2-Cy1	1.78	0.39	4.55	P= <0.001
Cy3-Cy1	2.06	0.39	5.26	P= <0.001
Cy4-Cy1	2.71	0.43	6.37	P= <0.001
Cy5-Cy1	3.77	0.91	4.16	P= <0.001
Cy3-Cy2	0.28	0.22	1.27	0.68
Cy4-Cy2	0.93	0.28	3.31	P= <0.01
Cy5-Cy2	1.98	0.85	2.32	0.12
Cy4-Cy3	0.65	0.27	2.38	0.10
Cy5-Cy3	1.71	0.85	2.01	0.24
Cy5-Cy4	1.05	0.86	1.22	0.71

Table 5. Multipe comparisons of elevational means: Tukey Contrasts

Elevation pairwise comparison	Estimate	SE	Z value	P-value
Lowland-Highland	0.94	0.24	3.90	P= <0.01
Mid-elevation-Highland	0.26	0.27	0.99	P= 0.58
Mid-elevation-Lowland	-0.67	0.22	-3.04	P= 0.01

Table 6. Multipe comparisons of seasonal means: Tukey Contrasts

Season pairwise comparison	Estimate	SE	Z value	P-value
November 2018-January 2017	-0.17	0.24	-0.73	P= 0.75
October 2016-January 2017	0.59	0.23	2.57	P= 0.02
October 2016-November 2018	0.77	0.23	3.40	P= <0.01

Table 7. Dissimilarity within seasons

Dissimilarity measure	**October 2016**	**January 2017**	**November 2018**
β_{SIM}	0.77	0.86	0.80
β_{SNE}	0.07	0.04	0.05
β_{SOR}	0.84	0.90	0.85

Table 8. Dissimilarity between October/November 2016 and January 2017

Dissimilarity measure	**Between Seasons**
β_{SIM}	0.59
β_{SNE}	0.02
β_{SOR}	0.61

Table 9. Dissimilarity between January 2017 and November 2018

Dissimilarity measure	**Between Seasons**
β_{SIM}	0.72
β_{SNE}	0.03
β_{SOR}	0.75

Table 10. Dissimilarity between October/November 2016 and November 2018

Dissimilarity measure	**Between Seasons**
β_{SIM}	0.58
β_{SNE}	0.06
β_{SOR}	0.64

Table 11. Taxonomic distinctness (Δ^+) for the sites surveyed in October 2016

Site	Species richness	Δ^+	P
Jebel Shams 2	6	72.1	0.11
Buwah	16	83.7	0.86
Yiti	21	84.4	0.97
Taww	14	85.6	0.72
Birkat Al-Mouz 1	11	85.9	0.71
Birkat Al-Mouz 2	9	86.6	0.66
Jebel Shams 1	8	90.8	0.32

Table 12. Taxonomic distinctness (Δ^+) for the sites surveyed in January 2017

Site	Species richness	Δ^+	P
Yiti	15	80.6	0.01
Al Hodinia	8	81.4	0.22
Ghubrah Canyon	10	81.5	0.13
Taww	6	85.0	0.77
A’Tekhah	11	85.5	0.70
Buwah	4	89.3	0.76
Jebel Shams 1	6	91.4	0.39

Table 13. Taxonomic distinctness (Δ^+) for the sites surveyed in November 2018

Site	Species richness	Δ^+	P
Taww	10	86.3	0.98
Old Road to Sur	11	86.5	0.97
Salma Plateau	3	86.8	0.98
Buwah	10	87.0	0.89
Yiti	11	87.3	0.80
Jebel Shams	6	92.1	0.39
Ghubrah Canyon	7	92.5	0.29

Table 14. Community-level weighted means (CWM) of trait values for the October 2016 surveys

Survey Sites	Total species richness	Lifestyle	Body form	Scopa?
Yiti	21	Secondary pollinators	Hairy	No
Taww	15	Secondary pollinators	Smooth	No
Buwah	16	Secondary pollinators	Smooth	No
Birkat Al Mouz 1	11	Secondary pollinators	Hairy	No
Birkat Al Mouz 2	9	Secondary pollinators	Hairy	No
Jebel Shams 1	6	Secondary pollinators	Hairy	No
Jebel Shams 2	6	Secondary pollinators	Smooth	No

Table 15. Community-level weighted means (CWM) of trait values for the January 2017 surveys

Survey Sites	Total species richness	Lifestyle	Body form	Scopa?
Yiti	15	Secondary pollinators	Smooth	No
Taww	8	Secondary pollinators	Smooth	No
Buwah	10	Pollinator	Hairy	No
Ghubrah Canyon	6	Secondary pollinators	Smooth	No
A'Tekhah	11	Secondary pollinators	Hairy	No
Al Hodinia	4	Secondary pollinators	Smooth	No
Jebel Shams	6	Secondary pollinators	Hairy	No

Table 16. Community-level weighted means (CWM) of trait values for the November 2018 surveys

Survey Sites	Total species richness	Lifestyle	Body form	Scopa?
Yiti	10	Secondary pollinators	Smooth	No
Taww	11	Secondary pollinators	Scales	No
Buwah	3	Secondary pollinators	Smooth	No
Ghubrah Canyon	10	Secondary pollinators	Smooth	No
Old Road to Sur	11	Secondary pollinators	Hairy	No
Jebel Shams	6	Secondary pollinators	Hairy	No
Salma Plateau	7	Pollinator	Hairy	No

Supplementary information. Species lists

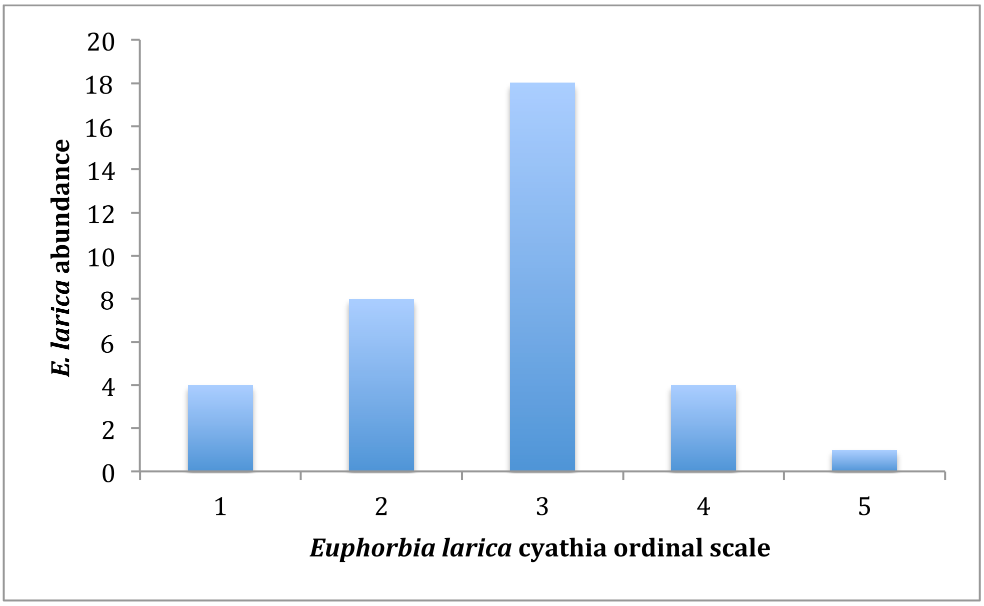


Figure S1. Cyathia abundance in October/November 2016

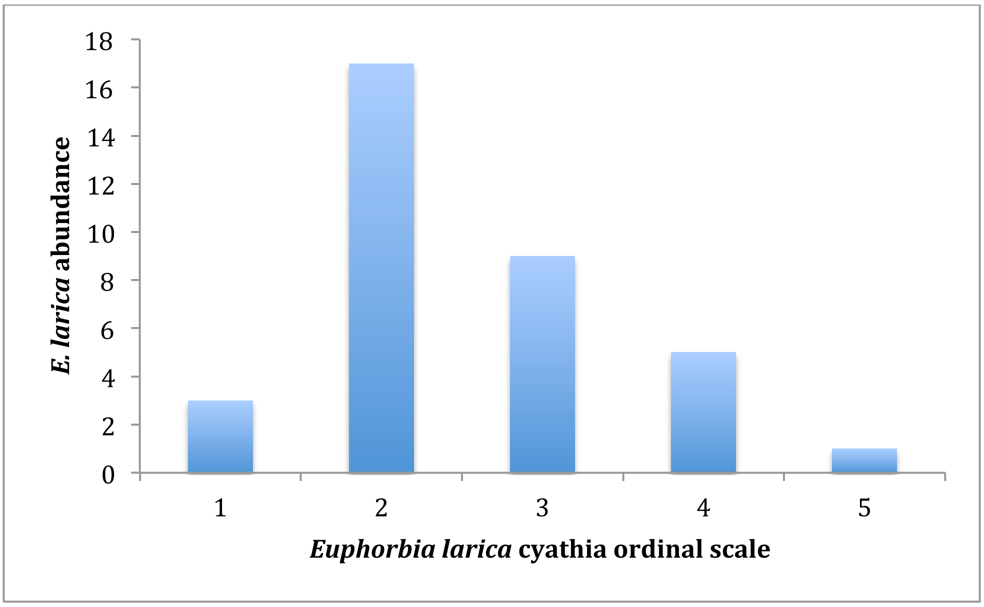


Figure S2. Cyathia abundance in January 2017

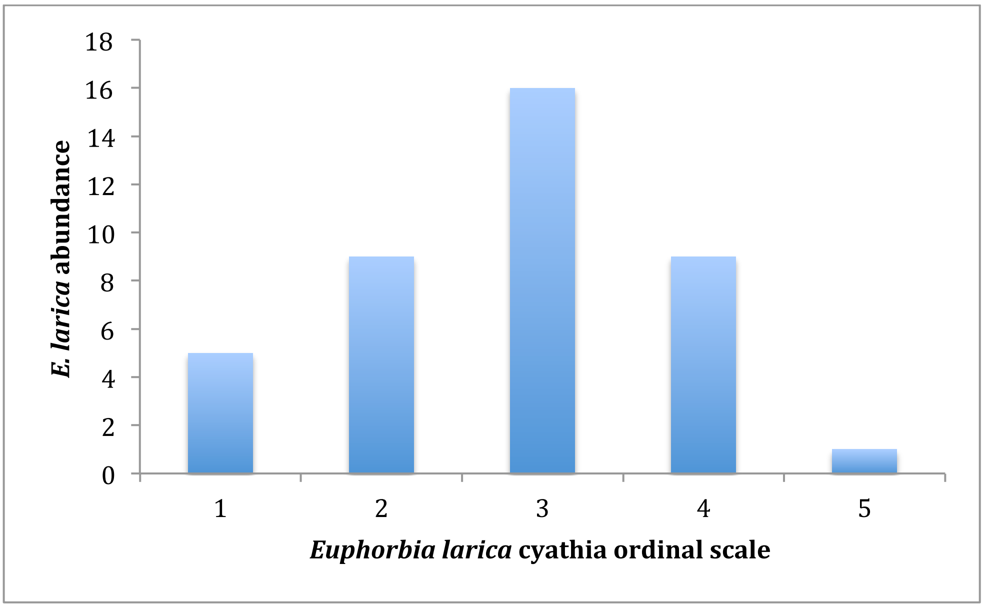


Figure S3. Cyathia abundance in November 2018

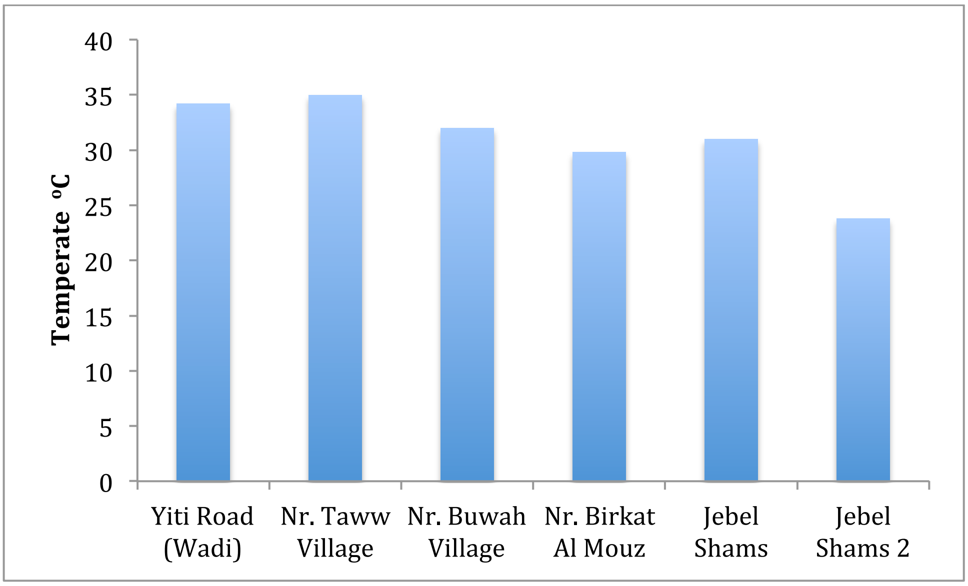


Figure S4. Temperatures recorded at the start of every sampling period, October/November 2016

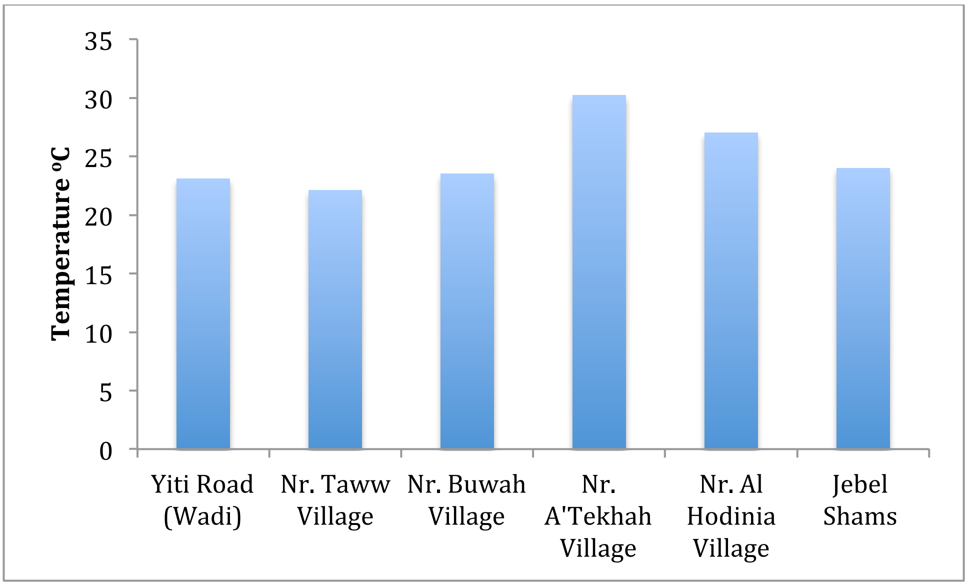


Figure S5. Temperatures recorded at the start of every sampling period, January 2017

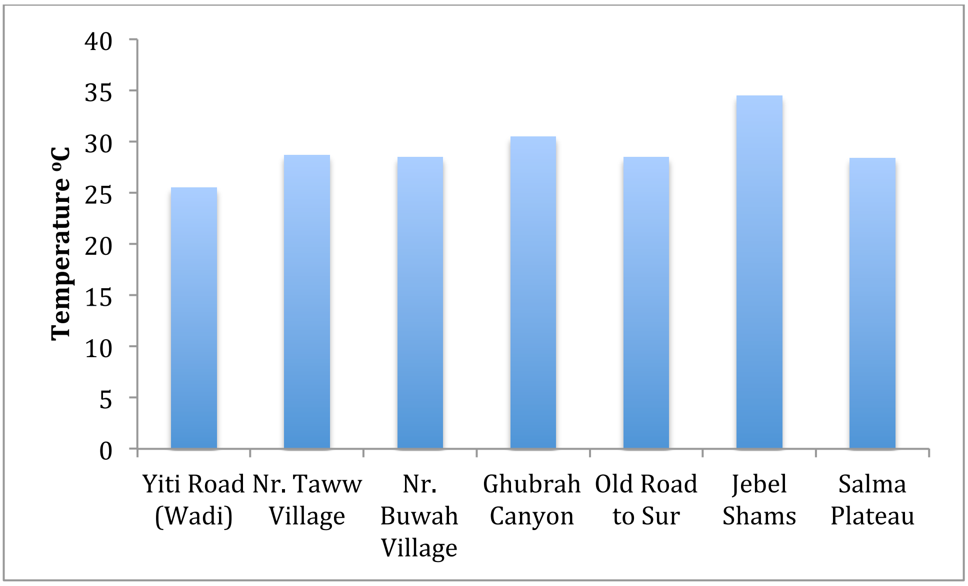


Figure S6. Temperatures recorded at the start of every sampling period, November 2018

Table S1. List of other *Euphorbia* species found in the Hajar Mountains

Species	**Date of expected flowering and fruiting**
E. hirta	February-April
E. indica	February-April
E. serpens	February-April
E. arabica	February-April; September
E. granulata var. *granulata*	February-April; September
E. riebeckii	February-March
E. heterophylla	February-April
E. helioscopia	February-April
E. peplus	February-March/April

Table S2. Survey sites

Survey site October/November 2016	**Altitudinal band**	**Survey site January 2017**	**Altitudinal band**	**Survey site November 2018**	**Altitudinal band**
Yiti 23°31’74” N 58°37’42” E	0-100 m	Yiti 23°31’74” N 58°37’42” E	0-100 m	Yiti 23°31’74” N 58°37’42” E	0-100 m
Taww 23°31’48” N 57°58’07” E	100-200 m	Taww 23°31’48” N 57°58’07” E	100-200 m	Taww 23°31’48” N 57°58’07” E	100-200 m
Buwah 23°30’84” N 58°00’69” E	200-300 m	Buwah 23°30’84” N 58°00’69” E	200-300 m	Buwah 23°30’84” N 58°00’69” E	200-300 m
Birkat Al Mouz 1 22°57’34” N 57°39’65” E	600-700 m	Ghubrah Canyon 23°26’74” N 57°52’91” E	300-400 m	Ghubrah Canyon 23°26’74” N 57°52’91” E	300-400 m
Birkat Al Mouz 2 22°57’42” N 57°39’66” E	700-800 m	A’Tekhah 23°15’71” N 57°26’70” E	500-600 m	Old Road to Sur 23°10’02” N 58°06’11” E	600-700 m
Jebel Shams 1 23°12’42” N	1200-1300 m	Al Hodinia 23°11’34” N	800-900 m	Jebel Shams 1 23°12’42” N	1200-1300 m

57°08’86” E		57°37”19” E		57°08’86” E	
3°06’40” N57°24’27” E	1300-1400 m	Jebel Shams 1 23°12’42” N 57°08’86” E	1200-1300 m	Salma Plateau 22°22’40” N 59°07’07” E	1300-1400 m

Table S3. October 2016 metaweb of insect visitors to *E. larica*

Order	**Family**	**Genus**	**Species**	**Abundance**
Coleoptera	Chrysomelidae	*Acanthoscelides*	Sp. 1	5
Coleoptera	Chrysomelidae	*Bruchidius*	Sp. 1	13
Coleoptera	Chrysomelidae	*Callosobruchus*	Sp. 1	29
Coleoptera	Chrysomelidae	*Callosobruchus*	*C. cherensis*	7
Coleoptera	Chrysomelidae	*Spermophagus*	Sp. 1	84
Coleoptera	Dermestidae	*Anthrenus*	Sp. 1	32
Coleoptera	Dermestidae	*Phradonoma*	Sp. 1	6
Coleoptera	Melyridae	?	Malachinae sp. 2	28
Diptera	Bombyliidae	*Anthrax*	*A. trifasciatus*	8
Diptera	Bombyliidae	*Apolysis*	Sp. 1	1
Diptera	Bombyliidae	*Desmatoneura*	*D. brevipennis*	1
Diptera	Bombyliidae	*Exhyalanthrax*	Sp. 1	5
Diptera	Bombyliidae	*Exoprosopa*	*E. efflatouni*	1
Diptera	Bombyliidae	*Exoprosopa*	*E. minios*	1
Diptera	Bombyliidae	*Oligodranes*	*O.* sp. aff. *flavus*	1
Diptera	Bombyliidae	*Petrorossia*	Sp. 1	1
Diptera	Bombyliidae	*Petrorossia*	Sp. 2	1
Diptera	Bombyliidae	*Petrorossia*	Sp. 4	1
Diptera	Bombyliidae	*Petrorossia*	*P. albula*	2
Diptera	Bombyliidae	*Petrorossia*	*P. letho*	2
Diptera	Bombyliidae	*Petrorossia*	*P. tropicalis*	4
Diptera	Bombyliidae	*Spogostylum*	Sp. 1	2
Diptera	Bombyliidae	*Systoechus*	*S. aurifacies*	7

Diptera	Bombyliidae	*Toxophora*	*T. aegyptiaca*	1
Diptera	Milichiidae	*Milichiella*	*M. argentiventris*	1
Diptera	Mythicomyiidae	*Cephalodromia*	*C. ktantesula*	1
Diptera	Tephritidae	*Trupanea*	*T. stellata*	1
Hymenoptera	Braconidae	?	Doryctinae sp. 1	1
Hymenoptera	Braconidae	*Cardochiles*	Sp. 1	1
Hymenoptera	Braconidae	*Glyptomorpha*	Sp. 1	1
Hymenoptera	Braconidae	*Glyptomorpha*	*G. irreptor*	3
Hymenoptera	Pteromalidae	?	Pteromalidae sp. 1	1
Hymenoptera	Formicidae	*Camponotus*	*C. sericeus*	34
Hymenoptera	Formicidae	*Lepisiota*	*L. gracilicornis*	43
Hymenoptera	Formicidae	*Lepisiota*	*L. omanensis*	4
Hymenoptera	Formicidae	*Monomorium*	*M. exiguum*	1
Hymenoptera	Formicidae	*Monomorium*	*M. niloticum*	36
Hymenoptera	Formicidae	*Trichomyrmex*	*T. mayri*	2
Hymenoptera	Vespidae	*Cyrtolabulus*	Sp. 1	11
Hymenoptera	Vespidae	*Delta*	Sp. 1	1
Hymenoptera	Vespidae	*Delta*	*D. hottentottum elegans*	1
Hymenoptera	Vespidae	*Delta*	*D. esuriens*	1
Hymenoptera	Vespidae	*Eumenes*	Sp. 1	1
Hymenoptera	Megachilidae	*Icteranthidium*	Sp. 1	2
Hymenoptera	Crabronidae	*Cerceris*	*C. alboatra*	1
Hymenoptera	Crabronidae	*Gastrosericus*	Sp. 1	1
Lepidoptera	Lycaenidae	*Chilades*	*C. trochylus*	1
Lepidoptera	Pieridae	*Colotis*	Sp. 1	1

Table S4. January 2017 metaweb of insect visitors to *E. larica*

Order	**Family**	**Genus**	**Species**	**Abundance**
Coleoptera	Cerambycidae	*Idactus*	*I. iranicus*	1
Coleoptera	Chrysomelidae	*Spermophagus*	Sp. 1	1
Coleoptera	Dermestidae	*Anthrenus*	Sp. 1	7
Coleoptera	Dermestidae	*Anthrenus*	*A. flavipes*	5
Coleoptera	Dermestidae	*Attagenus*	Sp. 1	7
Coleoptera	Dermestidae	*Phradonoma*	Sp. 1	2
Coleoptera	Malachiidae	?	Malachinae sp. 1	2
Coleoptera	Malachiidae	?	Malachinae sp. 2	1
Coleoptera	Scarabaeidae	*Stalagmosoma*	*S. cynanki*	1
Diptera	Bombyliidae	*Petrorossia*	Sp. 1	1
Diptera	Bombyliidae	*Petrorossia*	Sp. 2	1
Diptera	Bombyliidae	*Petrorossia*	*P. albula*	1
Diptera	Chloropidae	*Lagaroceras*	*L. albolineatum*	1
Diptera	Milichiidae	*Milichiella*	*M. argentiventris*	1
Diptera	Muscidae	*Musca*	*M. domestica*	2
Diptera	Mythicomyiidae	*Empidideicus*	Sp.1	1
Diptera	Rhiniidae	*Cosmina*	*C. viridis*	1
Diptera	Rhiniidae	*Rhyncomya*	*R. bullata*	2
Diptera	Syrphidae	*Paragus*	*P. compeditus*	1
Diptera	Syrphidae	*Syritta*	*S. fasciata*	2
Diptera	Tephritidae	*Microtreta*	*M. deemingi*	1
Diptera	Tephritidae	*Paraoxyna*	Sp. 1	1
Hymenoptera	Braconidae	*Glyptomorpha*	Sp. 2	3
Hymenoptera	Braconidae	*Glyptomorpha*	*G. irreptor*	5
Hymenoptera	Formicidae	*Lepisiota*	*L. gracilicornis*	33
Hymenoptera	Formicidae	*Lepisiota*	*L. omanensis*	2
Hymenoptera	Formicidae	*Monomorium*	*M. niloticum*	21

Hymenoptera	Formicidae	*Trichomyrmex*	*T. mayri*	2
Hymenoptera	Formicidae	*Paratrechina*	Sp. 1	1
Hymenoptera	Vespidae	*Antepipona*	Sp. 1	1
Hymenoptera	Vespidae	*Cyrtolabulus*	Sp. 1	6
Hymenoptera	Vespidae	*Delta*	*D. hottentottum elegans*	2
Hymenoptera	Pompilidae	*Aporinellus*	Sp. 1	1
Hymenoptera	Crabronidae	*Cerceris*	*C. alboatra*	1
Hymenoptera	Crabronidae	*Dasyproctus*	*D. arabs*	1
Hymenoptera	Crabronidae	*Philanthus*	Sp. 1	1
Hymenoptera	Crabronidae	?	Crabronidae sp. 1	2
Hymenoptera	Sphecidae	*Ammophila*	Sp. 1	1
Hymenoptera	Colletidae	*Hylaeus*	Sp. 1	3
Hymenoptera	Halictidae	*Lasioglossum*	*L. dathei*	2
Hymenoptera	Halictidae	*Lasioglossum*	*L. mose*	1
Hymenoptera	Halictidae	*Pseudapis*	Sp. 1	5
Hymenoptera	Megachilidae	*Icteranthidium*	Sp. 1	1

Table S5. November 2018 metaweb of insect visitors to *E. larica*

Order	**Family**	**Genus**	**Species**	**Abundance**
Coleoptera	Chrysomelidae	*Bruchidius*	Sp. 1	7
Coleoptera	Chrysomelidae	*Bruchidius*	Sp. 2	1
Coleoptera	Chrysomelidae	*Spermophagus*	Sp. 1	4
Coleoptera	Dermestidae	*Anthrenus*	Sp. 1	79
Coleoptera	Malachiidae	?	Malachinae sp. 2	3
Coleoptera	Malachiidae	*Troglops*	Sp. 1	2
Diptera	Agromyzidae	?	Agromyzidae sp. 1	1
Diptera	Bombyliidae	*Anthrax*	*A. trifasciatus*	2
Diptera	Bombyliidae	*Exhyalanthrax*	*E. beckerianus*	4
Diptera	Bombyliidae	*Exoprosopa*	*E. linearis*	2
Diptera	Bombyliidae	*Petrorossia*	*P. hespera*	5
Diptera	Bombyliidae	*Petrorossia*	*P. letho*	3
Diptera	Bombyliidae	*Nr. Reissa*	Sp. 1	1
Diptera	Bombyliidae	*Systoechus*	*S. aurifacies*	1
Diptera	Bombyliidae	*Toxophora*	*T. fasciculata*	1
Diptera	Cecidomyiidae	?	Cecidomyiidae sp. 1	2
Diptera	Empididae	*Empidideius*	Sp. 1	1
Diptera	Muscidae	*Musca*	*M. sorbens*	1
Diptera	Sciaridae	?	Sciaridae sp. 1	4
Diptera	Syrphidae	*Paragus*	*P. azureus*	1
Hymenoptera	Braconidae	?	Doryctinae sp. 1	1
Hymenoptera	Braconidae	*Glyptomorpha*	Sp. 1	1
Hymenoptera	Encyrtidae	?	Encyrtidae sp. 1	1
Hymenoptera	Eurytomidae	*Tetramesa*	Sp. 1	1
Hymenoptera	Formicidae	?	Formicidae sp. 1	4
Hymenoptera	Formicidae	*Monomorium*	*M. niloticum*	18
Hymenoptera	Formicidae	*Lepisiota*	*L. gracilicornis*	22
Hymenoptera	Vespidae	*Cyrtolabulus*	Sp. 1	1

Hymenoptera	Vespidae	*Eumenes*	Sp. 1	3
Hymenoptera	Vespidae	*Vespa*	*V. orientalis*	4
Hymenoptera	Sphecidae	*Ammophila*	Sp.1	3
Hymenoptera	Megachilidae	*Icteranthidium*	Sp. 1	1
Lepidoptera	Lycaenidae	*Azanus*	*A. jesous*	2
Lepidoptera	Lycaenidae	*Chilades*	*C. trochylus*	1

Table S6. Species found in all three-survey periods.

Order	**Family**	**Genus**	**Species**
Coleoptera	Chrysomelidae	*Spermophagus*	Sp. 1
Coleoptera	Dermestidae	*Anthrenus*	Sp. 1
Hymenoptera	Formicidae	*Lepisiota*	*L. gracilicornis*
Hymenoptera	Formicidae	*Monomorium*	*M. niloticum*
Hymenoptera	Vespidae	*Cyrtolabulus*	Sp. 1
Hymenoptera	Megachilidae	*Icteranthidium*	Sp. 1

Table S7. Temperatures recorded at each sampling sites at the start of a survey, October/November 2016

Survey Site	Temperature (^{o}C)
Yiti Road	34.2
Nr. Taww Village	35.0
Nr. Buwah Village	32.0
Nr. Birkat Al Mouz 1	29.8
Nr. Birkat Al Mouz 2	N/A
Jebel Shams 1	31.0

Jebel Shams 2	23.8

Table S8. Temperatures recorded at each sampling sites at the start of a survey, January 2017

Survey Site	Temperature (^{o}C)
Yiti Road	23.1
Nr. Taww Village	22.1
Nr. Buwah Village	23.5
Ghubrah Canyon	N/A
Nr. A'Tekhah Village	30.2
Nr. Hodinia Village	27.0
Jebel Shams 1	24.0

Table S9. Temperatures recorded at each sampling sites at the start of a survey, November 2018

Survey Site	Temperature (^{o}C)
Yiti Road	25.5
Nr. Taww Village	28.7
Nr. Buwah Village	28.5
Ghubrah Canyon	30.5
Old Road to Sur	28.5
Jebel Shams 1	34.5

Salma Plateau	28.4

Chapter 4.

Do rainfall events cause spikes in bee abundance in a desert environment?

Do rainfall events cause spikes in bee abundance in a desert environment?

Abstract

Temporal sampling of bee populations across multiple seasons still remains comparatively rare in comparison to studies of spatial differences in community structure. In desert environments there are some suggestions that bees use rainfall as a cue for emergence from diapause in order to synchronise their flight activity with flowering plants. This would imply bee community assembly is due to abiotic filtering. This study used yellow pan traps to sample the local bee assemblage over almost two years at a single locality within the lowland Hajar Mountains in northern Oman. Species richness and abundance of bee species was low throughout the study, with a high level of turnover in the form of species replacement. Change within the assemblage was directional and while species richness was highest in the spring months, there was no definitive evidence that rainfall events resulted in spikes in bee abundance.

Introduction

While bees are recognised as being the primary pollinators of 87.5% of all angiosperms (Dorchin et al., 2017), an understanding of how community structure responds to temporal changes due to abiotic factors is still understudied in comparison to how patterns of species richness change spatially (Magurran et al., 2010). The structure of pollination networks is recognised as being temporally fluid, with a high turnover of species and links from year to year (Collins et al., 2008; Olesen et al., 2008; Fantinato et al., 2019). Nevertheless, a lack of baseline data on pollinator community structure in most of the world makes it difficult to track the potential effects of climate change on communities (Knight et al., 2018).

Insect abundance shows large fluctuations as a response to changes in climate and food resources during the year (Wolda, 1988; Pinheiro et al., 2002). While this may be particularly evident in the northern hemisphere with definite cold and warm seasons (Gezon et al., 2018), subtropical environments, especially those which experience severe dry and wet periods, may also see clear oscillations in abundance and turnover of certain orders of insect (Pinheiro et al., 2002).

Many insects that rely on plant hosts during their lifecycle synchronise their emergence from eggs or diapause with their respective resource(s) in order to reduce the likelihood of mortality or reduced fitness (Dixon, 2003). Diapause is a physiological process (Kostal, 2006) that allows insects to escape unsuitable conditions through dormancy during periods when resources fluctuate temporally (Yocum et al., 2006). For instance eggs of the aphid species *Drepanosiphum platanoidis* hatch at the same time as *Acer pseudoplatanus* bud burst (Dixon, 1976). Both the tree and aphid species respond to a period of chilling in the spring, which initiates bud-burst and egg hatching (Dixon, 2003), thus the synchronisation of these two species is based around their responses to changing temperatures.

While photoperiod and temperature have previously been considered the most important phenological cue for insects (Tauber et al., 1998; Danforth, 1999), in xeric environments, hotspots for solitary bee diversity (Michener, 2007), precipitation (along with temperature) is probably the key climatic factor. This is because water availability is a limiting factor for plant growth (Crimmins et al., 2010) and hence the availability of flowers. Deserts in the Middle East typically experience two types of rainfall (Sharon, 1972), light rain falling over a generalised area over a few hours, or intense downpours that may only last a few minutes. This second type can lead to localised flooding and comes from small widely spaced convective cells that cause rainfall to be extremely localised (Sharon, 1972). This so-called 'spottiness' of rainfall (Sharon, 1972) in turn leads to patchiness in plants flowering across a landscape (Ghazanfar & Osborne, 2010). In deserts, the phenology of plants is believed to be controlled predominantly by water availability (Abd El-Ghani, 1997) with flowering in Middle Eastern deserts principally occurring in the spring after winter rains. Phenological patterns in ten plant species recorded from Saudi Arabia found flowering was constrained to a relatively brief period, with the peak occurring in March-May after winter rainfall and before maximum daily temperatures reached 50°C (Abd El-Ghani, 1997). Plant communities may show two types of flowering events: plants, flower together over a short, intense period (defined as a “big-bang” scenario), or instead flower at lower intensities over a more prolonged period, defined as a “steady-state” scenario (Gentry, 1974; Oleques et al., 2017). In bees, this would be demonstrated either by mass emergence with rainfall, or by a slower accumulative emergence throughout the season.

In tropical environments rainfall has also been recorded as an important trigger in insect development and reproduction. In Panama the beetle *Stenotarsus rotundus* remains inactive until the first rains of the wet season trigger dispersal and mating (Wolda & Denlinger, 1984; Tanaka et al., 1987; Wolda, 1988). Likewise beetle emergence in deciduous forests in southern India is initiated by precipitation (Murali & Sukumar, 1993). In deserts a wide range of insect taxa including wasps, lepidopterans, and tephritid flies are recorded as becoming active almost immediately after rainfall events (Tauber et al., 1986).

Heavy, irregular rainfall events in deserts act as resource pulses as defined by Yang (2004) as “uncommon events of ephemeral resource superabundance”. Rainfall events in turn trigger other resource pulses (Chesson et al., 2004), such as mass flowering, reproductive events

(Keeley & Bond, 1999; Jentsch & White, 2019) and the sudden increased aggregated abundances of insects (Yang, 2004). There have been suggestions that some oligolectic bees in xeric habitats have adapted to use rainfall as a cue (Danforth, 1999) to emerge from diapause in synchronization with germinating annual plants (Minckley et al., 2000; Danforth et al., 2003). Hurd, (1957), Linsley (1958), and Rust (1988) suggested or provided evidence for this proposition. For example Hurd (1957) recorded that after an unusual summer rainfall event, individuals of the usually univoltine species *Hesperapis fulvipes* (Melittidae) emerged a second time. Likewise, Rust (1988) noted that over eight years of observations, 5 cm or more of rainfall triggered a species of *Calliopsis* (Andrenidae) to emerge (Danforth, 1999). Aside from the honeybee, *Apis mellifera*, and a small number of other species, nearly all non-tropical species of bee have phenologies involving adults or larva entering a period of diapause before emergence in the spring (Bartomeus et al., 2011), although these events can be extended if there is insufficient rainfall. As pulse events are considered to be any type of sudden change of resources within an ecosystem (Jentsch & White, 2019), mass emergence by bees from diapause occurring after rainfall in xeric habitats could be described as a pulse event in itself. If synchronisation of bees and their host plants does occur, drought events in desert environments over successive years may result it what Yang et al (2008) describe as "temporal accumulation and then release". Accumulation in this case refers to a situation where, across a landscape, limited rainfall results in bee populations remaining in diapause. This is similar to the situation where seeds remain in storage within a seed bank until a rainfall event of sufficient magnitude triggers their mass germination (release). This type of temporal accumulation and release event is most clearly seen in other insect taxa, such as the lifecycle of periodical cicadas, which show mass, synchronised emergence every 13-17 years (Marlatt, 1907; Yang et al., 2008).

Minckley et al's (2013) three-year study of the bee community in the Chihuahuan Desert in southwestern North America found that a drought in one of the years of the study had a considerable effect on the composition of the bee community. Not only were specialist bees less abundant during the drought year, but also those oligolectic species that did emerge tended to be specialists of plants that were not dependent on rainfall in order to flower. This reinforces the argument that certain oligolectic bees use rainfall as a trigger to synchronise their emergence with plant species that germinate after rainfall. Thus selection acts on highly specialised bees to use cues that predict if their host(s) are in flower or not (Minckley et al., 2013).

On the contrary, solitary bees in South Africa's arid winter rainfall area of the Succulent Karoo do not appear to use rainfall as a trigger to emerge in synchrony with plants (Mayer & Kuhlmann, 2004). In this region rainfall usually occurs in the winter months, followed by a peak in flowering in August, which coincides with the greatest abundance and species richness of oligolectic bees. During a drought year where floral resources were low, bee abundance was still recorded as being high in August even though the main flowering occurred late in September due to the drought (Mayer & Kuhlmann, 2004). The authors suggest this demonstrates that bees in this region are not using rainfall itself to trigger emergence in synchrony with flowering plants. In contrast to the use of rainfall as a trigger, the authors suggest the breaking of dormancy may in fact be caused by internal factors (e.g. a body clock) (Mayer & Kuhlmann, 2004).

The above examples of bee phenological patterns from the Chihuahuan Desert and Succulent Karoo appear to show similarities to the two extreme types of plant flowering strategies, “big-bang” scenario or “steady state” scenario. The bees of the Succulent Karoo show that desert species do not automatically reflect a “big-bang” emergence strategy using rainfall as a trigger. Oman has a short flowering season of about three months, suggesting that a 'big bang' phenology might be more appropriate.

Climate change is predicted to disrupt phenological processes (Flo et al., 2018) and consequently have a detrimental effect on plant-pollinator community structure (Devoto et al., 2009). The decoupling of synchronised interactions may have particularly severe effects in xeric habitats, where the bee communities are dominated by short-lived oligolectic bee species only active at certain times of the year (Michener, 1979; Minckley, 2008). Halictid bees have been recorded as having a 10% reduction in foraging time because of a single day’s lack of synchrony with their host plants (Gezon et al., 2017, 2018). Over time, such disruptions can threaten the stability of networks and lead to a loss of seed production (Memmott et al., 2007).

Studies of how seasonality influences patterns of insect abundance are few outside of Europe and North America (Michel & Cadet, 2009). In addition, as originally highlighted in Wolda’s (1988) influential paper on seasonality in tropical insects, there is a taxonomic bias in seasonality studies towards certain insect groups such as Lepidoptera and Coleoptera. Kishimoto-Yamada & Itioka (2015) suggest this bias remains a problem. Outside the temperate regions, studies of the seasonal changes in bee communities are mostly confined to the Neotropics, focused on orchid bees (the Euglossini: Roubik & Ackerman, 1987; Becker et al., 1991; Knol, 2016; Margatto et al., 2019).

This study quantifies the phenology of different bee species in northern Oman in order to understand how seasonality affects bee communities in an arid environment. It tests the prediction that winter/spring rainfall triggers surges in the abundance of bee species.

Methods

Study site

The study was carried out at a site adjacent to the Oman Botanic Garden (OBG) (23^{o}33’14” N 58^{o}07’49” E, 106m a.s.l) located in Al Khoud Village near Muscat in the foothills of the Hajar Mountains. The immediate area around the OBG is fenced, and hence there is no disturbance to the plant community from grazing livestock or off-road vehicles. The site offers a pristine example of the floral assemblage found within lowland northern Oman.

At 106 m elevation, the plant community at the site is typical of the open drought-deciduous *Euphorbia larica - Vachellia tortilis* woodland (0-450m) (Patzelt, 2015) habitat found throughout northern Oman outside of the true Hajar Mountains and along the coasts. The lowlands of northern Oman have a mean annual temperature of 28.4^{o}C with rainfall in the north of the country generally confined to December-March (Ghazanfar & Osborne, 2010), coinciding with the main flowering period. Average annual precipitation is 59 mm (Patzelt, 2015), although precipitation can be very unpredictable in space and time. As in other arid environments, seasonal changes are likely to be reflected by high turnover in insect species, synchronising to varying resource availability (Barretto et al., 2018).

Annual plants are common in the lowlands of the Hajar Mountains, typically germinating in January after rainfall (Patzelt, 2015). Common perennials found at the study site include *Euphorbia larica*, *Fagonia indica*, *Ochradenus aucheri*, *Tephrosia apollinea* and two species of *Convolvulus* (Table S1 gives a plant list of the site).

Daily precipitation data (mm per day) was obtained from the nearest weather station, the Public Civil Aviation Authority weather station at Bawsher, Muscat, 15 km from the survey site.

Sampling procedure

The study ran for twenty-two months from January 2017 until November 2018. Within this time period 35 yellow pan traps were set out for 24 hours every 11 days, resulting in a total of 53 trapping events. There was some variation in the length of time between collections due to collecting dates falling on weekends or public holidays. Yellow pans, measuring 4x15 cm, were set out in a line spaced six metres apart. On collection, specimens were dried and pinned for identification. Dr Alain Pauly of the Royal Belgian Institute of Natural Sciences, Brussels, identified the Halictidae, where possible to species level. Other specimens were separated into morpho-species using Michener (2007), whose taxonomy was followed.

Yellow pans are considered a useful standardised collecting method, especially as regular hand netting was not possible due to the length of the study and would depend on a collector's skill/knowledge of bees, which can lead to biased collecting. In desert environments, the traps have the advantage of attracting bees when flowers are rare as well as collecting transients in search of infrequent floral resources (Minckley et al., 2013).

Data Analysis

1. Community structure

To investigate how the structure of the bee assemblage within the study site changed during the two years of the study, the R package *betapart* was used. Using the function *beta.multi*, the Sørensen index of beta diversity was calculated. This index calculates three aspects of dissimilarity, spatial turnover (β_{SIM}), nestedness (β_{SNE}), and the sum of both (β_{SOR}) (Baselga et al., 2013). A value of 0-1 is returned. A zero value indicates no nestedness or species turnover, while a score of one shows total nestedness or species turnover between sites.

To understand further the temporal dynamics occurring during the study, two temporal diversity indices in the R package *codyn* were also employed (Hallett et al., 2016). These indices measure species turnover (function *turnover*), and the rate of community change (function *rate_change*) (Hallett et al., 2016). *Turnover* returns three metrics: total turnover, and species appearances and disappearances through time, all of which calculate the proportion of species that change between time points (Hallett et al., 2016).

The *rate_change* function ascertains the type of temporal change occurring within a community, for instance whether it is 'cyclic, directional, stochastic, or chaotic' (Collins et al., 2000). It uses time-series data to measure the similarity within the community through time and to pick out patterns that emerge temporally (Collins et al., 2000).

Finally, the *codyn* function *synchrony* was used with the default 'Loreau' parameter (Loreau & Mazancourt, 2008). This measures the degree of synchrony between the bee species recorded in the study. The function returns a score between 0 and 1, 0 being perfect asynchrony and 1 being perfect synchrony. Unlike the other *codyn* functions, which measure aspects of temporal diversity, the *synchrony* function measures community stability (Hallett et al., 2016). Species evenness was calculated using Pielou's evenness, which measures relative evenness (Jost, 2010), using the function '*diversity*' in the R package *vegan* (Oksanen et al., 2018).

2. Phylogenetic Diversity

In order to view how phylogenetic diversity changed throughout the survey period, the R packages *ape* and *picante* were used. Bees were classified using Michener (2007) for the taxonomy from family, to subfamily, tribe, and genus. An ultra-metric tree including branch lengths with the *p* parameter set to 1 (based on Hoiss et al., 2012; Dorchin et al., 2017) was constructed using the function *as.phylo.formula* and *compute.brlen* in *ape* (Figure 1).

The function *ses.pd* in the *picante* package was used to calculate the standardized effect size (SES) of Faith's phylogenetic diversity (PD)

(Kembel et al., 2019). The SES is calculated by 'dividing the effect size by the standard deviation of the null distribution' (Swenson, 2014). *Ses.pd* returns the SES of the PD as against that of null communities (Kembel et al., 2019). These values will be negative or positive depending on whether the observed values are higher or low than the random SES (Swenson, 2014). A P-value (quantile) is also returned, showing whether the observed PD is significantly different from that of the null distribution (Kembel et al., 2019). A significant negative value indicates phylogenetic underdispersion, i.e. less phylogenetic diversity than expected from the null model (high species to genus ratio), implying that the dominant mechanism of community assembly is abiotic filtering (Swenson, 2014). The opposite, a significant positive value, is known as phylogenetic overdispersion (low species to genus ratio), implying that the dominant mechanism of community assembly is biotic, such as the competitive exclusion of closely related species (Presley et al., 2018).

3. Weather variables

To test whether precipitation resulted in a significant relationship against bee species richness or abundance, two Pearson product-moment correlation coefficients were calculated. The relationship between the bee species richness and bee abundance (totals per month of the study) was assessed against precipitation (total per month of the study).

Results

1. Bee assemblage composition

A total of 274 bee specimens from 30 species were collected during the study (Table 1). These included genera in the families Colletidae (1 species), Andrenidae (1 species), Halictidae (10 species), Megachilidae (14 species), and Apidae (4 species) (Table 1). From examining the collections in the Natural History Museum (London) and Oxford University Museum of Natural History, a preliminary checklist for Oman of 71 species was compiled (Table S2).

Species richness was extremely low throughout most of the study, with only five of the trapping periods collecting six or more species of bee. As expected, species richness and abundance was greatest in both years during spring, February-March in 2017 and March-April in 2018 (Figures 2 & 3).

151 specimens of the species *Systropha* sp. 1 were collected, making this by far the most abundant species, especially as the next most abundant species was *Halictus tibialis,* with 29 specimens (Figure 4). Most species were rare, with 25 of the 30 species being recorded from five or fewer specimens (Table 1). While species richness was almost the same for the two years, 18 in 2017 and 17 in 2018, abundance was far higher in the first year, 232 vs. 42 individuals. The Halictidae were the most species-

rich family in 2017 with eight species, while in 2018 Megachilidae replaced them with eleven species recorded.

In both years, abundance was greatest in March, although in 2017 numbers of bees were much higher than the following year (135 individuals vs. 19) (Figure 5). The results from Pielou's evenness index showed that throughout the study, where trapping events collected more than one species of bee, the local assemblage was mostly even with low levels of abundance for all species (Figure 5).

Only three trapping events showed low Pielou values (below 0.50) indicating unevenness within the local assemblage. These events all occurred in the first year, two during March and then again in May (0.24, 0.23 in March and 0.49 in May). Unevenness within the communities was due to spikes in abundance of the species *Systropha* sp.1.

A species abundance curve (Figure 4) for the two years emphasises the abundance of the *Systropha* species and a few other relatively abundant species followed by a long tail of rare species. Other than *Apis mellifera* and *Systropha* sp. 1, all species recorded from more than five specimens were from the genera *Halictus* and *Lasioglossum* of the family Halictidae.

2. Temporal turnover and species synchronization

The Sørensen index of beta diversity revealed high species replacement between all surveys, as well as between the summed collections made in 2017 and 2018. The particularly low levels of nestedness (β_{SNE} 0.01) within the 'between years' analysis suggest almost two different communities of bees during the two years of the study. In both datasets species replacement is the driving factor in temporal turnover (Table 2).

The measures from the *turnover* function agreed with the Sørensen index in showing that the assemblage structure was highly dynamic, with half of the trapping events recording a total turnover of species of 1.00. Turnover was lower in the early spring months (February-April), indicating more stability with some species being recorded multiple times. Outside of the spring months, nearly all species appeared once and then were lost from the site. This may be a reflection of the low abundance of flowering plants at the study site, and hence that these species were transients (Table 3)

The rate of change within the assemblage over the survey period was 0.85. As the slope is positive and linear, the type of change showed a directional pattern. Therefore the assemblage showed a succession of different bee species appearing throughout the study (Figure 6). The synchrony function (Loreau metric) in the package *codyn* returned a score of 0.32, implying that the local species assemblage is asynchronous.

Hence all metrics imply that there was little pattern to when species appeared during the study. While abundance and species richness were highest in the spring, the majority of species appeared and then were rapidly lost from the study site.

3. Phylogenetic Diversity within the local assemblage

Apart from two of the surveys in May 2017, all surveys that calculated a SES for collection dates with more than one species returned a negative SES score (Table 4). This indicates that PD was lower than expected based on the null model. However, only three surveys (16.03.17, 27.03.17, and 30.05.18) returned a significant negative SES, suggesting phylogenetic underdispersion (high species to genus ratio).

4. Climatic conditions

Total annual rainfall was low in both years of the study, 27.4 mm in 2017 and 18 mm in 2018. A total of eighteen rainfall events were recorded (Figure 7), all occurring during February-May and September-December. The amount of rain ranged from 0.2 mm to 11.4 mm, with October 2018 seeing the greatest amount of rainfall (three rainfall events totalling 15.6 mm) for any month.

The Pearson product-moment correlation coefficient (Figure 8) calculated to assess the relationship between total bee abundance per month and the total amount of precipitation per month found no significant correlation between the two variables (r= 0.061, p= >0.5). The second correlation coefficient (Figure 9) looking at the relationship between total bee species richness per month and the total amount of precipitation per month also showed no significant correlation (r= 0.052, p= >0.5).

Discussion

The results of this study suggest a dynamic assemblage of bees with many rare species and a high level of turnover that continued throughout the study. Change within the local assemblage was directional because a succession of different species was added throughout the period of study. Dominance in species numbers shifted from the family Halictidae in the first year to Megachilidae in the second year, demonstrating turnover at the family as well as the species level. Most species were scarce with 83% of species being recorded from five or less specimens. This scarcity in abundance appears to be a common observation in many bee community studies (Williams et al., 2001; Roubik et al., 2001; Potts et al., 2003; Dorchin et al., 2017). A possible explanation to this pattern given by Williams et al (2001) is that the rarity is due to transient species entering an environment to which they are less adapted, hence the low numbers (Dorchin et al., 2017). This concept may be applicable to this study as the Oman Botanic Gardens is situated in a transitional zone between the Western Hajar Mountains and the Batinah Coastal plain, with both areas containing distinctive floral communities (Patzelt, 2015). Further research is needed on the plant choices of foraging bees in this region in order understand how different species are using different habitat types.

The histogram showing the abundance of bees over the two years (Figure 4) reveals the pattern of assemblage, with a few dominant species and many rare species. This is a pattern in abundance seen in other studies looking at the species richness of insects through time. Moreover this skewed pattern is reflected in the levels of interactions seen within pollination networks, with a few highly connected species and many specialised species (Maia et al., 2019) creating an asymmetric pattern that is typical for many networks (Fantinato et al., 2019). A similar pattern of a mostly low abundant species with a limited number of very common species is recorded for certain oligarchic beetle species in the family Mordellidae inhabiting the canopy of the Amazon rainforest (Erwin et al., 2017). Erwin et al (2017) suggest investigating the taxonomic relationship between species in order to understand why this type of pattern would develop. Thompson (2005) highlights that related species might show similar phylogenetic conservatism and ecological specialisation in terms of the species they coevolve with. Consequently related bee species may visit the same plant families or genera and hence would show similar levels of abundance as they respond to the same abiotic and biotic factors that affect they're host plants.

The dissimilarity results showed species replacement rather than nestedness was the defining feature of turnover within this local assemblage (Table 2). While species richness was similar in both years, apart from three low Pielou index scores (all in 2017) due to large numbers of *Systropha* (a Convolvulaceae specialist: Baker, 1996), the abundance of individual species was low and the assemblage structure was even. Low abundance was particularly clear in the second year of the study when the Megachilidae replaced the Halictidae as the dominant component of the bee fauna and the abundance of individual species was lower. The fact that replacement was such an important aspect of assemblage structure in this habitat underlined the importance of sampling bee communities at multiple time periods (Basilio et al., 2006) and over several years to capture rare and transient species. Sampling in only one of the two years would have created a biased view of how the assemblage was structured.

In contrast to my initial hypothesis, the evidence suggested that rainfall was not supported as a trigger for spikes in bee abundance: there was no evidence of the "big-bang" type of emergence seen in germinating annual plants in xeric habitats after rainfall. The low synchrony score (0.32) shows the local assemblage was asynchronous; again implying rainfall was not structuring species to emerge at the same time. The generally high levels of turnover throughout the study, the non-significant result of the correlation, and the lack of significant phylogenetic underdispersion in the assemblage likewise all point towards bee abundance in this habitat not being influenced by rainfall. While both abundance and species richness were greatest during the spring months as expected, this did not correlate with rainfall events during the study, which were more sporadic than the literature on the climate of Oman suggests. For instance in 2017, the heaviest rain occurred in May after the main flowering season had finished in northern Oman. Likewise in 2018 90% of the rainfall was recorded during September and October, three months before the flowering period started. Only one bee was recorded during this period, and so the autumn rainfall events appeared to have had no immediate effect on bee populations. Climate change is likely to cause further disruption to rainfall patterns in the region, potentially leading to periods of extreme drought or more regular flash flooding (Sowers, et al., 2011; Terink et al., 2013). This could be disastrous for local bee populations who rely on floral resources from specific plant species, especially if rainfall events trigger seed germination at unusual times of the year. Phenological mismatching between bee and plant species would threaten pollination networks.

Nevertheless there are two caveats. Firstly while phylogenetic underdispersion, an indication that community assembly is influenced primarily by abiotic factors (Swenson, 2014), was only recorded three times, nine of the surveys that collected specimens only collected a single individual. Therefore it was not possible to calculate PD during these surveys. Nevertheless, there was a clear separation between the communities during the two years, Halictidae dominant in the first year of the study, Megachilidae in the second year. Therefore phylogenetic underdispersion (indicated by a high species to genus ratio) was apparent when the species were summed for all surveys for each of the two years.

Secondly, during both years rainfall was low, 28 mm in 2017 and 18 mm in 2018. Therefore it may be a case that the amount of rain did not meet a threshold to trigger emergence and most bees simply remained in diapause, hence the low abundance levels. As highlighted in Minckley et al (2013), in drought years species observed in the Chihuahuan Desert were predominately generalist species, while specialised species were suspected to have remained in diapause. Adaptation to limited water is seen in many desert annual plant species, which tolerate dry interpulse years by not germinating and remaining in the seed bank (Miao & Bazzaz, 1990). Support for the idea that many bee species remained in diapause could be reflected in the extremely low levels of species richness recorded during most of the study. 58% of surveys failed to record a single bee and only one survey (23.02.17) collected more than ten species. This was surprising, as northern Oman has been declared both as a hotspot for bee diversity (Patiny & Michez, 2007) and plant species richness (Patzelt et al., 2014) and so high bee species richness was expected, particularly in the spring months. In order to gain a clearer insight it would be necessary to continue this study in years of heavy rainfall during the winter and spring months, as well as recording floral choices to see if generalist species are more common in drought years (Minckley et al., 2013).

A possible explanation for the low-recorded species richness and abundance seen during much of the study may be due to the trapping methodology itself. One of the major benefits of pan trapping is that it is avoids collector bias (Toler et al., 2005), is cost effective (Spafford & Lortie, 2013), and can be easy to maintain for long time periods. Alternatively surveying with a hand net can be problematic. Unless the same collector is present during every survey, less experienced researchers may risk missing taxa such as *Hylaeus*, which don't necessarily appear to be bees to the non-expert.

Nevertheless, several studies have highlighted that pan trapping can lead to species bias within a sample and only capture a subset of a local species assemblage (Roulston et al., 2007). For instance, species of the family Halictidae are recorded as being particularly common in pans (Toler et al., 2005; Roulston et al., 2007). Vrdoljak & Samways (2012) cautioned that the colour of pan traps might influence trapping results. The authors found when pan traps were trialled in South Africa's Cape Floristic Region, while yellow and white pan traps provided relatively good estimates of species richness, only using these two colours meant 20% of the entire species pool were missed. Colour may also lead to biases in the sex of species, for instance blue pans have been noted as being especially attractive to females of the species *Andrena lamnanthis* (Leong & Thorp, 1999). Not only did Vrdoljak & Samways (2012) find species richness was influenced by colour but colour of a trap influenced levels of individual species abundance (Southwood & Henderson, 2000). Therefore, it must be recognised that only using a single colour of pan may have influenced the species that were collected during this study.

In the current study, ignoring *Apis mellifera*, all of the most common species belonged to the family Halictidae, and nearly all of these were *Halictus* and *Lasioglossum*, two genera known to contain eusocial species (Brady et al., 2006). Two of the three *Halictus* species belonged to the same subgenus *Seladonia*, and likewise two of the three *Lasioglossum* species belonged to the subgenus *Sphecodogastra.* It would be useful to know which plant species are visited by these bees, because this might help to explain their levels of abundance, especially compared to rarer distantly related species. This might indicate whether phylogenetic conservatism influences patterns of emergence. Pan trapping in other locations, including different habitat types, may also allow an exploration of whether pan trapping itself was influencing the high number of Halicitdae species caught during the study.

The greatest abundance of bees was collected in the spring and winter of both years, as predicted. Nevertheless, three species (*Pseudapis* sp.1, *Megachile* sp. 6, and *Amegilla* sp. 2) were collected in September and October of the two years. As no bees were recorded during the summer months (June-August) of both years, it may be the case that a limited number of species emerges from diapause in the autumn and continues flight activity until the end of May. Therefore the community probably does not simply emerge after the main period of rainfall in late winter/early spring, as initially expected. *Pseudapis* sp. 1 and *Amegilla* sp. 2 were collected in September and October 2017. The last recorded rainfall for that year was the 14th May 2017 (8.2mm), and so clearly these species do not use rainfall as a trigger to synchronise their emergence with late-flowering host plants.

The three species active in autumn, belong to three different families (Halictidae, Megachilidae and Apidae), and represent both short and long-tongued species. This suggests there is enough floral diversity present at that time of the year to support different guilds of bees. All three species were then recorded again in February to April. Whether populations remain active throughout this period or are bivoltine/multivoltine is unknown, although Megachilidae and ground nesting Apidae are usually regarded as being univoltine (Danforth et al., 2019). Bivoltine lifestyles have been recorded in the subfamily Nomminae, the subfamily that includes *Pseudapis.* Therefore it is possible the records for *Pseudapis* sp. 1 represent two separate generations although this requires further research to determine.

Conclusions

There was insufficient evidence to rule out or support the proposition that xeric-adapted bee species synchronise their emergence from diapause with germinating plants using rainfall as a cue. Bee occurrence was low throughout the study, with no obvious relationship with precipitation. This is similar to the findings of Mayer & Kuhlmann (2009) from the Succulent Karoo of South Africa.

However, the low diversity and abundance of the catch may indicate that as surveys were conducted during low-rainfall years, the majority of species simply remained in diapause. More surveys are needed to understand if the observed patterns represent abnormally low species richness, which seems likely as Patiny & Michez (2007) recognised the Hajar Mountains as being a bee diversity hotspot. The scarcity of rainfall events during the study years may have failed to reach a threshold to initiate mass emergence. However, without survyes conducted in years with greater rainfall it is not possible to confirm whether or not rainfall is a trigger to bee emergence. Additionally, future studies should use several different colours of pan traps to test whether this influences the range of species collected. While this study caught a wide diversity of bee taxa, including all known families found in Oman apart from the family Melittidae (only one species of Melittidae, *Dasypoda albipila*, has been recorded from Oman), additional surveys in the same habitat type but at other sites are needed, trialling different colour pans. This will allow estimates to be made on whether the results in this study reflect the true species composition found in lowland Oman or are instead a reflection of the collecting methodology.

Figures and Tables

Figure 1. Phylogenetic tree of the bee fauna at the OBG site. The families Halictidae and Megachilidae dominate the recorded bee fauna. *Megachile* was the most species-rich taxon.

Figure 2. Bee abundance shown throughout the study period.

Figure 3. Bee species richness shown throghout the study period.

Figure 4. Distribution curve for bee abundance over the two years of the study. Species 1= *Systropha* sp. 1, Species 2= *Halictus tibialis*

Figure 5. Species richness and Pielou's evenness index scores for all successful trapping events.

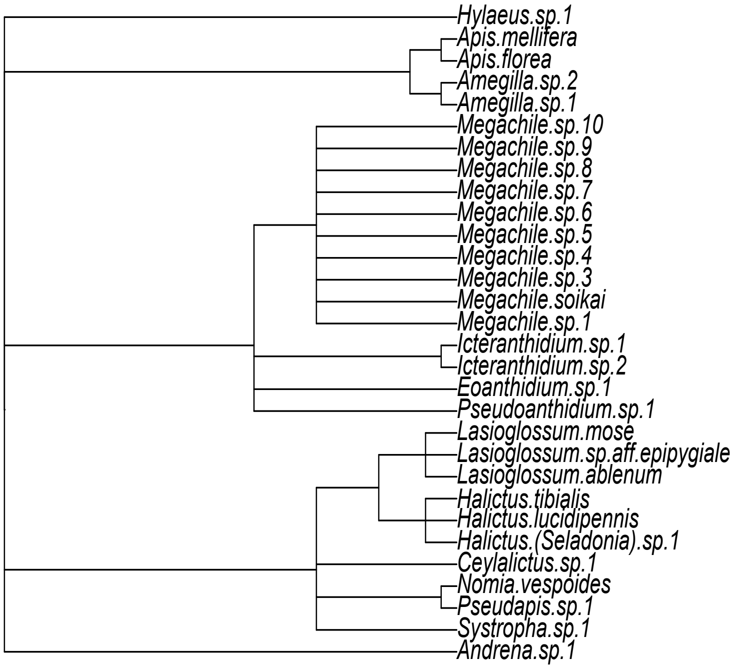
Figure 6. The top graph shows turnover within the bee assemblage between trapping events (blue line= total turnover, green line= appearances within the assemblage, yellow line= disappearances within the assemblage). The bottom graph shows rate and direction of change within the local assemblage. The compositional change to the assemblage is measured using Euclidean distances. These are calculated on pair-wise communities throughout the whole of the study period. As the data set had 53 trapping events there are distance values for 52-one interval time lags (e.g. t_1 vs. t_2, t_2 vs. t_3...), 51-two-interval time lags (e.g. e.g. t_1 vs. t_3, t_2 vs. t_4…) etc. The distance values are then regressed against the time lag interval

(Hallett et al., 2016) to reveal the rate and type of change (directional, stochastic, cyclic etc.). The positive and linear shape of the slope indicates directional change is occurring throughout the study period.

Figure 7. Temperature (°C) and rainfall events (mm) during the study period.

Figure 8. Total bee abudance per month against total rainfall per month.

Figure 9. Total bee species richness per month against total rainfall per month.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Amegilla.sp.1
Megachile.sp.10
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Megachile.sp.8
Megachile.sp.7
Megachile.sp.6
Megachile.sp.5
Megachile.sp.4
Megachile.sp.3
Megachile.soikai
Megachile.sp.1
Icteranthidium.sp.1
Icteranthidium.sp.2
Eoanthidium.sp.1
Pseudoanthidium.sp.1
Lasioglossum.mose
Lasioglossum.sp.aff.epipygiale
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Halictus.tibialis
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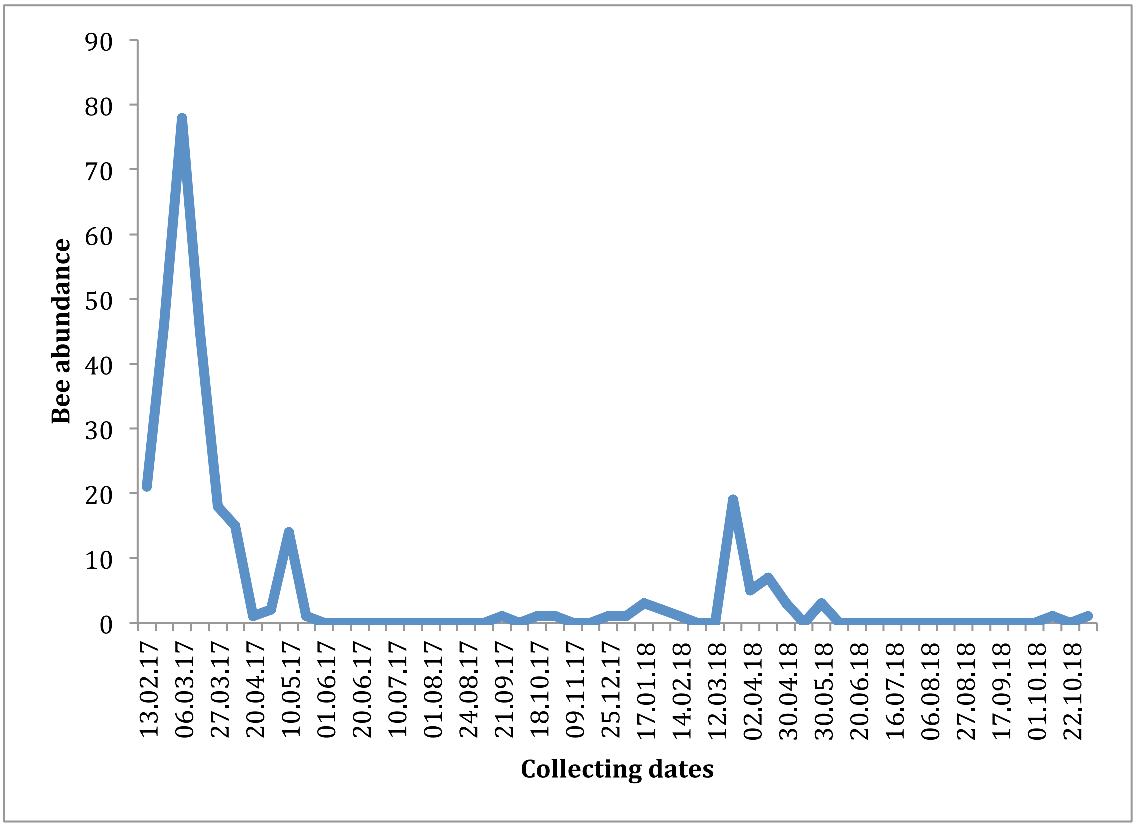
Fig 1.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21.09.17
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25.12.17
17.01.18
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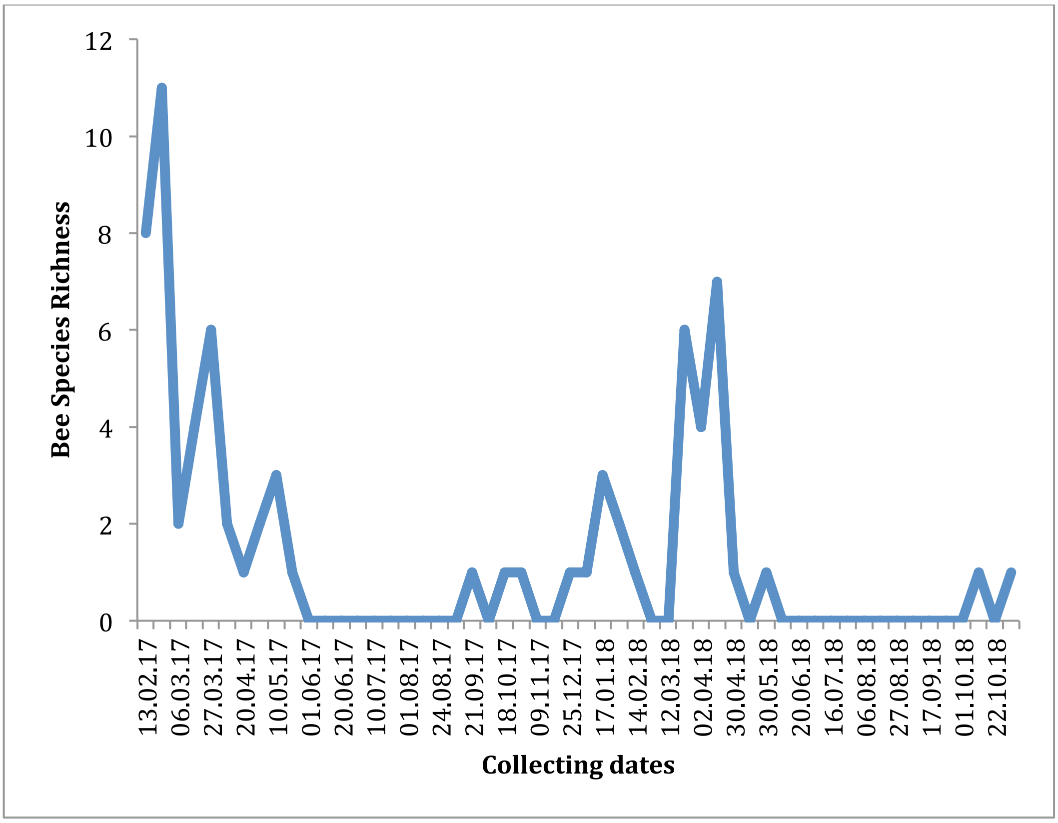
22.10.18
Collecting dates

Fig 2.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Bee Species Richness
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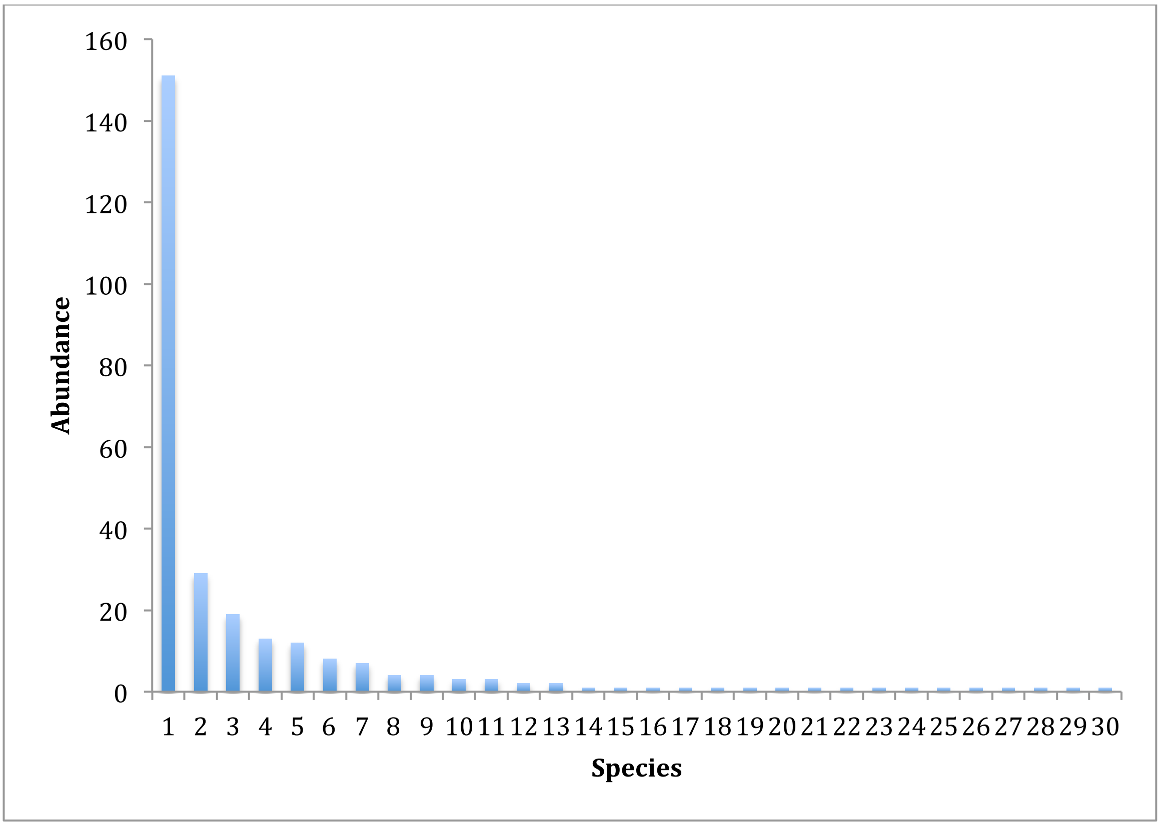
22.10.18
Collecting dates

Fig 3.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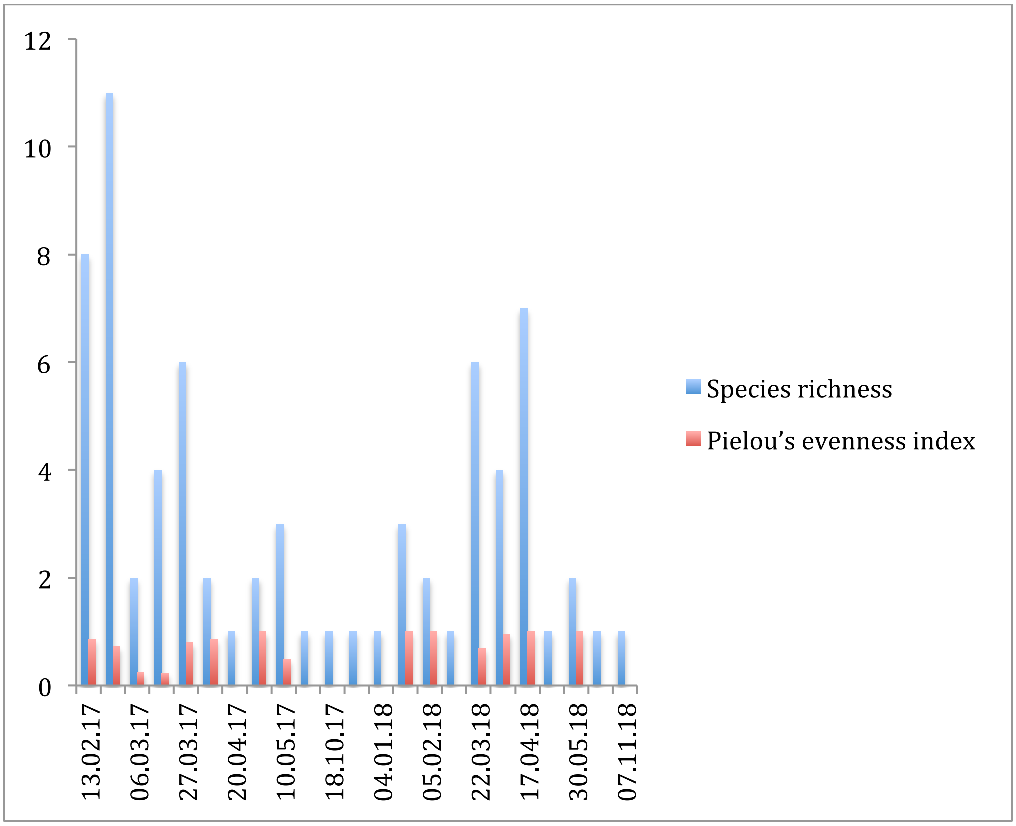
Species

Fig 4.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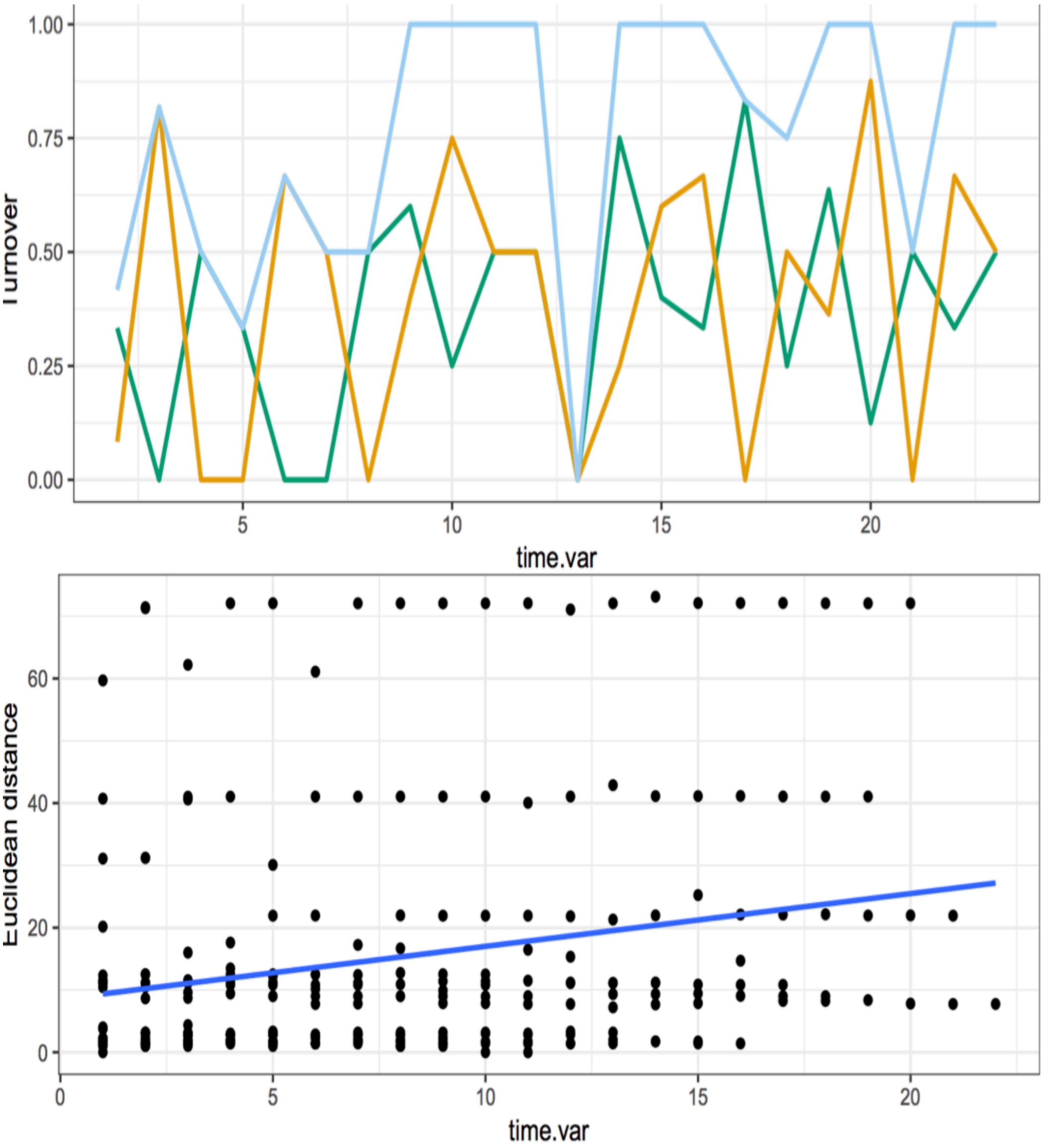
30.05.18
07.11.18
Species richness
Pielou's evenness index

Fig 5.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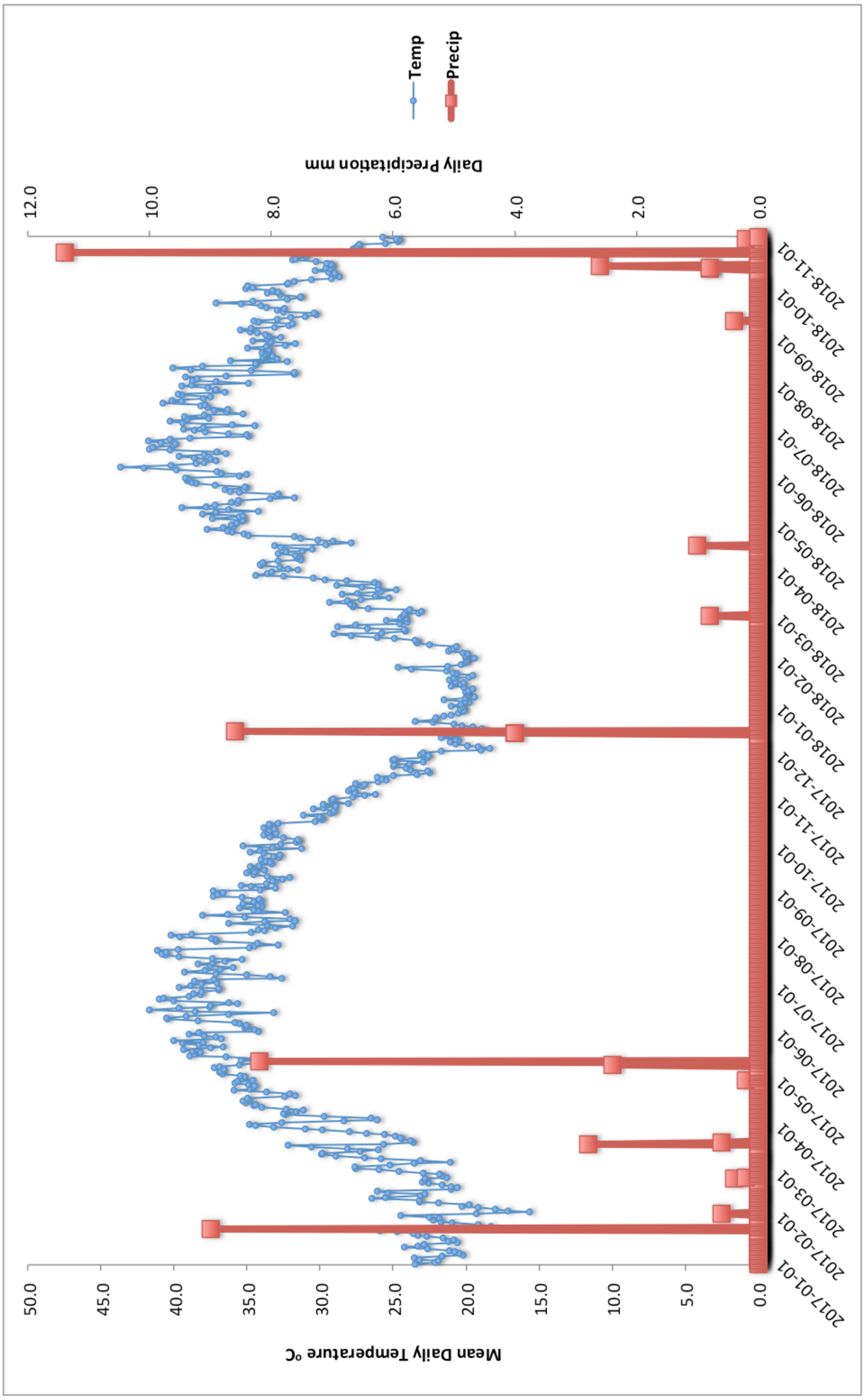
time.var

Fig 6.


Temp
Precip
Daily Precipitation mm
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6.0
4.0
2.0
0.0
Mean Daily Temperature °C
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40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
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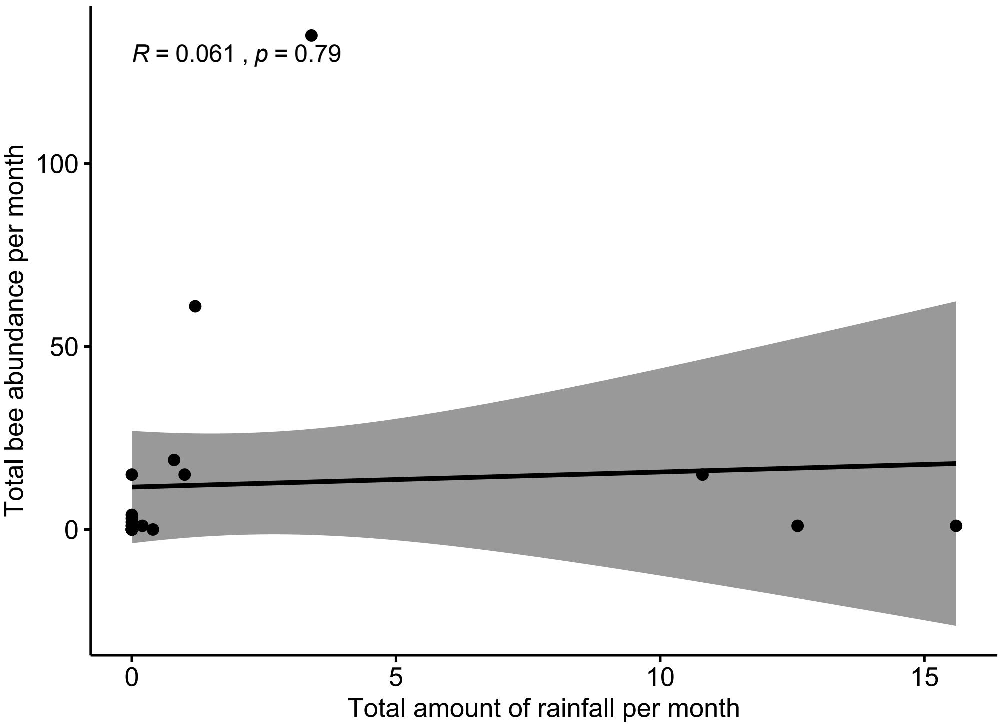
2018-07-01
2018-08-01
2018-09-01
2018-10-01
2018-11-01

Fig 7.



R = 0.061 , p = 0.79
Total bee abundance per month
100
50
0
0
5
10
15
Total amount of rainfall per month

Fig 8.

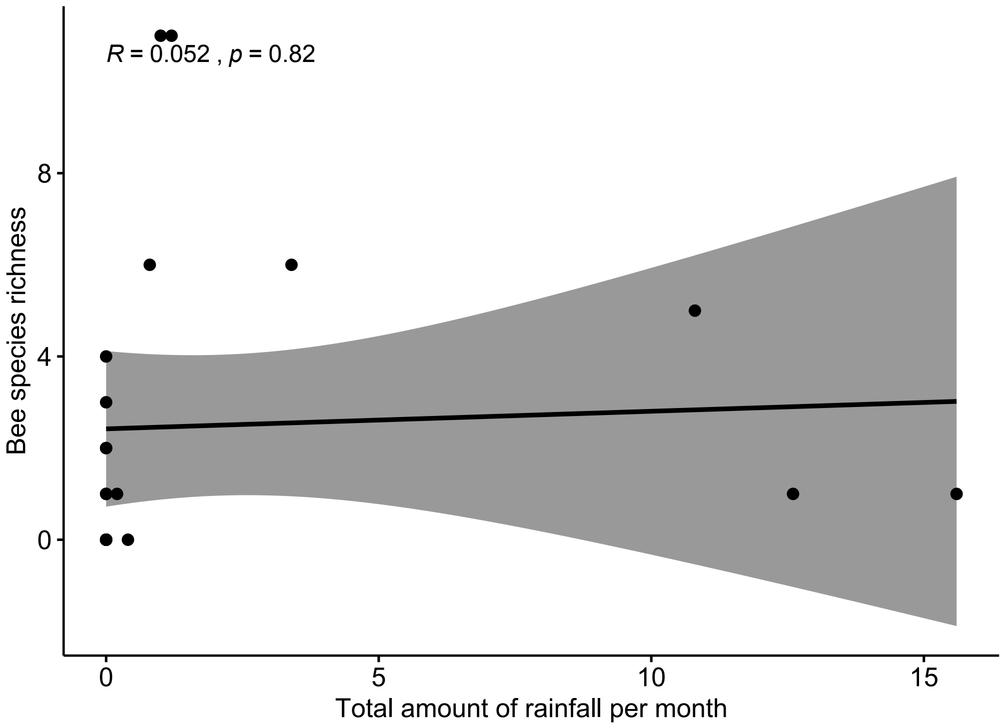

R = 0.052 , p = 0.82
Bee species richness
8
4
0
0
5
10
15
Total amount of rainfall per month

Fig 9.

Table 1.

Monthly totals for each species of bee recorded during the study.

Species	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**Total abundance**
Hylaeus sp. 1	0	1	0	0	0	0	0	0	0	0	0	0	1
Andrena sp. 1	0	1	0	0	0	0	0	0	0	0	0	0	1
Systropha sp. 1	0	16	114	10	11	0	0	0	0	0	0	0	151
Pseudapis sp. 1	0	0	1	1	0	0	0	0	1	0	0	0	3
Nomia vespoides	0	0	0	1	0	0	0	0	0	0	0	0	1
Ceylalictus sp. 1	0	1	0	0	0	0	0	0	0	0	0	0	1
Halictus (Seladonia) sp. 1	1	1	12	4	1	0	0	0	0	0	0	0	19
Halictus lucidipennis	2	4	5	1	0	0	0	0	0	0	0	0	12
Halictus tibialis	0	17	12	0	0	0	0	0	0	0	0	0	29
Lasioglossum ablenum	0	6	2	0	0	0	0	0	0	0	0	0	8
Lasioglossum sp. aff. *epipygiale*	0	4	0	0	0	0	0	0	0	0	0	0	4
Lasioglossum mose	1	10	2	0	0	0	0	0	0	0	0	0	13
Anthidiini sp. 1	0	0	2	1	0	0	0	0	0	0	0	0	3
Anthidiini sp. 2	0	0	0	1	0	0	0	0	0	0	0	0	1
Anthidiini sp. 3	0	0	1	0	0	0	0	0	0	0	0	0	1
Icteranthidium sp. 1	0	0	0	0	1	0	0	0	0	0	0	0	1
Megachile sp. 1	0	0	0	0	1	0	0	0	0	0	0	0	1
Megachile sp. 2	0	0	2	2	0	0	0	0	0	0	0	0	4

(*Megachile* *soikai*)												
Megachile sp. 3	0	0	0	1	0	0	0	0	0	0	0	0	1
Megachile sp. 4	0	0	0	1	0	0	0	0	0	0	0	0	1
Megachile sp. 5	0	0	0	1	0	0	0	0	0	0	0	0	1
Megachile sp. 6	0	1	0	0	0	0	0	0	0	1	0	0	2
Megachile sp. 7	0	0	0	0	1	0	0	0	0	0	0	0	1
Megachile sp. 8	0	0	1	0	0	0	0	0	0	0	0	0	1
Megachile sp. 9	0	0	0	1	0	0	0	0	0	0	0	0	1
Megachile sp. 10	0	0	0	1	0	0	0	0	0	0	0	0	1
Amegilla sp. 1	1	0	0	0	0	0	0	0	0	0	0	0	1
Amegilla sp. 2	0	1	0	0	0	0	0	0	0	1	0	0	2
Apis florea	0	0	1	0	0	0	0	0	0	0	0	0	1
Apis mellifera	1	3	0	0	1	0	0	0	0	0	1	1	7

Table 2.

Sørensen index of beta diversity results. Nestedness was low across all surveys as well as between the two years of the study. Species replacement is the main driver of species turnover.

Surveys	**Dissimilarity values**
All surveys:	β_{SIM}: 0.88
	β_{SNE}: 0.06
	β_{SOR}: 0.94
Between 2017 & 2018:	β_{SIM}: 0.70
	β_{SNE}: 0.01
	β_{SOR}: 0.71

Table 3.

Turnover of species (function *turnover* in the R package *Codyn*)

Collection Date	**Total Turnover**	**Appearances**	**Disappearances**
13.02.17	0.42	0.33	0.08
23.02.17	0.82	0.00	0.82
06.03.17	0.50	0.50	0.00
16.03.17	0.33	0.33	0.00
27.03.17	0.67	0.00	0.67
10.04.17	0.50	0.00	0.50
20.04.17	0.50	0.50	0.00
01.05.17	1.00	0.60	0.40
10.05.17	1.00	0.25	0.75
21.09.17	1.00	0.50	0.50
18.10.17	1.00	0.50	0.50
25.12.17	0.00	0.00	0.00
04.01.18	1.00	0.75	0.25
17.01.18	1.00	0.40	0.60
05.02.18	1.00	0.33	0.67
14.02.18	0.83	0.83	0.00
22.03.18	0.75	0.25	0.50
02.04.18	1.00	0.64	0.36
17.04.18	1.00	0.13	0.87
30.04.18	0.50	0.50	0.00
30.05.18	1.00	0.33	0.67
10.10.18	1.00	0.50	0.50

Table 4.

PD with richness null model

	SR	PD	Mean PD in null communities	SD of PD in null communities	Rank of PD vs. null communities	Z	P-value
13.02.17	8	3.62	4.49	0.60	66	-1.45	0.07
23.02.17	11	5.04	5.53	0.65	232	-0.77	0.23
06.03.17	2	0.31	1.43	0.73	99.5	-1.53	0.10
16.03.17	4	0.79	2.76	0.62	9	-3.16	0.01
27.03.17	6	2.55	3.73	0.59	14	-1.98	0.01
10.04.17	2	0.62	1.42	0.74	223	-1.08	0.22
20.04.17	1	NA	NaN	NA	NA	NA	NA
01.05.17	2	2.00	1.39	0.73	713	0.83	0.71
10.05.17	3	2.31	2.17	0.68	509.5	0.20	0.51
21.09.17	1	NA	NaN	NA	NA	NA	NA
18.10.17	1	NA	NaN	NA	NA	NA	NA
25.12.17	1	NA	NaN	NA	NA	NA	NA
04.01.18	1	NA	NaN	NA	NA	NA	NA
17.01.18	3	2.00	2.18	0.68	237	-2.66	0.24
05.02.18	2	2.00	1.39	0.75	705.5	0.81	0.71
14.02.18	1	NA	NaN	NA	NA	NA	NA
22.03.18	6	3.21	3.74	0.58	188.5	-0.92	0.19
02.04.18	4	2.45	2.80	0.63	229	-0.57	0.23
17.04.18	7	3.69	4.08	0.59	238.5	-0.66	0.24
30.04.18	1	NA	NaN	NA	NA	NA	NA
30.05.18	2	0.03	1.41	0.74	21	-1.87	0.02
10.10.18	1	NA	NaN	NA	NA	NA	NA
07.11.18	1	NA	NaN	NA	NA	NA	NA

Supplementary Information

Table S1. Vascular plant species list from the Oman Botanic Garden Yellow Pan site (In the area of ca. 100 m around the yellow pan trap site, made on the 25.06.2019). Family names and circumscriptions follow the APG IV (Angiosperm Phylogeny Group). Species names follow the 'Plants of the World Online' database. All plants listed flower between February-April, expect *Vachellia tortilis*, which flowers in May *(Dr Annette Patzelt, Scientific Director at the Oman Botanic Garden, compiled the plant list on request).*

Species	Family
Blepharis ciliaris (L.) B. L. Burtt	Acanthaceae
Aizoon canariense L.	Aizoaceae
Pentatropis nivalis (J.F. Gmel.) D.V. Field & J.R.I. Wood	Apocynaceae
Launaea massauensis (Fres.) Chiov	Asteraceae
Heliotropium calcareum Stocks	Boraginaceae
Morettia philaeana DC	Brassicaceae
Cleome quinquenervia DC	Cleomaceae
Convolvulus virgatus Boiss.	Convolvulaceae
Chrozophora oblongifolia (Delile) A. Juss. ex Spreng.	Euphorbiaceae
Euphorbia arabica Hochst. & Steud. ex T. Anderson	Euphorbiaceae
Euphorbia larica Boiss.	Euphorbiaceae
Vachellia tortilis (Forssk.) Hayne	Fabaceae
Tephrosia apollinea (Del.) DC	Fabaceae
Ochradenus aucheri Boiss.	Resedaceae
Ziziphus spina-christi (L.) Willd.	Rhamnaceae

Plocama aucheri (Guill.) M. Backlund & Thulin	Rubiaceae
Lycium shawii Roem. & Schult.	Solanaceae
Forsskaolea tenacissima L.	Urticaceae
Asphodelus fistulosus L.	Xanthorrhoeaceae
Fagonia paulayana Wagner & Vierh.	Zygophyllaceae

Table S2. A preliminary species list of bees of Oman based on Museum collections (*an "*" indicates a species that I've added from my DNA barcoded specimens*)

Family: Colletidae

Subfamily: Colletinae

Tribe: Colletini

Colletes fuscicornis Noskiewicz, 1936

Colletes guichardi Kuhlmann, 2003

Colletes nanus Friese, 1898

Colletes salsolae Cockerell, 1934

Subfamily: Hylaeinae

Hylaeus (Paraprosopis) albonotatus Walker, 1871

Family: Andrenidae

Subfamily: Andreninae

Andrena (Melandrena) albifacies Alfken, 1927

Andrena (Suandrena) savignyi Spinola, 1838

Subfamily: Panurginae

Tribe: Panurgini

Camptopoeum (Camptopoeum) negevense (Warncke, 1972)

Panurgus (Pachycephalopanurgus) nigriscopus Perez, 1895

Tribe: Melitturgini

Borgatomelissa brevipennis (Walker, 1871)

Family: Halictidae

Subfamily: Rophitinae

Systropha (Austrosystropha) aethiopica Friese, 1911

Systropha (Systropha) diacantha Baker, 1996

Subfamily: Nomiinae

Lipotriches (Armatriches) pallidicincta (Cockerell, 1932)

Lipotriches (Clavinomia) clavicornis (Warncke, 1980)

Nomia (Crocisaspidia) forbesi (W.F. Kirby, 1900)

Nomia (Crocisaspidia) vespoides Walker, 1871

Nomia (Leuconomia) omanica (Pauly, 2000)

Pseudapis (Pseudapis) nilotica (Smith, 1875)

Pseudapis (Pseudapis) patellata (Magretti, 1884)

Subfamily: Nomioidinae

Ceylalictus (Ceylalictus) punjabensis (Cameron, 1907)

Ceylalictus (Ceylalictus) variegatus (Olivier, 1789)

Nomioides rotundiceps Handlirsch, 1888

Nomioides turanicus Morawitz, 1876

Subfamily: Halictinae

Tribe: Halictini

Halictus (Argalictus) tibialis Walker, 1871 *

Halictus (Seladonia) lucidipennis Smith, 1853

Halictus (Seladonia) seladonius (Fabricius, 1794)

Halictus (Seladonia) subauratus (Rossi, 1792)

Halictus (Vestitohalictus) pici Perez, 1895

Lasioglossum (Ctenonomia) gibber (Vachal, 1892)

Lasioglossum (Ctenonomia) vagans (Smith, 1857)

Lasioglossum (Hemihalictus) ablenum (Blüthgen, 1934) *

Lasioglossum (Hemihalictus) villosulum (Kirby, 1802)

Lasioglossum (Sphecodogastra) elbanum (Blüthgen, 1934)

Lasioglossum (Sphecodogastra) epipygiale (Blüthgen, 1924) *

Lasioglossum (Sphecodogastra) mose Ebmer, 1974

Family: Melittidae

Subfamily: Dasypodainae

Tribe: Dasypodaini

Dasypoda (Dasypoda) albipila Spinola, 1838

Family: Megachilidae

Subfamily: Megachilinae

Tribe: Lithurgini

Lithurgus atratus Smith, 1853

Tribe: Osmiini

Hoplitis (Alcidamea) hofferi Tkalcu, 1977 *

Hoplitis (Alcidamea) limassolica (Mavromoustakis, 1937)

Hoplitis (Anthocopa) batyamae (van der Zanden, 1986) *

Hoplitis (Hoplitis) parana (Warncke, 1991) *

Stenoheriades eingeddicus Griswold, 1994

Tribe: Anthidiini

Anthidium (Anthidium) tesselatum Klug, 1832

Anthidium (Gulanthidium) anguliventre Morawitz, 1888

Eoanthidium (Eoanthidium) arabicum Pasteels, 1980

Icteranthidium afrum (Lepeletier, 1841)

Icteranthidium ferrugineum (Fabricius, 1787)

Icteranthidium sinuatum Pasteels, 1969 (invalid???)

Pseudoanthidium (Exanthidium) guichardi (Pasteels, 1980)

Stelis (Stelidomorpha) nasuta (Latreille, 1809)

Tribe: Megachilini

Coelioxys (Allocoelioxys) afra Lepeletier, 1841

Megachile (Chalicodoma) sicula (Rossi, 1792)

Megachile (Creightonella) arabica Friese, 1901

Megachile (Creightonella) felix (Pasteels, 1979)

Megachile (Eurymella) patellimana Spinola, 1838

Megachile (Eutricharaea) deceptoria Perez, 1890

Megachile (Eutricharaea) malangensis Friese, 1904

Megachile (Pseudomegachile) lanata (Fabricius, 1775) *

Megachile (Pseudomegachile) rubripes Morawitz, 1875

Megachile (Pseudomegachile) soikai Benoist, 1961 *

Megachile (Pseudomegachile) walkeri Dalla Torre, 1896 *

Family: Apidae

Subfamily: Xylocopinae

Xylocopa (Koptortosoma) pubescens Spinola, 1838

Tribe: Ceratinini

Ceratina (Pithitis) tarsata Morawitz, 1872

Subfamily: Apinae

Tribe: Anthophorini

Amegilla crocea (Klug, 1845)

Anthophora priesneri Alfken, 1932

Anthophora semirufa (Friese, 1898)

Tribe: Melectini

Melecta (Paracrocisa) sinaitica (Alfken, 1937)

Thyreus hyalinatus (Vachal, 1903)

Thyreus ramosus (Lepeletier, 1841)

Tribe: Apini

Apis florea Fabricius, 1787

Apis mellifera Linnaeus, 1758

Chapter 5.

Using species distributions models to understand the current and future distributions of bees in the Middle East

Using species distributions models to understand the current and future distributions of bees in the Middle East

Abstract

Species distribution models (SDMs) are now regularly employed to map current distributions and to investigate how this may vary with climate change. However, there has been a dearth of studies for bees of true xeric habitats, surprising due to their abundance in this habitat type. This study uses museum specimens collected from across the Middle East to look for biogeographical patterns and to explore how species are likely to respond to a relatively poor climate prediction (RCP 8.5). While abiotic niches remained similar, on the whole species distributions contracted, with Southern Arabia worst affected. While future climate change did not appear to have a catastrophic effect, the results imply that on a local level the ranges of species will decline, and this may have consequential effects on pollination network stability.

Introduction

Although bees are recognised as being most species-rich in xeric environments (Michener, 2007), their biogeography is still relatively unknown (Patiny & Michez, 2007), both in terms of where species are distributed but also the main influencing processes (Patiny et al., 2008). In relation to the broad-scale distributions of bees, the main known hotspots include South Africa (Kuhlmann et al., 2012), the peripheries of the Arabian and Saharan deserts (Patiny & Michez, 2007; Patiny et al., 2008), the Mediterranean basin (Petanidou & Ellis, 1993), California, and the deserts of southwest North America, Central Asia and Chile (Michener, 1979; 2007). Within these areas, detailed knowledge of bee distributions and communities at a finer scale is still lacking. An added challenge is predicting how bees might respond to climate change (Biella et al., 2017), one of multiple factors with the potential to disrupt links within pollination networks. Beyond certain temperature thresholds, dependent on the species in question, bees will reduce foraging time in order to cool their body temperature (Rader et al., 2013) and so climate change is predicted to cause declines in bee activity and therefore seed set. As climates change in the long-term range shifts may occur further distrupting networks.

In their study of bee biogeography in the Saharan desert, Patiny et al. (2008) suggest species are distributed mainly in response to water availability. Too much rainfall will negatively affect ground-nesting bees, and too little will result in a plant community and biomass too small to support a rich bee community. The study found that species richness within the Saharan region is greatest along the periphery of the true desert i.e. along the Mediterranean and Atlantic coasts. Within the Saharan desert itself, species richness was greatest in areas with strong ecological gradients, such as mountains, river valleys and inland waters (Patiny et al., 2008). These data suggest water availability is a key determinant of bee species richness.

Knowledge of bees in the Middle East (Figure 1 in Chapter 1) suffers from the so-called Linnean and Wallacean shortfalls, meaning many species remain to be scientifically described (Linnean shortfall) and distributions are poorly known (Wallacean shortfall) (Bini et al., 2006). Species distribution models (SDMs), which use locality records and environmental variables to predict the 'true' range based on the realised abiotic niche (Guisan & Thuiller, 2005; Pearson et al., 2007), can be employed to improve understanding of bee biodiversity in this region. SDMs have been used multiple times to map the potential responses of tropical and subtropical bees to climate change (Giannini et al., 2012; Giannini et al., 2013; Nemésio et al., 2016). This type of study is important, as it allows an understanding of whether a species niche will change or remain similar (niche shifts vs. niche conservatism) (Peterson, 2011; Guisan et al., 2014). However, only very few studies have been applied to truly xeric environments (Silva et al., 2015; Giannini et al., 2017; Silva et al., 2018), surprising given the rich faunas found in this type of habitat. Silva et al

(2018), suggest this may be because of the view that pollination services play a more limited role in human uses of deserts, where the grazing of livestock is the dominant agricultural practice. Therefore SDMs within this habitat type are not considered a priority for mapping projects.

Unlike angiosperms and many other taxa, which reach their highest diversity in moist, warm, wet tropical conditions (Pimm & Raven, 2000), bees have remained most abundant and species-rich in their proposed ancestral environment of dry Mediterranean and desert conditions. This is the case for environments such as present-day California and the deserts of southwest North America (Michener, 2007). The general link between low bee diversity and tropical forests may be to do with precipitation, because heavy rainfall may prevent the diversification of ground-nesting species. Rozen (in Michener, 1979) suggested damp soil conditions could result in the growth of pathogens and fungi that damage developing larvae and/or larval pollen supplies in ground-nesting species. In addition there is the threat of nest flooding during rainy seasons.

Hyper-arid conditions are inimical to all organisms, and so true sand-dune deserts, such as the interior of the Sahara and the Rub' al Khali in Arabia, have a depauperate bee fauna (and all taxa). Although bee diversity is relatively high in the rainforests of the Neotropical realm, partially due to their close proximity to species-rich areas such as Argentina (Michener, 1979), the faunas of the other major tropical forest regions of central Africa and particularly Southeast Asia are small (Michener, 1979). This suggests that unlike other phytophagous insects, which diversified due to their association with angiosperms, angiosperm species richness in itself is not the main driver for bee diversification (Farrell, 1998; Litman et al., 2011). The only bee hotspot that overlaps with a plant hotspot is the Cape Floral Kingdom (Kuhlmann, 2005) in South Africa. This is as a result of South Africa being the only centre of phytodiversity that occurs in an arid environment (Kuhlmann, 2009).

Although a clear link between bee species richness and xeric habitats is established, what drives this high level of diversity is still unclear. Numerous hypotheses have been proposed in explanation, including several that suggest that this type of habitat is favourable to nesting requirements. For instance Moldenke (1976a, 1979b) suggested abundant areas of bare ground in arid habitats could provide suitable habitat for ground-nesting species, while regular forest fires provide appropriate material for taxa that nest in dead wood (Petanidou & Ellis, 1993). However, although the idea that fire provides ideal conditions for offspring seems possible in some xeric habitats, such as the Mediterranean where wildfires are regular, it would not explain the diversity found in areas of the Middle East. For example in the Hajar Mountains in Oman, the thinly dispersed vegetation provides little ground litter and hence prevents regular fires (personal observation).

Another possible explanation for the extremely high diversity of bees in arid conditions is believed to be as a result of a bet-hedging lifestyle

(Danforth, 1999), an adaptation for surviving in an extremely variable environment created by unpredictable intermittent rainfall (Davidowitz, 2002). This life-history strategy is most commonly described in desert annual plants. By remaining dormant in a seed bank during dry years, plants sacrifice short-term fitness but survive to germinate in a range of future more favourable conditions, thus improving long-term average fitness (Venable & Kimball, 2013).

This strategy is also seen in desert oligolectic bees, which have the ability to remain in diapause during drought years and emerge in synchronization with the flowering of their plant host. For instance *Amegilla dawsoni* in the deserts of Western Australia is able to remain in diapause for up to ten years (Houston, 1991). In Sonoran and Mojave deserts in the southwest United States, where rainfall is the most unpredictable of all the deserts in North America (Davidowitz, 2000), the creosote bush, *Larrea tridentata*, is the pollen host to a wide range of solitary oligolectic bee species that are able to time their emergence with the blooming of this plant after rainfall (Minckley et al., 2000). Although it is not known whether bees are responding to the actual water itself or an unknown trigger from the plant, clearly they can emerge in synchronisation with a flowering host plant (Danforth, 1999) when resources are most available. This ability to emerge during the peak blooming period creates predictability out of an unpredictable environment (Minckley et al., 2000).

Danforth (1999) suggests bet-hedging leads to gene flow disruption between populations emerging in different years and so leading to speciation. Although a bet-hedging lifestyle has been proposed as a driver for speciation, not all bee hotspots show such clear synchronisation between host-plant germination and bee emergence, as seen in *Larrea tridentata*. As described in Chapter 4, in South Africa, which contains 50% of all bee species found in the Afrotropical region (Kuhlmann, 2009), bee species richness is particularly high in the Cape Floral Kingdom, where winter rains are predictable. Here bees are noticeably unsynchronized with the peak flowering period (Kuhlmann, 2009), suggesting that here unpredictable rainfall does not drive bee species richness, and therefore patterns of rainfall cannot be a general explanation for bee species richness.

Asynchronization of plant flowering phenology and peak abundance of pollinators may be due to factors other than abiotic factors such as precipitation. Other factors include the selection on flowering times due to florivores, granivores, and seed dispersers (Strauss & Whittall, 2006), which can have a significant effect. In Patagonia, some populations of the hemiparasitic mistletoe *Tristerix corymbosus* flower during winter and spring when the visitation rate of the hummingbird pollinator *Sephanoides galeritus* is at its lowest, resulting in pollinator limitation (Aizen, 2003). Nevertheless, fruits that then develop in the summer coincide with the period when the primary disperser, the marsupial *Dromiciops australis*, is raising young, and hence fruits are collected abundantly and the seeds are successfully dispersed (Aizen, 2003).

Xeric and tropical habitats clearly differ in bee species richness, but there is also a general difference in the level of pollen specialisation. For instance in the Lower Sonoran and Mojave deserts in southwest USA, oligolectic bees are more abundant than polylectic bees in terms of both species richness and biomass (Minckley et al., 2000). Tropical forest habitats tend to contain a higher percentage of polylectic social species, whereas xeric habitats favour oligolectic solitary bees (Minckley et al., 2008). This may again be linked to water availability, i.e. the frequent rainfall in tropical habitats generate reliable regular floral resources, reducing temporal variation in availability and hence favouring social species which maintain large colonies needing a constant supply of nectar and pollen. Although plants in xeric habitats are able to respond rapidly to unpredictable and inconsistent rainfall events (Venable & Kimball, 2013), this unpredictability makes them an unsuitable pollen host for the maintenance of large colonies. Thus another hypothesis to explain the species richness in xeric habitats is that a lack of competition with social species has allowed the diversification of solitary species (Minckley, 2008).

In Patiny & Michez's (2007) study of bee biogeography in the Saharan and Arabian deserts, the authors used a taxonomic diversity index based on published literature and museum specimen records to designate three regions (Nile Valley, Jordan Valley and Oman's Al Hajar Mountains) as hotspots for bee biodiversity within the Middle East and North Africa. However, as the number of species used in the study was relatively small (291), it is possible other hotspots were missed, such as in the subtropical region of Dhofar in southern Oman and mountainous areas of Yemen and western Saudi Arabia. Locating specific areas/regions as species hotspots or 'diversity centres' is one of the major purposes to mapping biodiversity (Barthlott et al., 1999).

Currently there is no overall complete checklist of bees for the region, although Dathe (2009) produced a checklist of 140 species for the series of Arthropod Fauna of the UAE volumes. As the author pointed out, Central Europe, a region not considered to be a hotspot for diversity, has a fauna of 300-400 species, and so this current list is likely greatly to underestimate the true levels of diversity. There are some subsequent studies on individual genera (*Sphecodes* - Schwarz, 2010; *Braunsapis* - Engel & Dathe, 2011; *Colletes* - Kuhlmann, 2014), and some recent descriptions of new species and records collected in Iran, Saudi Arabia and Qatar (e.g., Engel, 2008; Alqarni et al., 2012; Alqarni et al., 2013). Studies addressing pollination networks are absent for the Arabian Peninsula, although one study lists the plant species visited by 25 species of bee in the Dubai Desert Conservation Reserve, UAE (Gess & Roosenschoon, 2016).

Pollinators are declining globally, mainly due to human influences (Colla & Packer, 2008), while at the same time farmers rely on insects to pollinate most of the world's crops (Klein et al., 2008). For these reasons, providing faunal checklists for taxonomically understudied regions is a vital first step in conservation. This study uses species distribution models to understand which climatic variables influence bee niches and to locate hotspots within the Middle East that harbour the greatest diversity.

Methods

Study region

The Middle East (Figure 1, Chapter 1) has a surface area of 7,207,575 km^2 and contains a wide range of habitat types, including multiple mountain ranges, both sand sea and gravel deserts, and extensive wetlands. This transcontinental region is unique, being the only region worldwide where three biogeographical realms, the Palaearctic, Afrotropical and Oriental, meet (Krupp et al., 2009). The region contains a rich and diverse fauna and flora, with areas such as eastern Yemen and the Dhofar Mountains of Oman (Ghazanfar, 1998; Patzelt, 2015), the Socotra Archipelago (Krupp et al., 2009), and Al-Sarawat Mountains in Saudi Arabia (El-Hawagry et al., 2013) being particularly species-rich.

Species records

A list of 636 species (Table S2) occurring within the Middle East (excluding Turkey and Cyprus) was compiled based on the collections of the Natural History Museum, London (NHM), Oxford University Museum of Natural History (OUMNH), and American Museum of Natural History (AMNH). Specimens from Turkey were excluded because although this country contains xeric habitats, the fauna shows considerable overlap with those of more temperate Palaearctic habitats. As the aim was to assess desert-adapted species, it was therefore decided not to include those species recorded from Turkey. Hence when discussing the “Middle East”, I include Bahrain, Egypt, Iran, Iraq, Israel, Jordan, Kuwait, Lebanon, Oman, Palestine, Qatar, Saudi Arabia, Syria, United Arab Emirates, and Yemen.

Specimens held in the AMNH collection included coordinates, but the NHM and OUMNH specimens did not. Therefore to georeference the specimens, Google Earth Pro was used to locate the coordinates of the collecting locality based on the information provided on the specimen label. If a specimen only gave the name of a village, then the latitude and longitude at the centre of the village was recorded (see Figure 1 for a map of all 2127 collection localities).

Of the 636 species, 67 were recorded from 8 or more localities, meaning I selected them for analysis using MaxEnt. As specimens from museum collections tend to be collected from localities found close together, due to areas near roads and settlements being easier to access (Pearson et al., 2007), this can lead to geographic bias. This may be particularly true for the Middle East, where desert conditions prevent collecting occurring long distances from roads. When creating an SDM this geographic bias can create environmental bias, a situation where environmental (climatic) conditions of a certain region are over-represented within a model (Aiello-Lammens et al., 2015). A simple example would be a species where ten of its records are collected from an alpine environment all within a few kilometres of each other. Another ten records are equally spread over several other habitat types separated by 100 kilometres from each other. Unless the alpine records that are found close together were thinned, the alpine sites would create an environmental bias for this habitat type. As the species is found in multiple habitat types the model could be unrepresentative of the true habitat choices for the species in question.

To avoid autocorrelation of species localities within the dataset, the r package *spThin* (Aiello-Lammens et al., 2015) was used to thin species records. The package *spThin* reduces bias in the analysis by using a randomization algorithm that sets a minimum distance between occurrences. A minimum distance of 10 km was set, meaning species records that were closer than 10 km were removed from the dataset. The bee specimens used to build the SDM's were all collected by a limited number of researchers (Baker, 2004), and so geographic bias was present in the dataset. As the number of specimens per species was low, 10 km was selected as a suitable tradeoff in an attempt to overcome the bias, while still retaining enough specimens to build an SDM. Increasing the thinning distance between collection localities above 10 km resulted in too few specimens to build models for many of the species. 10 km appears to be a standard distance in several SDM studies due to similar issues regarding low specimen record numbers (Radosavljevic & Anderson, 2014; Aiello-Lammens et al., 2015). A final total of 45 species (Table 1) with more than eight independent records per species was used to build the SDMs. Eight records was chosen as the cutoff point for deciding whether or not to include a species based on the fact that the museum collections used held few long series of specimens for each species. While MaxEnt can model species based on a few records, too few records will mean a model is not based on the full range of environmental conditions normally associated with a particular species (Anderson & Martinez-Meyer, 2004; Pearson, 2007). This creates poor estimates of species distributions.

Sample sizes were small for most species (mean ± SD= 13.5 ± 6.4) because in the Middle East many bees are rare and transitory, a factor reflected in the low numbers of specimens per species held in museum collections. Another issue reducing numbers is the political reasons that make many regions within the Middle East difficult to visit, both in the past and present. This may increase bias within the dataset, but is currently unavoidable.

Climate variables

Nineteen bioclimatic variables with 30 arc-second resolutions were downloaded from WorldClim (http://www.worldclim.org). These variables were trimmed in QGIS version 2.18.2 to fit the Middle East region. In order to prevent multi-colinearity being an issue amongst the weather variables, the function *vif* in the R package *usdm* was used (Naimi, 2015). This function calculates the variance inflation factor (VIF) and selects the variables that should be removed as a result of collinearity, meaning those predictor variables that show strong correlation with each other. The VIF records the square of the multiple correlation coefficient that is calculated when a predictor variable is regressed against all other predictor variables (Naimi, 2015). The correlation coefficient will be close to 1 when a variable and at least one other variable have a strong linear relationship. This gives a large VIF, which if it is over 10, suggests the problem of collinearity (Naimi, 2015). Predictor variables with a VIF greater than 10 were excluded from further analysis (Table S1 for the VIFs of the predictor variables included to build the SDMs).

After running the VIF, ten predictors remained: mean diurnal range (Bio2), temperature annual range (Bio7), mean temperature of wettest quarter (Bio8), mean temperature of driest quarter (Bio9), mean temperature of warmest quarter (Bio10), precipitation of wettest month (Bio13), precipitation of driest month (Bio14), precipitation seasonality (Coefficient of Variation) (Bio15), precipitation of warmest quarter (Bio18), and precipitation of coldest quarter (Bio19). These variables were selected for use in the final models.

To analyse the future habitat suitability of each species within the Middle East, HadGEM2-CC's Representative Concentration Pathway (RCP) 8.5 for the year 2070 was downloaded from the WorldClim website. The same variables as for the current scenario were applied. RCP 8.5 is considered a negative scenario, because assumptions are made that the human population will continue to grow to high densities and there will be few technological advances to combat the emissions causing climate change (Riahi et al., 2011).

Species distribution modelling

MaxEnt (maximum entropy algorithm, version 3.4.1: Philips et al., 2006) was selected to build the SDMs because this algorithm has been recognised as performing well with small sample sizes, as well as presence-only data (Wisz et al., 2008).

Model accuracy was assessed using the MaxEnt output. This includes an AUC score (Area Under the Reciever Operating Characteristic Curve) that results from the ROC (Reciever Operating Characteristic Curve). A plot is given showing the ROC curve plotted as sensitivity (proportion of observed presences correctly predicted) against 1-specificity (proportion of oberserved absences incorrectly predicted) (Pearson, 2007). A 1:1 line is given on the plot. If a model is unable to predict sites where species are present or absent and is random, then the curve will follow this line. Alternatively, a model that is accurate in predicting species occurrences will show a curve that rises rapidly on the left axis and runs along the top of the plot (Pearson, 2007). The AUC score may lie between 0.5 (models no better than random) to 1.0 (perfectly predicts presences). Thus, a high AUC implies a site with "high predicted suitability values that tend to be areas of known presence and locations with lower model prediction values tend to be areas where the species in not known to be present" (Hijmans & Elith, 2017)

In addition to the AUC score, MaxEnt also provides estimates of the most important climatic variable within the model, expressed as a percentage as well as variable importance measured by the resampling method, a jackknife test (Phillips, 2006). When the jackknife test is run a model is created: jackknife test of variable importance. To create the model each predictor variable is excluded in turn, while a model is created with the remaining variables (Phillips, 2017). This is shown visually by a bar chart with the environmental variables along the y-axis and regularised training gain along the x-axis. The importance of each variable is shown by a light blue bar (regularised training gain when the variable is removed from the model) and dark blue bar (regularised training gain with only the variable in the model). The variable with the shortest dark blue bar (achieves almost no gain) represents the variable that (by itself) is the least useful for estimating the distribution of the species under question. The opposite is true for the variable with the longest dark blue bar. A variable with a short light blue bar would imply this is an important variable as when it is omitted from the model it's loss decreases the gain. This implies it contains information that is not present in the other variables included in the model.

To examine how current and future predicted distributions differ, the output maps from MaxEnt were converted into binary maps using QGIS. A cell containing a species was given a score of 1 and therefore total counts could be made for each distribution using the attribute table in QGIS. Present and future distribution maps could then be compared to look for range increases/decreases.

Results

A checklist of the 636 species (six families, 67 genera) with their collection localities recorded from the collections of the NHM, OUMNH and AMNH is included in the Supplementary Information (Table S2). While only preliminary, this is the most complete list to date of the bee fauna of the Middle East.

A total of 45 species were modelled using MaxEnt to predict their current distributions and how these would potentially change with future climate change. All models performed well with a mean AUC of 0.928 ± 0.087 (mean ± standard deviation). The lowest AUC score was 0.817 and therefore no model was excluded from further analysis (Table 2). Due to the high AUC scores the model results can be considered to be excellent predictors of the distributions.

The results of the jackknife tests in the MaxEnt output showed that the weather variables 'precipitation of the warmest quarter' (Bio18) and 'temperature annual range' (Bio7) were the most important of the climatic predictors for the majority of species (19 and 16 species respectively) (Figure 2).

The response curves showed that species that were affected most by Bio18 all showed the same extreme decline in suitabilities with increased summer precipitation above ~30mm. (see Figure 3 for the example of *Osmia lhotelleriei*). Species that nest or go into diapause in the ground may be particularly susceptible to losses in areas that experience heavy summer rainfall.

91% of the species modelled showed similar predicted ranges based on current climatic conditions. Areas with high-predicted habitat suitability for many species included the northern half of the UAE, the southern Iranian coast opposite the Musandam peninsula, the western coast of

Saudi Arabia, Israel, southern Lebanon, and northern Egypt and the Sinai Peninsula. While the predicted habitat suitability was greatest around the periphery of the Peninsula, all but four of the species (*Ceratina bispinosa*, *C. cucurbitina*, *Lasioglossum politum* and *L. pseudosphecodimorphum*) showed predicted suitable habitat within the interior of the Arabian Peninsula. This suggests that these are all desert-adapted species and if suitable plant communities occur, then the abiotic conditions would not prevent their occurrence.

The ranges for all species apart from the four *Ceratina* and *Lasioglossum* species were distributed across the Peninsula and therefore small isolated populations did not appear to exist (Figure 4). Instead, species appeared to occupy similar niches and therefore the species pool of bees throughout the Peninsula may be rather uniform. Where suitabilities did differ were in the high-altitude areas where, for instance, only 28% of species were predicted in the higher elevations of the Hajar Mountains. Due to their relative isolation, therefore, these high altitude areas may contain endemic or relict species.

The four *Ceratina* and *Lasioglossum* species showed high habitat suitabilities within the Levant and northern coastline of Egypt and Libya. This suggests these species are not truly adapted to the desert environment of the Peninsula, but instead could be considered Mediterranean or Palaearctic species that reach their southern limits along the North African coastline.

The binarized maps describe the increase or decrease in bee distributions under climate change. In terms of the 2070 predictions, of the 45 species modelled, eight species were predicted a range increase, while the remaining 37 had declines to their predicted distributions. Only eleven of the latter group increased their ranges in the south. As 82% of species were predicted to decline, overall future climate change is predicted to have a negative effect on bees within the Middle East, with the southern half of the Arabian Peninsula worst affected (Figure 4). While most species ranges physically shifted northwards, *L. gibber* showed an extreme reduction of its predicted southern distribution, leading to areas of isolation (Figure 5).

The future predictions showed little variation in species composition at high altitude in the Hajar Mountains, although two species (*Colletes pumilus* and *Lasioglossum ablenum*) showed predicted declines in habitat suitability, and *Anthidium tesselatum* was predicted to expand its range into the high elevations of the Hajar Mountains. Rather than species moving higher up the mountains, the majority of species ranges were predicted to decline around the Hajar Mountains or shift their ranges northwards.

Discussion

The results of this study found that although there was a general decline/shift in predicted distributions, apart from *Lasioglossum gibber,* this decline was not extreme and the majority of the species showed relatively similar ranges. This minimal change to most species distributions agrees with Silva et al's (2018) study of the Australian bee *Exoneurella tridentata,* one of the few studies investigating how climate change might affect bees in xeric habitats. Silva et al (2018) suggest a possible explanation for the apparent stability in *E. tridentata* populations experiencing climate change, is due to the fact that central Australia is topographically monotonous and therefore the future climate is stable. Likewise the Arabian Peninsula outside of the peripheral Hajar and Asir Mountains is topographically similar and therefore this stability of climate may be reflected in stable bee populations. As Silva et al (2018) point out, this result contrasts with studies that have investigated bee species response to climate change in tropical or temperate regions, where a greater range of climatic variables exist (Kerr et al., 2015; Martins et al., 2015; Rasmont et al., 2015).

Bees form the core of most pollination networks globally (Larson et al., 2001) and therefore any disruption to the links within a network will have cascading effects to ecosystem functioning. While the results of this study indicate climate change will have a negative effect on the distributions of most modelled bee species in the Middle East, the results were mixed since a minority of species were predicted to respond positively. Several other studies have had similar findings, with varied responses of bees to climate change including declines, some shifting their ranges but remaining at a similar extent (Giannini et al., 2017), and others responding positively (Silva et al., 2015). This varied response to climate change is known as response diversity (Rader et al., 2013) meaning ecosystem functioning is preserved because different species have different responses. Generalist plants that receive multiple pollinators may be buffered from declines in pollination services if this is the case. Silva et al (2015) suggest these varied types of response by bees may be due to their patterns of visitation, with generalists able to adapt to new environments/floral hosts while specialists declining if their host plants respond negatively to climate change. As most bees of xeric habitats are considered to be oligolectic in their choice of floral hosts (Michener, 2007), it consequently appears that the bee communities within the Middle East will see general (if not dramatic) declines in abundance.

Conversely, it is important to note that the belief in the oligolecty of xeric bees may in fact be based on insufficient data, as the ecology of bees in the Middle East remains largely unknown. Taking the species *Megachile walkerii* as an example, my surveys carried out in Oman to record the topology of the lowland visitation network revealed that over relatively few surveys this species was recorded visiting five different plant families (Amaranthaceae, Apiaceae, Brassicaceae, Fabaceae, and Resedaceae). While *M. walkerii* may simply be one of a limited number of generalist species, this highlights the paucity of data upon which this idea, based on a few studies in the deserts of the southwest USA (Minckley et al., 2000; Minckley, 2008). Further research is needed before this statement can be universally applied to bee faunas in all xeric ecosystems.

The overall future declines of the majority of the species, especially in their southern ranges, indicates that in southern Arabia not only will wild plant populations be under threat from disrupted pollination networks, but also there will be potentially significant threats to agro-biodiversity. The results are consistent with the theory that with rising temperatures, species will tend to shift their distributions northwards to avoid increasing temperatures (Wilson et al., 2005). Using Oman as an example, villages in the Hajar Mountains contain 107 different crops, including relicts such as faba bean *(Vicia faba* L. var*. minor* Peterm. em. Harz) and lentil (*Lens culinaris* Medik.) (Gebauer et al., 2007). The majority of these crops, which include fruit, can currently only be grown at high altitudes (to avoid the high temperatures of the lowlands) and are largely insect pollinated. While current high-altitude species may be replaced with lowland species as average temperatures rise, there is also the issue of phenological mismatches (Bartomeus et al., 2011). The pollinators are likely to be synchronised with plant communities that flower earlier in the year in the lowlands.

Though the suitability maps showed mostly uniform current distributions throughout the Arabian Peninsula, the high-altitude areas contained more distinct bee communities, which are at greatest risk from climate change. Montane species are believed to show more negative trends with climate change (Flousek et al., 2015): cold-adapted plants are unable to expand their range any higher, and also experience increased competition with species moving up from lower altitudes. Since the 1950s temperatures are estimated to have increased by 0.13°C per decade, and mountain ecosystems are at the forefront of the effects of such climate change (Pepin & Seidel, 2005; Biella et al., 2017). While only two species are predicted to be lost from the Hajar Mountains in the future scenarios, these also occur elsewhere throughout the Middle East. The species included in this study are not high-altitude specialists, but true specialists to high altitudes are likely to show much more severe declines than my results suggest. Like the plants, they are predicted to suffer from the warming temperatures and competition with invading lowland species such as *Anthidium tesselatum*. Climate change and habitat fragmentation are predicted to hit specialist species with poor dispersal abilities hardest (Bommarco et al., 2010).

The records of the museum specimens (Figure 1) were highly clustered around Israel/Lebanon, Egypt, and then to a lesser extent the UAE and northern Oman. Records from Iran, Yemen and Saudi Arabia were sparse, while specimens from Iraq and Syria were almost completely absent from the three collections. This meant that the presences in the MaxEnt models matched climate variables from mountainous, Mediterranean, coastal and riverine habitats. Few records exist from true desert environments, which make up the majority of the land surface of the Arabian Peninsula.

Sand sea deserts in the Arabian Peninsula clearly have lower species richness compared to Mediterranean habitats in Israel. Nevertheless, the results of the Royal Geographical Society's Oman Wahiba Sands Project demonstrate that sand sea deserts can harbour complex plant (and hence insect) communities. During that study, 162 plant species within 44 families (Cope, 1988), as well as twenty Orders of insect (Büttiker & Büttiker, 1988), were recorded from the Sharqiya (Wahiba) Sands in northern Oman. Likewise the extensive gravel deserts of Oman, though comparatively low in plant species richness, contain the majority of Oman's endemic plants and form part of the Horn of Africa global biodiversity hotspot (Mittermeier et al., 2005; Borrell et al., 2019). Therefore, while species richness may be clustered along mountain ranges and rivers (principally the Nile and Jordan River in this study), as suggested in Patiny et al's (2008) study of bee species richness patterns in the Saharan Desert, the low suitabilities produced by the MaxEnt models in the deserts of the Arabian Peninsula may be partially affected by bias within the museum collections.

Conclusions

The results from this broad-scale study indicate that the majority of bee species are predicted to decline in distribution with climate change.

However, if the plant communities with which these species interact are buffered from climate change, the results do not suggest a significant collapse in the bee community and their associated ecosystem services for most regions of the Middle East. Nevertheless, there are two important caveats.

The first comes from the suspected bias in the choice of species used to create the models. As previously noted, numbers of specimens per species in all three museum collections were low. Whilst museum collections can offer an excellent and at times the sole resource for the mapping of many species distributions (Newbold, 2010), until more standardised collecting and hence the probable 'absences' from specific areas can be recorded, bias will remain a major issue when using opportunistic collections to map distributions (Fletcher Jr et al., 2019). Although steps were taken to remove bias by spatial thinning of records, it is likely this still remains an issue in this study because of the low numbers of records used per species, which are clustered in specific regions of greater collecting efforts. The collections of Middle Eastern bees held in the NHM and OUMNH were primarily made by three individuals: I. L. Hamer, C. G. Roche, and K. Guichard (Baker 2004). Many oligolectic bees are rare, and hence easily missed, and therefore it is likely that the few long series of specimens held in the collections are generalists. For example, *Amegilla mucorea* showed a trans-peninsula distribution, having being collected in both Egypt and the UAE. Due to the differences in the floral communities of these two countries, it is likely this bee visits different plants in different parts of its range, and therefore can be considered a generalist.

Itinerant generalist pollinators are believed to show greater resistance to change and fragmentation of the communities in which they occur (Bommarco et al., 2010; Jauker et al., 2018). This indicates that the effects of climate change will not be as significant compared to those that affect specialist species, assumed to form the majority of the bee fauna of the Middle East (Michener, 2007) (although as I have highlighted, this is probably an erroneous statement). The issue of collecting bias emphasises the need for greater numbers of specimens, especially of known specialist desert species, to conduct a better test of whether the effects of future climate change are likely to be limited to generalists.

A second issue in the study was that only abiotic predictors were used to determine a species range. To improve the models, other important biotic aspects (Broennimann et al., 2012) that may affect bee populations, such as the distributions of host plants or parasitoids, would need to be included. This is an important next step in order to refine the models.

Nevertheless, from the specimen data available, the results of the models suggest that future climate change across the Arabian Peninsula may not cause severe collapses in bee community structure. This does not imply climate change will have a neutral effect at a more local level, as indicated by the declines predicted in southern Arabia. An increase in collecting efforts, especially of known specialists, is needed to build upon this initial biogeographical study.

Figures and Tables

Figure 1. Collecting localities of the 636 bee species held in the Natural History Museum (London), Oxford University Museum of Natural History, and American Museum of Natural History

Figure 2. Most important climatic predictors (Bio18, Precipitation of warmest quarter; Bio7, Temperature annual range; Bio19, Precipitation of coldest quarter; Bio13, Precipitation of warmest month; Bio9, Mean temperature of driest quarter; Bio10, Mean temperature of warmest quarter; Bio2, Mean diurnal range (Mean of monthly (max temp- min temp)).

Figure 3. Example of a response curve showing *Osmia lhotelleriei* declining with increased summer precipitation.

Figure 4. Examples of MaxEnt graphs showing suitability for the species *Ceratina tarsata,* typical of most species included in this study. The upper graph shows the current predicted distribution, while the lower graph shows the 2070-projected distribution. While the species shows a similar distribution in both maps, suitability in the future map is lower particularly in southern Arabia and parts of the range in Oman and Yemen have been lost. On a local scale this type of decline could have a significant impact on pollination networks.

Figure 5. Maps of *Lasioglossum gibber*, the upper graph showing the current distribution and lower graph showing the 2070-projected distribution. The maps demonstrate the most extreme shift of the modelled species highlighting how climate change will lead to both disruption of pollination networks when a species is lost (southern Arabia) and when/if that species invades new territory (northern Egypt).

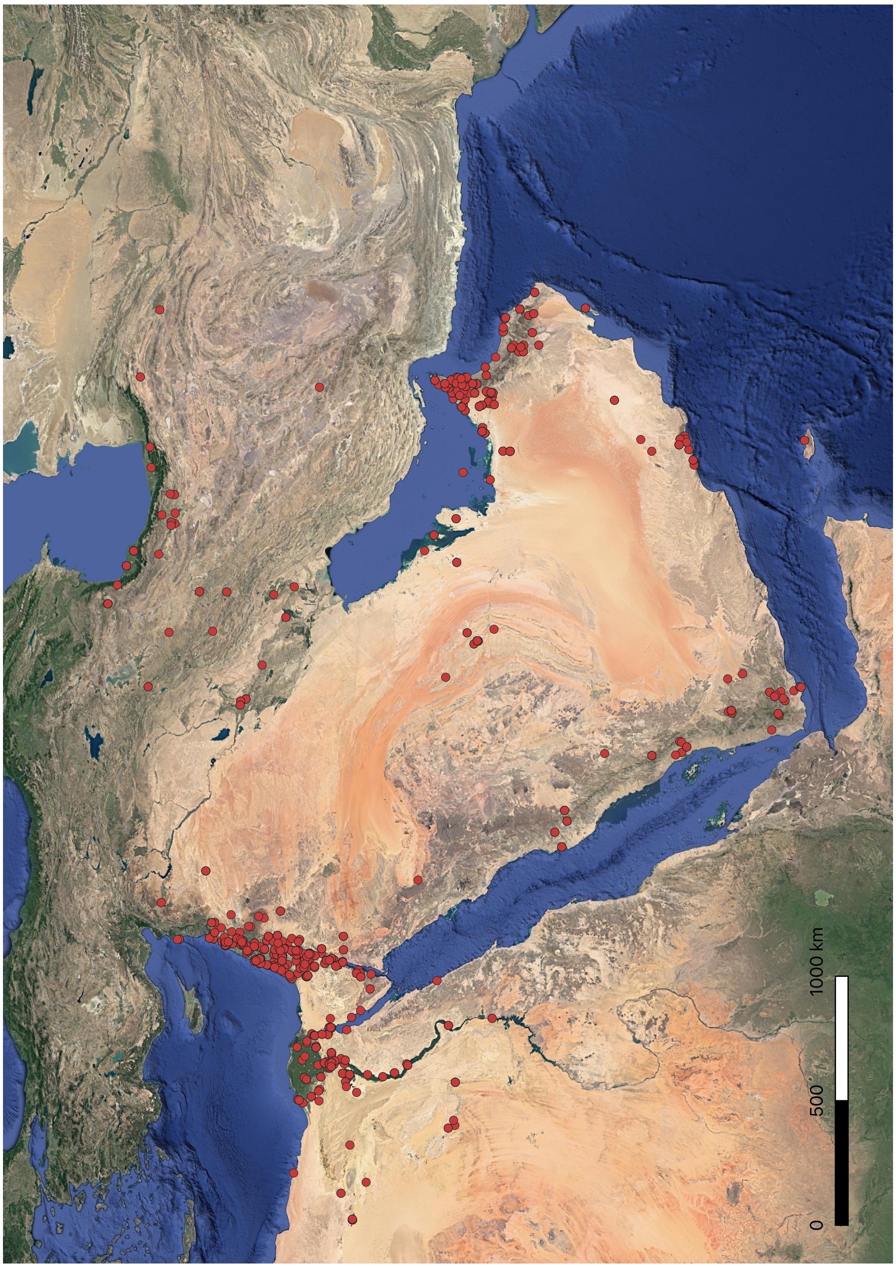


Fig 1.

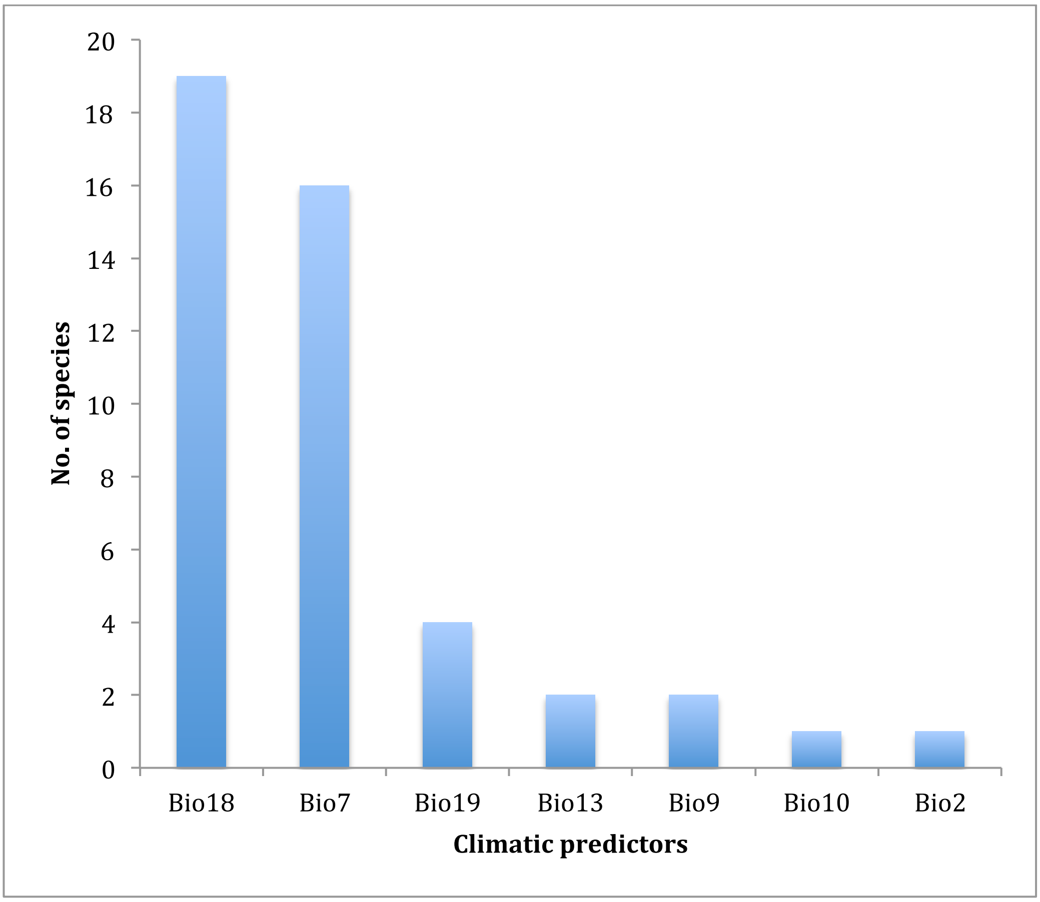

No. of species
20
18
16
14
12
10
8
6
4
2
0
Bio18
Bio7
Bio19
Bio13
Bio9
Bio10
Bio2
Climatic predictors

Fig 2.

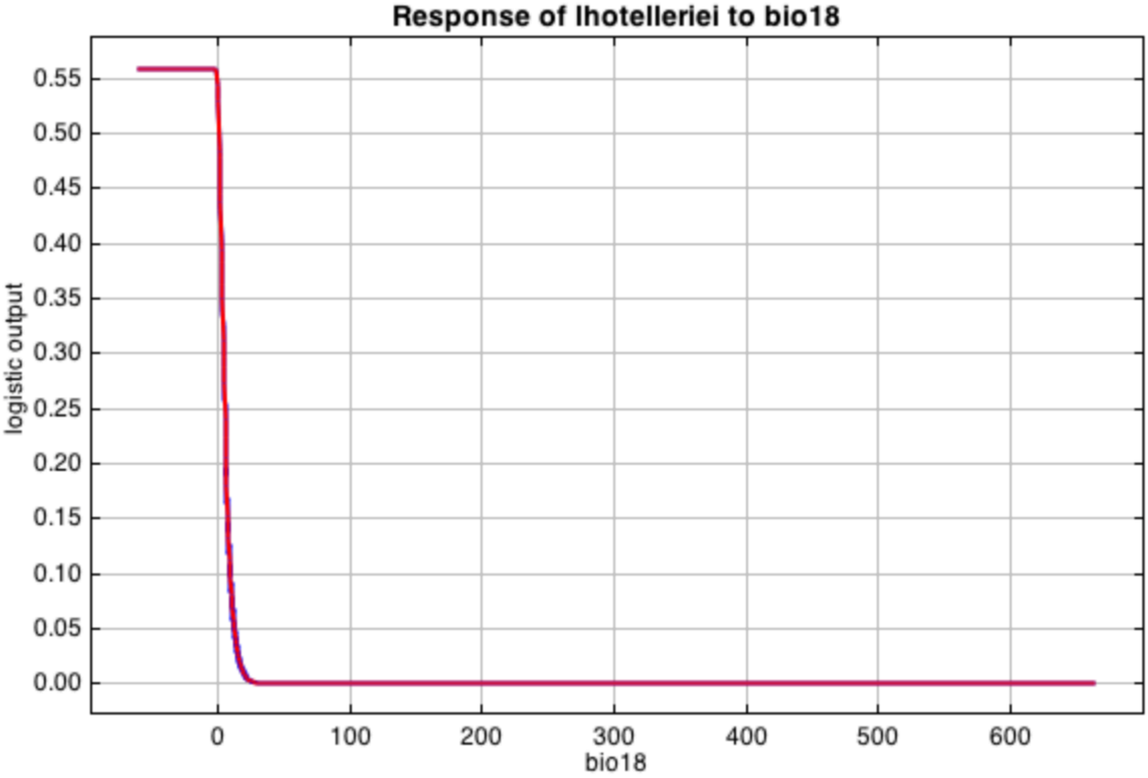

Response of lhotelleriei to bio18
logistic output
bio18
0.55
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
100
200
300
400
500
600

Fig 3.

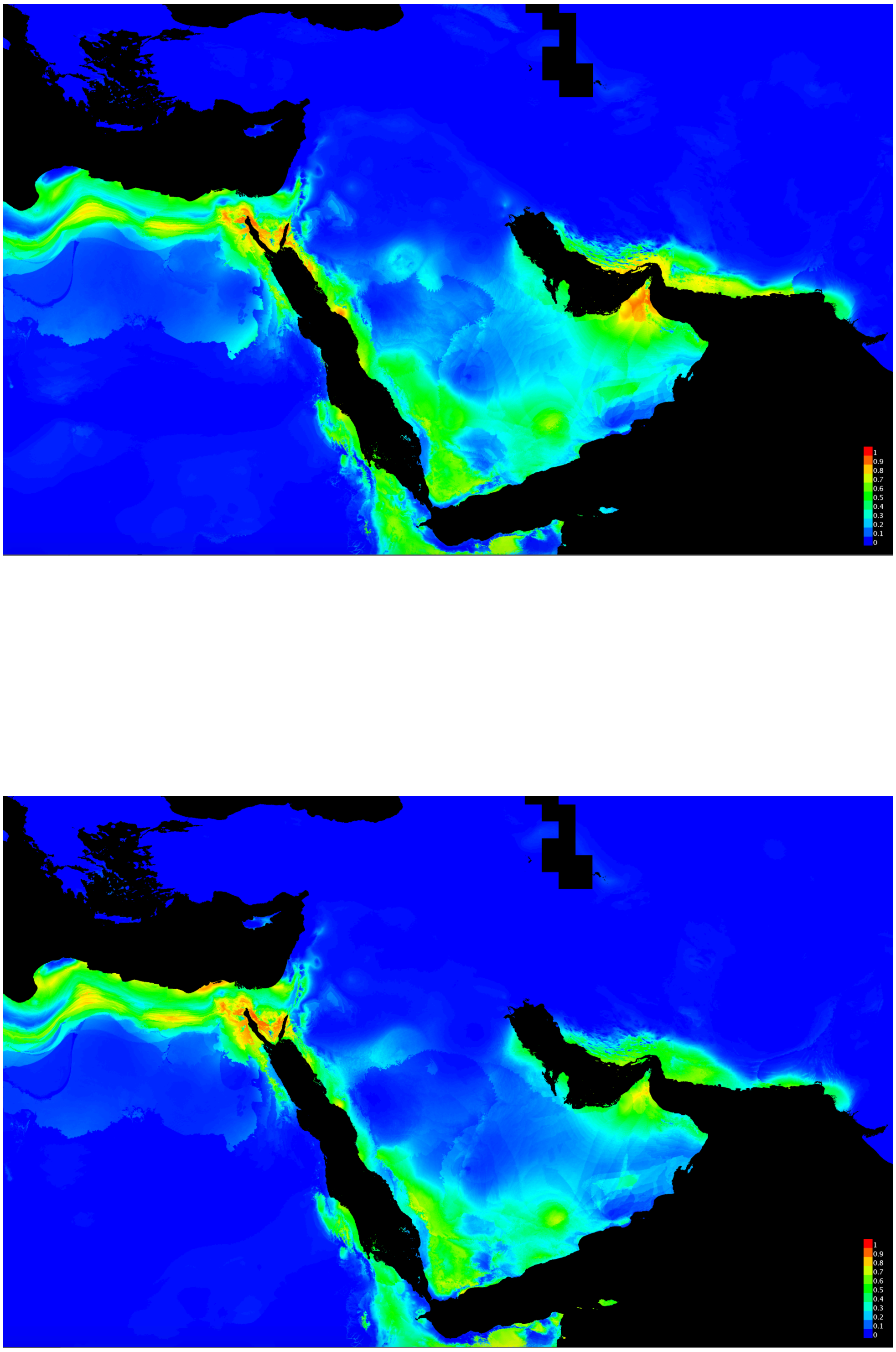


Fig. 4

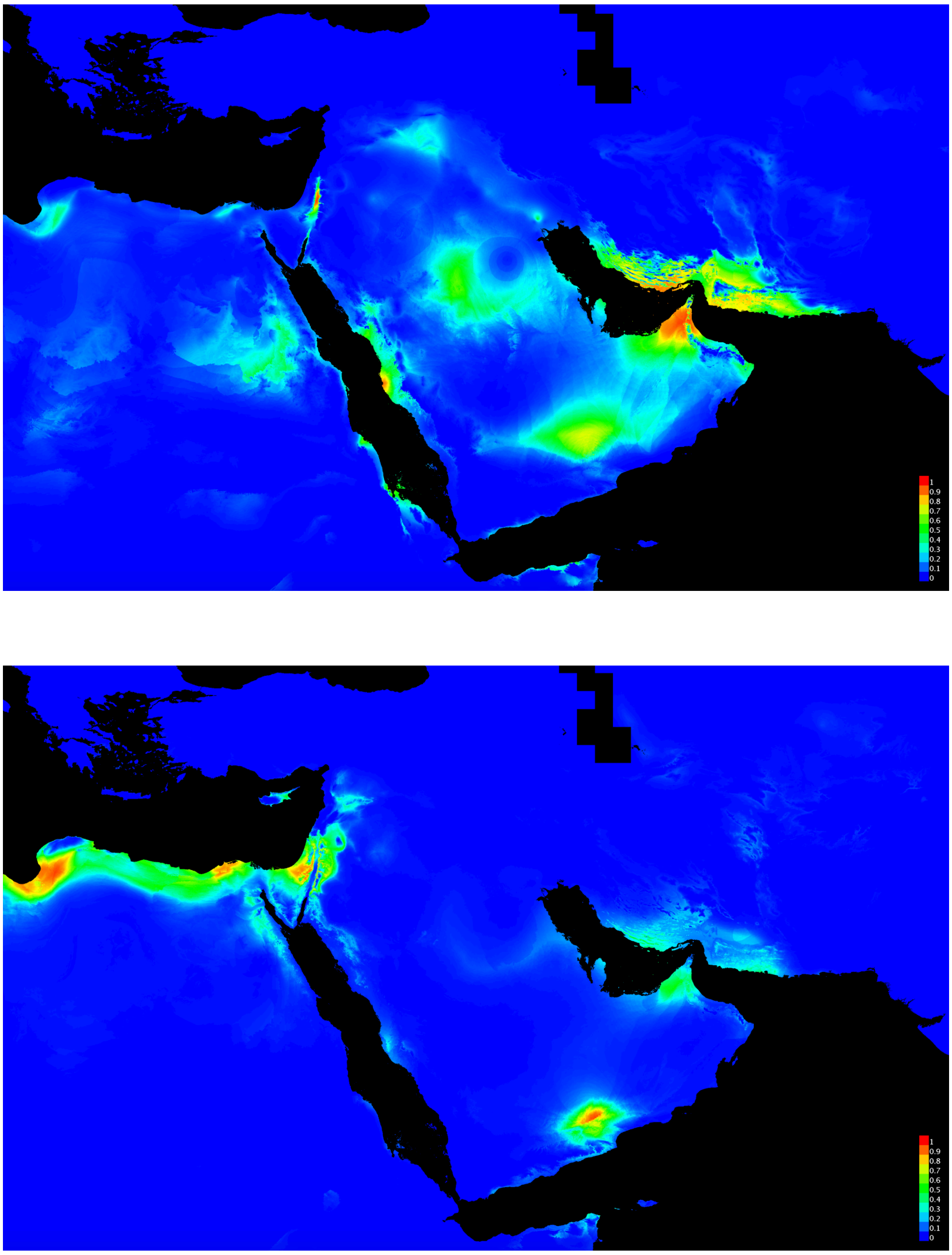


Fig. 5

Table 1. Bee families used in the models

Family	**Selected species**	**Unselected species**	**Total number**
Colletidae	8	51	59
Andrenidae	1	45	46
Melittidae	0 (0 %)	8	8
Halictidae	17	125	142
Megachilidae	9	185	194
Apidae	10	144	154
Total	**45**	**558**	**603**

Table 2. AUC scores for the species included within the study.

Species	**AUC**	**SD**
Colletes lacunatus	0.947	0.036
Colletes nanus	0.942	0.058
Colletes perezi	0.908	0.107
Colletes pumilus	0.850	0.225
Hylaeus albonotatus	0.950	0.074
Hylaeus dinkleri	0.957	0.046
Hylaeus gujaraticus	0.953	0.024
Hylaeus xanthopoda	0.985	0.016
Panurgus nigriscopus	0.947	0.030
Pseudapis patellata	0.962	0.053
Ceylalictus punjabensis	0.896	0.111
Ceylalictus variegatus	0.920	0.080
Nomioides turanicus	0.817	0.206
Sphecodes olivieri	0.937	0.116
Halictus cupidus	0.962	0.018
Halictus seladonius	0.952	0.050
Halictus subauratus	0.851	0.272
Halictus tibialis	0.832	0.198
Lasioglossum ablenum	0.915	0.216
Lasioglossum gibber	0.936	0.077
Lasioglossum mose	0.950	0.083
Lasioglossum politum	0.998	0.003
Lasioglossum pseudosphecodimorphum	0.999	0.002
Lasioglossum transitorium	0.969	0.019
Lasioglossum vagans	0.801	0.193
Lasioglossum villosulum	0.924	0.062
Hoplitis helouanensis	0.969	0.036
Osmia lhotelleriei	0.993	0.006
Osmia submicans	0.972	0.018

Anthidium tesselatum	0.884	0.132
Icteranthidium ferrugineum	0.924	0.054
Megachile flavipes	0.973	0.040
Megachile incerta	0.970	0.013
Megachile minutissima	0.907	0.073
Megachile sicula	0.935	0.099
Ceratina bispinosa	0.969	0.078
Ceratina citriphila	0.831	0.202
Ceratina cucurbitina	0.998	0.001
Ceratina parvula	0.945	0.030
Ceratina tarsata	0.923	0.061
Nomada fenestrata	0.909	0.075
Amegilla byssina	0.906	0.145
Amegilla crocea	0.884	0.174
Amegilla mucorea	0.892	0.172
Anthophora priesneri	0.902	0.128

Supplementary Information

Table S1

Variance inflation factor scores of the predictor variables used to build the Species distribution models

Table S2

Species list for the Middle East compiled from the following sources:

AMNH: *American Museum of Natural History*

CAvH: Collection of A. van Harten, UAE Insect Project, Sharjah (Dathe, et al., 2009)

CAM: Collection of A. Müller, Zurich, Switzerland

CAWE: Collection of A. W. Ebmer, Puchenau, Austria

CES: Collection of E. Scheuchl, Velden, Germany (Dathe, et al., 2009)

CMH: Collection of M. Hauser, Sacramento, USA (Dathe, et al., 2009)

CMK: Collection of M. Kuhlmann, London, UK (Dathe, et al., 2009)

CMS: Collection of M. Schwarz, Ansfelden, Austria

DEI: Senckenburg Deutsches Entomologisches Institut, ZALF Müncheberg, Germany (Dathe, et al., 2009)

INHRCM: *Iraq Natural History Research Centre and Museum, University of Baghdad*

NHM: *Natural History Museum, London*

NHML: National Natuurhistorisch Museum, Leiden, Netherlands

OUMNH: *Oxford University Museum of Natural History*

SCU: *Department of Plant Protection, Faculty of Agriculture, Suez Canal University*

SEMC: Division of Entomology, University of Kansas, Lawrence, USA

UAEIC: UAE Invertebrate Collection (Dathe, et al., 2009)

Table S1.

Variables	**VIF**
bio2	2.25
bio7	2.84
bio8	6.26
bio9	3.54
bio10	6.87
bio13	4.50
bio14	2.75
bio15	1.93
bio18	4.03
bio19	2.66

Colletidae

Colletinae

Colletini

***Colletes arabicus* Kuhlmann, 2002**
Saudi Arabia: Jafura Al Qa'd: AMNH
UAE: Abu Samrah, Liwa: NHM

***Colletes arztbergi* Kuhlmann, 2003**
Syria: Palmyra: NHM

***Colletes brevigena* Noskiewicz, 1936**
Synonym: *succinctus brevigena* Noskiewicz, 1936
Egypt: Fayid: AMNH

***Colletes bytinskii* Noskiewicz, 1955**
UAE: Sweihan: NHM

***Colletes cariniger* Perez, 1903**
Synonyms: *Colletes cariniger graecus* Noskiewicz, 1959
Israel: Mt. Carmel, Tel Aviv, Wadi Loz: AMNH

***Colletes chengtehensis* Yasumatsu, 1935**
Iran: Sarein: AMNH

***Colletes coriandri* Perez, 1895**
Egypt: Ein Khudra: NHM

***Colletes eatoni* Morice, 1904**
Synonym: *Colletes caspicus eatoni* Morice, 1904
Egypt: Cairo: NHM

***Colletes formosus* Perez, 1895**
Jordan: Petra: NHM

***Colletes fuscicornis* Noskiewicz, 1936**
Israel: Ein Gedi: AMNH
Oman: Dhofar (Ayun Pools): NHM

***Colletes guichardi* Kuhlmann, 2003**
Oman: Arzat, Dhofar (Qara Hills): NHM
Saudi Arabia: Fayfa, Taif: NHM

***Colletes hehiticus* Warncke, 1978**
Iran: Karaj: AMNHM

***Colletes intricans* Spinola, 1838**
Synonyms: *Colletes kervillei* Pérez, 1908; *Colletes succinctus aegyptiacus* Noskiewicz, 1936
Egypt: Tel El Kebir: AMNH

***Colletes jejunus* Noskiewicz, 1936**
Synonyms: *Colletes askhabadensis jejunus* Noskiewicz, 1936
Egypt: Kom Oshim: NHM
Saudi Arabia: Jeddah: NHM
UAE: Jebel Dhana: NHM

***Colletes judaicus* Noskiewicz, 1955**
Synonyms: *Colletes coriandri judaicus* Noskiewicz, 1955
Israel: Shizzafon Junction, nr. Telamim, nr. Yeroham, nr. Zihor Junction: AMNH

***Colletes lacunatus* Dours, 1872**

Synonyms: *Colletes bracatus* Perez, 1895; *Colletes grandis* Friese, 1898; *Colletes nursei* Cameron, 1907; *Colletes deesensis* Cockerell, 1922
Egypt: Asyut, Cairo, Faiyum, Ismailia, Kerdasha, Suez Canal University: NHM
Israel: Ein Gedi, En Tamar, Haifa, nr. Shizzafon Junction, nr. Telamim, nr. Zohar Junction: AMNH
UAE: Abu Dhabi, Al Ain Road, Dubai, Liwa, Sweihan: NHM

***Colletes maidli* Noskiewicz, 1936**
Synonyms: *Colletes caspicus maidli* Noskiewicz, 1936; *Colletes caspicus lebedewi* Noskiewicz, 1936; *Colletes lebedewi* Noskiewicz, 1936
Egypt: Abo Aref nr. Suez, Tel El Kebir: AMNH

***Colletes maroccanus* Warncke, 1978**
UAE: Hatta, Wadi Wurayah: **CAvH**

***Colletes microdontoides* Kuhlmann, 2003**
Saudi Arabia: Fayfa: NHM

***Colletes nanus* Friese, 1898**
Synonyms: *Colletes (Nanocolletes) nanus* Friese, 1898
Egypt: Alexandria Montaza, nr. Bahariya Oasis, Cairo, Dahab, Dakhla Oasis, Helwan, Kom Oshim, Nuweiba, nr. Suez: NHM
Israel: Eiliat, Ein Gedi, nr. Ir Ovot: AMNHM & NHM
Oman: Adam, Al, Ghaftain, Al Wafi, Dawkah, Sur (Wadi Rafsah)
Saudi Arabia: Riyadh, Wadi Majarish: NHM
UAE: Abu Dhabi, Asimah, Hatta, Khor Fakkan, Liwa, Remah, Shuwaib, Sweihan, Wadi Helo, Wadi Maidaq, Wadi Wurayah: NHM

***Colletes omanus* Kuhlmann, 2003**
UAE: Al Ajban, Jebel Hafit, Liwa, Sharjah Desert Park: CMH, CMK, DEI, UAEIC

***Colletes perezi* Morice, 1904**
Synonyms: *Colletes resedae* Cockerell, 1934
Egypt: Cairo, Dahab, El Qesir, Giza, Hammam Faraun, Ismailia, Kom Oshim, Meadi, Neviot, Siwa, Suez Canal University: NHM
Israel: Eiliat, Ein Gedi, nr. Zihor Junction: AMNH & NHM

***Colletes pseudojejunus* Noskiewicz, 1959**
Synonyms: *Colletes askhabadensis pseudojejunus* Noskiewicz, 1959
Israel: En Tamar: AMNH
UAE: Liwa, Shuwaib: NHM

***Colletes pumilus* Morice, 1904**
Egypt: El Amarna, Ismailia, Kerdasha, Kom Oshim, Muhafazat al Qanal, Suez Canal University, Wadi El Natrum: NHM
Israel: Eiliat, Ein Gedi, Zohar Junction: AMNH
Jordan: Wadi Rum: NHM
Saudi Arabia: Abha, Riyadh: NHM

Colletes pusillus
Synonym of C. inconspicuus?
UAE: Al Saad: NHM

Colletes rozeni **Kuhlmann, 2005**
Israel: Telamim: AMNH
Colletes salsolae **Cockerell, 1934**
Synonym: *Colletes omanus* Kuhlmann, 2003
Oman: Bareimi: NHM
Saudi Arabia: Abyan, Sabya (Asir): NHM
Yemen: Lahij (Nr. Aden): NHM
Colletes schmideggeri **Kuhlmann, 2014**
UAE: Liwa: NHM
Colletes similis **Schenck, 1853**
Synonyms: *Colletes picistigma* Thomson, 1872; *Colletes (Simcolletes) similis* Schenck, 1853
Iran: Damavand: AMNH
Israel: Tel Aviv: AMNH
Colletes tuberculatus **Morawitz, 1893**
Synonyms: *Colletes tuberculatus anatolicus* Noskiewicz, 1959; *Colletes tuberculatus siculus* Noskiewicz, 1959
Israel: Wadi Loz: AMNH
Colletes yemensis **Noskiewicz, 1929**
Saudi Arabia: Abha: NHM
Yemen: Sana'a: NHM

Subfamily: Hylaeinae
Hylaeus (Abrupta) cornutus **Curtis, 1831**
Synonyms: *Hylaeus cornutus_homonym* Smith, 1842; *Hylaeus plantaris* Smith, 1842; *Hylaeus plumicornis* Costa, 1884; *Prosopis (Abrupta) cornuta* (Curtis, 1831); *Prosopis cornuta porzana* Warncke, 1992
Israel: Baram ruins, Tiberius, Wadi Kakara: NHM
Hylaeus (Dentigera) brevicornis **Nylander, 1852**
Synonyms: *Prosopis brevicornis* (Nylander, 1852); *Prosopis pygmaea* Schenck, 1853; *Prosopis rubicola_homonym* Smith, 1869; *Hylaeus discretus* Förster, 1871; *Hylaeus atratulus* Förster, 1871; *Hylaeus suspectus* Förster, 1871; *Hylaeus breviceps* Morawitz, 1876; *Hylaeus laticeps* Morawitz, 1876; *Hylaeus nigritarsis* Morawitz, 1876; *Prosopis brevicornis sardoa* Alfken, 1934; *Prosopis (Dentigera) brevicornis* (Nylander, 1852)
Israel: Bet Oren, Har Gillo: AMNH
Hylaeus (Dentigera) imparilis **Forster, 1871**
Synonyms: *Hylaeus ambiguus* Forster, 1871; *Hylaeus medullitus* Forster, 1871; *Hylaeus blandus* Forster, 1871; *Hylaeus exaequatus* Forster, 1871; *Hylaeus seductus* Forster, 1871; *Prosopis imparilis* (Forster, 1871); *Prosopis cognata_homonym* Perez, 1903; *Hylaeus (Paraprosopis) diplonymus* (Schulz, 1906); *Prosopis brevicornis var cypria* Alfken, 1928
Israel: Nr. Bet Shean, Har Gillo, Tiberius: AMNH
Lebanon: Al Montazah nr. Mansourieh, Jdeide: NHM
Hylaeus (Dentigera) kahri **Forster, 1871**

Synonyms: *Hylaeus carbonaria* Förster, 1871; *Hylaeus assimilis* Förster, 1871; *Prosopis perforator* Smith, 1876
Israel: Mt. Hermon: AMNH

***Hylaeus (Dentigera) punctus* Forster, 1871**
Israel: Bet Oren, nr. Haifa, Ramat Ha Nadiv, Tel Aviv: AMNH

***Hylaeus (Hylaeus) hameri* Dathe, 1995**
UAE: Abu Dhabi, Badayah, Hatta, Lulayyah: NHM & OUMNH

***Hylaeus (Hylaeus) moricei* (Friese, 1898)**
Synonyms: *Prosopis moricei* Friese, 1898; *Prosopis gracilicornis var luteifrons* Strand, 1909; *Prosopis moricella* Bischoff, 1954; *Prosopis moricella f atricallosa* Bischoff, 1954; *Prosopis nigrifacies rhenana* Warncke, 1986; *Hylaeus (Hylaeus) moricei luteifrons* (Strand, 1909)
Egypt: Abo Aref nr. Suez, Ismailia, Faiyum: OUMNH
Israel: Kefar Masaryik: AMNH

***Hylaeus (Hylaeus) sidensis* (Warncke, 1981)**
Synonyms: *Prosopis sidensis* Warncke, 1981
Israel: Bet Oren: AMNH

***Hylaeus (Hylaeus) trifidus* (Alfken, 1936)**
Synonyms: *Prosopis trifida* Alfken, 1936
Israel: Har Gillo: AMNH

***Hylaeus (Hylaeus) tyrolensis* Forster, 1871**
Israel: Ramat Ha Nadiv, Upper Galilee (between Menara and Yiftah): AMNH

***Hylaeus (Lambdopsis) scutellatus* (Spinola, 1838)**
Israel: Kefar Masaryik: AMNH

***Hylaeus (Paraprosopis) albonotatus* Walker, 1871**
Synonyms: *Prosopis albonotata* Walker, 1871; *Prosopis klugii* Friese, 1898; *Prosopis klugi kermana* Warncke, 1981; *Prosopis klugii mesopotamae* Warncke, 1992
Egypt: Abo Aref nr. Suez, Cairo, El Ferdan, Giza, Ismailia, Maragi, Oasis Ain Hudra, Sitra Oasis, Siwa, Suez Canal University, Wadi Rayyan, Wadi Watir: NHM
Israel: Dead Sea (En Zeelim), Ein Gedi, Elat, Wadi En Agrabbim, Zohar Junction: AMNH
Oman: Rayy: NHM
UAE: Al Ain Road, Al Babha, Al Saad, Badayah, Hatta, Liwa, Lulayyah, Sweihan: NHM & OUMNH
Yemen: Harib: NHM

***Hylaeus (Paraprosopis) dinkleri* (Friese, 1898)**
Synonyms: *Prosopis dinkleri* Friese, 1898; *Prosopis falsifica* Alfken, 1930
Egypt: El Ferdan, Faiyum, Fayid, Giza, Ismailia, Suez Canal University: NHM & OUMNH
Israel: Ein Gedi, En Tamar, Nr. Qumeran: AMNH

***Hylaeus (Paraprosopis) donbakeri* Dathe, 1995**
UAE: Jebel Jibir: DEI

***Hylaeus (Paraprosopis) emir* Dathe, 2000**
UAE: Liwa: CAvH

***Hylaeus (Paraprosopis) gujaraticus* Nurse, 1903**

Synonyms: *Prosopis elata* Warncke, 1981; *Hylaeus (Paraprosopis) elatus* (Warncke, 1981)
Israel: Avara Valley, Ein Gedi, Shezaf Nature Preserve, Yotvata, Nr. Zihor Junction: AMNH
UAE: Asimah, Hatta, Hayl: NHM

***Hylaeus (Paraprosopis) lineolatus* (Schenck, 1861)**

Synonyms: *Prosopis lineolata* Schenck, 1861; *Hylaeus inaequalis* Forster, 1871; *Prosopis lineolata var nigrifacies_homonym* Alfken, 1913; *Prosopis creticola* Strand, 1915; *Prosopis lineolata rudis* Pittioni, 1950; *Prosopis lineolata farina* Warncke, 1992; *Hylaeus (Paraprosopis) lineolatus farina* (Warncke, 1992)
Israel: Bet Oren, Har Gillo, Hurfeish, Mt. Carmel: AMNH & NHM
Lebanon: Al Montazah nr. Mansourieh: NHM

***Hylaeus (Paraprosopis) taeniolatus* Forster, 1871**

Synonym: *Prosopis taeniolata* (Forster, 1871); *Prosopis arata* Vachal, 1895; *Prosopis luteipes* Benoist, 1943
Israel: nr. Haifa, Har Gillo, Ramat Ha Nadiv: AMNH
Lebanon: Al Montazah nr. Mansourieh: NHM

***Hylaeus (Paraprosopis) xanthopoda* (Vachal, 1895)**

Synonyms: *Prosopis xanthopoda* Vachal, 1895
Egypt: Hammam Faraun, Suez, Wadi Digla, Wadi Watir: OUMNH
Israel: Ein Gedi, Elat, En Tamar, Timna Park, nr. Samar, nr. Shizzafon Junction, Timna Park, Wadi N'Aqev, Yotvata, nr. Zihor Junction, nr. Zohar Junction: AMNH

***Hylaeus (Prosopis) alexandrinus* (Warncke, 1992)**

Synonyms: *Prosopis (Nesoprosopis) alexandrina* Warncke, 1992
Egypt: Wadi Digla: OUMNH

***Hylaeus (Prosopis) luteus* (Alfken, 1939)**

Synonyms: *Prosopis lutea* Alfken, 1939
Egypt: Wadi Digla: AMNH

***Hylaeus (Prosopis) maculatus* (Alfken, 1904)**

Israel: Tiberius: AMNH

***Hylaeus (Prosopis) meridionalis* Forster, 1871**

Synonyms: *Prosopis meridionalis* (Förster, 1871); *Prosopis variegata var brevimaculata* Strand, 1909; *Prosopis maculiscutum* Alfken, 1928; *Prosopis effasciata* Alfken, 1931; *Hylaeus hookeri* Cockerell, 1931
Iran: Karaj: AMNH

***Hylaeus (Prosopis) pictus* (Smith, 1853)**

Synonyms: *Prosopis gibba picta* Smith, 1853 *Prosopis picta* Smith, 1853; *Prosopis scutata* Lichtenstein, 1877; *Hylaeus psilurus* Cockerell, 1938
Israel: Kefar Masaryik: AMNH
Lebanon: Al Montazah nr. Mansourieh: NHM

***Hylaeus (Prosopis) variegatus* Fabricius, 1798**

Mellinus variegatus Fabricius, 1798; *Mellinus labiatus* Fabricius, 1798; *Prosopis variegata* (Fabricius, 1798); *Philanthus analis*

Fabricius, 1804; *Prosopis colorata* Panzer, 1805; *Prosopis coriacea* Perez, 1895; *Prosopis variegata var obscura* Hoppner, 1901; *Prosopis variegata var integra* Alfken, 1904; *Prosopis impressifrons_homonym* Gussakovsky, 1932; *Prosopis rufithorax* Alfken, 1933; *Prosopis variegata relicta* Warncke, 1981
Israel: Ekron: NHM
Lebanon: Al Montazah nr. Mansourieh, Jdeide: NHM

***Hylaeus (Spatulariella) armeniacus* (Warncke, 1981)**
Israel: Har Gillo: AMNH
Lebanon: Jdeide: NHM

***Hylaeus (Spatulariella) adspersus* (Alfken, 1935)**
Israel: Bet Oren: AMNH

***Hylaeus (Spatulariella) longimaculus* (Alfken, 1936)**
Synonyms: *Prosopis punctata var longimacula* Alfken, 1936
Egypt: Cairo: NHM
Israel: Bet Oren, Har Gillo, Hurfeish, Jerusalem, Maale Gilboa: AMNH
Lebanon: Al Montazah nr. Mansourieh, Deir Mar Maroun: NHM

***Hylaeus (Spatulariella) punctatus* (Brulle, 1832)**
Synonyms: *Prosopis punctata* Brullé, 1832; *Hylaeus subquadratus* Förster, 1871; *Hylaeus insignis* Förster, 1871; *Hylaeus corvinus* Förster, 1871; *Prosopis sinuata var atrifacialis* Strand, 1909
Egypt: Suez Canal University: AMNH

Family: Andrenidae

Subfamily: Andreninae

***Andrena (Aenandrena) aeneiventris* Morawitz, 1872**
Synonyms: *Andrena locularoides* Strand, 1915; *Andrena aeneiventris var punctata* Jaeger, 1934
Israel: Tiberius: AMNH

***Andrena (Aciandrena) judea* Scheuchl & Pisanty, 2016**
Israel: Lakhish: AMNH

***Andrena (Carandrena) aerinifrons* Dours, 1873**
Synonyms: *Andrena albo-virescens* Dours, 1873; *Andrena albovirescens* Dours, 1873; *Andrena viridata* Pérez, 1895; *Andrena viridi-aenea* Pérez, 1903; *Andrena viridiaenea* Pérez, 1903; *Andrena atlantis* Friese, 1924; *Andrena aerinifrons levantina* Hedicke, 1938
Israel: Nr. Telamim: AMNH

***Andrena (Chlorandrena) isis* Schmiedeknecht, 1900**
Egypt: Kerdasha: AMNH

***Andrena (Chrysandrena) aegyptiaca* Friese, 1899**
Egypt: Banhar Behar, Ismailia, Suez Canal University: AMNH
UAE: Nr. Al-Dhaid, Sharjah Desert Park: SCU

***Andrena (Cubiandrena) cubiceps* Friese, 1914**
Israel: Wadi Qelt: NHM

***Andrena (Distandrena) mariana* Warncke, 1968**

Synonyms: *Andrena mariana leptura* Warncke, 1974; *Andrena mariana mica* Warncke, 1974; *Andrena mariana solda* Warncke, 1974; *Andrena mariana tenostra* Warncke, 1975; *Andrena mariana alma* Warncke, 1975
Egypt: Maghagha, nr. Suez: AMNH

***Andrena (Graecandrena) arsinoe* Schmiedeknecht, 1900**
Synonyms: *Anthrena arsinoe* Schmiedeknecht, 1900
Egypt: Abu Rudeis: AMNH

***Andrena (Holandrena) variabilis* Smith, 1853**
Synonyms: *Andrena calabra* Costa, 1863; *Andrena fonscolombii* Dours, 1872; *Andrena picciolii* Dours, 1872; *Andrena piceicornis* Dours, 1872; *Andrena pulcherrima* Schmiedeknecht, 1884; *Andrena macedonica* Strand, 1919
Syria: Tekieh: NHM

***Andrena (Margandrena) menahemella* Scheuchl & Pisanty, 2016**
Israel: Lakhish: AMNH

***Andrena (Melanapis) fuscosa* Erichson, 1835**
Synonyms: *Andrena rutila* Spinola, 1838; *Andrena ephippium* Spinola, 1838; *Andrena xanthoscelis* Brulle, 1832; *Andrena dorsalis_homonym* Lepeletier, 1841; *Andrena lepeletieri* Lucas, 1849; *Andrena ruficornis* Smith, 1853; *Andrena atrocoerulea* Giraud, 1863; *Andrena dagestanica* Radoszkowski, 1867; *Andrena turcestanica* Morawitz, 1876; *Andrena dilecta* Mocsary, 1879; *Andrena lepeletieri var aschabadensis_homonym* Radoszkowski, 1893; *Andrena jucunda* Perez, 1895; *Andrena ephippium var cleopatra* Friese, 1899; *Melanapis violaceipennis_homonym* Cameron, 1902; *Melanapis rufifrons* Nurse, 1904; *Andrena cyprica* Cockerell, 1910; *Andrena ephippium var flavipennis* Friese, 1914; *Andrena ephippium var pallipes* Friese, 1914; *Andrena ephippium var rufocincta_homonym* Friese, 1914; *Andrena ephippium var rubriventris* Friese, 1922; *Andrena rutila ab carnea* Lebedev, 1933; *Andrena rutila ab zonaria* Lebedev, 1933; *Andrena ankarae* Alfken, 1935; *Andrena (Melanapis) rutila mauritanica* Patiny, 1997; *Andrena (Melanapis) canariensis* Patiny, 1997
Egypt: Faiyum, Kafr Hakim: AMNH & NHM
Iraq: Haj Omran: NHM
UAE: Jebel Jibir, Um al-Quwain, Wadi Shawkah: NHM

***Andrena (Melandrena) albifacies* Alfken, 1927**
Synonym: *Andrena rutila var albifacies* Alfken, 1927
Egypt: Helwan, Mansourieh: NHM
Israel: Nr. Zihor Junction: AMNH
Oman: Rostaq: NHM

***Andrena (Melandrena) morio* Brulle, 1832**
Synonyms: *Andrena lugubris_homonym* Erichson, 1841; *Andrena holomelana* Lepeletier, 1841; *Andrena violaceipennis* Dufour, 1841; *Andrena rhodia* Kriechbaumer, 1873; *Andrena occipitalis_homonym* Perez, 1895; *Andrena asterabadiae* Strand,

1921; *Andrena ephippium var scopipes* Friese, 1923; *Andrena ephippium var albicollis* Friese, 1923; *Andrena morio var scopipes* Friese, 1923; *Andrena morio athalassae* Pittioni, 1950
Egypt: Meadi: NHM
Iraq: Hinaidi: NHM
Israel: Deir al-Balah (Gaza Strip): NHM

***Andrena (Melandrena) pyropygia* Kriechbaumer, 1873**
Synonyms: *Andrena pyrrhopygia* Kriechbaumer, 1873
Israel: Mt. Carmel: NHM

***Andrena (Melandrena) thoracica* Fabricius, 1775**
Synonyms: *Apis thoracica* Fabricius, 1775; *Melitta melanocephala* Kirby, 1802; *Andrena sinensis* Cockerell, 1910; *Andrena (Gymnandrena) thoracica melanoptera* Hedicke, 1934; *Andrena thoracica kotschyi* Mavromoustakis, 1953
Israel: Nr. Jaffa: AMNH
Lebanon: Mt. Lebanon nr. Bhandoun, Jdeide: NHM

***Andrena (Melittoides) melittoides* Friese, 1899**
Israel: Amirim: AMNH

***Andrena (Nobandrena) iliaca* Warncke, 1969**
Israel: Hurfeish: AMNH

***Andrena (Notandrena) ungeri* Mavromoustakis, 1952**
Synonyms: *Andrena cyanescens var rufescens_homonym* Friese, 1922
Israel: Kefar Masaryik: AMNH

***Andrena (Parandrenella) legata* Nurse, 1904**
Iraq: Hinaidi: NHM

***Andrena (Plastandrena) bimaculata* (Kirby, 1802)**
Synonym: *Melitta bimaculata* Kirby, 1802; *Andrena decorata* Smith, 1847; *Andrena conjuncta* Smith, 1847; *Andrena articulata* Smith, 1847; *Andrena vitrea* Smith, 1847; *Andrena consobrina* Eversmann, 1852; *Andrena vitreipennis* Costa, 1861; *Andrena mystacea* Dours, 1861; *Andrena intermedia_homonym* Morawitz, 1871; *Andrena morawitzi* Thomson, 1872; *Andrena atro-rubricata* Dours, 1872; *Andrena atrorubricata* Dours, 1872; *Andrena aulica* Morawitz, 1876; *Andrena comparata* Morawitz, 1876; *Andrena melanura* Morawitz, 1877; *Andrena paveli* Schmiedeknecht, 1883; *Andrena magrettiana* Schmiedeknecht, 1884; *Andrena germabica* Radoszkowski, 1893; *Andrena atrorubricata var concolor_homonym* Alfken, 1914; *Andrena bimaculata var mondaensis* Friese, 1922; *Andrena bimaculata var serotinella* Friese, 1922; *Andrena morawitzi var hirtella* Friese, 1922; *Andrena tibialis var tricolorata* Friese, 1922; *Andrena florea var clavipes* Friese, 1924; *Andrena bluethgeni* Stoeckhert, 1930; *Andrena gaetula* Benoist, 1961
UAE: Jebel Jibir: CAvH

***Andrena (Poecilandrena) arabica* Scheuchl & Gusenleitner, 2007**

UAE: Nr. Al-Jazirat al-Hamra, Wadi Maidaq, Wadi Shawkah, Wadi Wurayah: CES, DEI, OÖLM, UAIEC

***Andrena (Poecilandrena) maidaqi* Scheuchl & Gusenleitner, 2007**

UAE: Nr. Al-Dhaid, Wadi Maidaqi, Wadi Shawkah: CES, CMH, DEI, OÖLM, UAIEC

***Andrena (Poecilandrena) sphecodimorpha* Hedicke, 1942**

Israel: Karei Deshe: AMNH

***Andrena (Poliandrena) unicincta* Friese, 1899**

Israel: Deir al-Balah (Gaza Strip), Mt. of Olives: NHM

***Andrena (Ptilandrena) vetula* Lepeletier, 1841**

Synonyms: *Andrena megacephala* Smith, 1853; *Andrena opaca* Morawitz, 1868; *Andrena tyrrhena* Alfken, 1938
Egypt: Assiut, Giza, Meadi: NHM
Israel: Jerusalem: AMNH & NHM
Lebanon: Al Montazah nr. Mansourieh: NHM

***Andrena (Platygalandrena) combaella* Warncke, 1966**

Israel: Shemona Golan: AMNH

***Andrena (Suandrena) aegypticola* Friese, 1922**

Synonyms: *Andrena larnacensis* Mavromoustakis, 1954
Israel: Nr. Telamim: AMNH

***Andrena (Suandrena) savignyi* Spinola, 1838**

Synonym: *Andrena bipartita_homonym* Brulle, 1840; *Andrena bicolorata_homonym* Smith, 1853; *Andrena uromelana* Costa, 1888; *Andrena antilope* Perez, 1895; *Andrena ilerda* Cameron, 1907; *Andrena ferozeporensis* Cameron, 1909; *Andrena ilerda inglisi* Cockerell, 1920; *Andrena bipartita aswanica* Cockerell, 1938
Egypt: Aswan, Dakhla; Meadi, nr. Suez: AMNH & NHM
Oman: Behla: NHM
Saudi Arabia: Sahanah: NHM
UAE: Al Ain, Fagsha, Ras al-Khaimah, Wadi Maidaq, Wadi Shawkah: NHM

***Andrena (Taeniandrena) ovatula* Kirby, 1802**

Synonyms: *Melitta ovatula* Kirby, 1802; *Melitta afzeliella* Kirby, 1802; *Melitta fuscata* Kirby, 1802; *Melitta picipes* Kirby, 1802; *Melitta barbata* Kirby, 1802; *Andrena hirticeps* Eversmann, 1852; *Andrena interrupta* Eversmann, 1852; *Andrena octostrigata* Schenck, 1853; *Andrena gibba* Schenck, 1853; *Andrena ovata* Schenck, 1853; *Andrena plantaris* Schenck, 1853; *Andrena canescens* Schenck, 1853; *Andrena albofimbriata* Schenck, 1853; *Andrena distincta_homonym* Schenck, 1861; *Andrena albo-fasciata* Thomson, 1870; *Andrena albofasciata* Thomson, 1870; *Andrena poupillieri* Dours, 1872; *Andrena meliloti* Verhoeff, 1890; *Andrena afzeliella var heliopolis* Friese, 1914; *Andrena pseudovatula* Alfken, 1926; *Andrena lecerfi* Benoist, 1961; *Andrena poupillieri incana* Warncke, 1975; *Andrena (Taeniandrena) ovatula transcaspiensis* Osytshnjuk, 1994

Egypt: Kerdasha, Meadi, Suez Canal University: AMNH & NHM

***Andrena (Thysandrena) helouanensis* Friese, 1899**

Egypt: Helwan, Wadi Hof: AMNH & NHM

***Andrena (Ulandrena) isabellina* Warncke, 1969**

Israel: Daliyat El Karmil: AMNH

***Andrena (Ulandrena) speciosa* Friese, 1899**

Egypt: Mariut: NHM
Israel: Jericho (Hisham Palace, Wadi Qelt): NHM
Syria: Banias: NHM

***Andrena (Zoandrena) flavipes* Panzer, 1799**

Synonyms: *Apis sordida_homonym* Gmelin, 1790; *Melitta fulvicrus* Kirby, 1802; *Melitta contigua* Kirby, 1802; *Andrena quadricincta_homonym* Brulle, 1832; *Andrena tricincta* Brulle, 1832; *Andrena fasciata_homonym* Imhoff, 1832; *Andrena puber* Erichson, 1835; *Andrena mactae* Lepeletier, 1841; *Andrena fulvicrus_homonym* Dufour, 1841; *Andrena capitalis* Smith, 1853; *Andrena interrupta_homonym* Schenck, 1870; *Andrena problematica* Perez, 1903; *Andrena levilabris* Cameron, 1908; *Andrena punjaubensis* Cameron, 1908; *Andrena kraussei* Strand, 1921; *Andrena kengracensis* Cockerell, 1930; *Andrena flavipes alexandrina* Warncke, 1965; *Andrena flavipes ibizensis* Warncke, 1984

Egypt: Cairo, Kafr Ammar, Meadi: AMNH & NHM
Iran: Tehran: NHM
Iraq: Al Mada'in: INHRCM
Israel: Daphne Oaks, Kefar Masaryik: AMNH & NHM

***Andrena (Zoandrena) vachali* Perez, 1895**

Synonyms: *Andrena creticola* Strand, 1915; *Andrena (Zonandrena) vachali creticola* Strand, 1915; *Andrena creticola var antennalis* Strand, 1915; *Andrena strigifrontalis* Strand, 1921; *Andrena pectoralis var cretensis* Friese, 1922; *Andrena hipomelaena* Gribodo, 1924;

Egypt: Helwan: AMNH

Subfamily: Panurginae

Tribe: Panurgini

***Camptopoeum (Camptopoeum) negevense* (Warncke, 1972)**

Synonym: *Panurgus (Camptopoeum) negevensis* Warncke, 1972
Israel: Nr. Shizzafon Junction: AMNH
Oman: Rostaq: NHM

***Camptopoeum (Camptopoeum) sacrum* Alfken, 1935**

Synonyms: *Camptopoeum frontale sacrum* Alfken, 1935
Jordan: Below Sait: NHM
Syria: Dibbin, Khabab: AMNH

***Camptopoeum (Epimethea) variegatum* (Morawitz, 1876)**

Synonyms: *Epimethea variegata* Morawitz, 1876; *Panurginus variegatus* (Morawitz, 1876); *Panurgus (Camptopoeum) variegatus berberus* Warncke, 1972; *Panurgus (Camptopoeum) variegatus graecus* Warncke, 1972; *Panurgus (Camptopoeum)*

variegatus israelensis Warncke, 1972; *Panurgus (Camptopoeum) variegatus kilikae* Warncke, 1972
Israel: Eshtaol (Kesalon Valley), Tiberius: NHM

***Panurginus turcomanicus* Popov, 1936**
Synonyms: *Panurgus (Panurginus) brullei bytinski* Warncke, 1972
Israel: Nr. Adam (Jordan Valley), Daliyat El-Karmil: AMNH

***Panurgus (Pachycephalopanurgus) nigriscopus* Perez, 1895**
Synonym: *Panurgus nigriscopa* Perez, 1895; *Panurgus (Panurgus) nigriscopus trigonus* Warncke, 1972
Israel: Arava Valley, Ein Gedi, En Zeelim, Shizzafon Junction: AMNH
Oman: Jebel Hawrah, Wadi Quryat: NHM
UAE: Hatta, Wadi Maidaq, Wadi Shawkah: NHM

***Panurgus (Panurgus) buteus* Warncke, 1972**
Egypt: Sinai, Wadi Rishrash: NHM
Israel: Ein Gedi, Hazeva, Shizzafon Junction, nr. Qumeran: AMNH & NHM
Jordan: Al-Karamah: AMNH

***Panurgus (Panurgus) dentatus* Friese, 1901**
Egypt: Ismailia, Suez, Suez Canal University: AMNH & SCU

***Panurgus (Panurgus) oblitus* Warncke, 1972**
Synonyms: *Panurgus (Panurgus) dentipes oblitus* Warncke, 1972
Jordan: Azraq Shisan Marsh: NHM

***Panurgus (Panurgus) platymerus* Perez, 1895**
Israel: Deir al-Balah (Gaza Strip): NHM
Saudi Arabia: Abha, Al Ha'ir: NHM

Tribe: Melitturgini:

***Borgatomelissa brevipennis* (Walker, 1871)**
Synonym: *Andrena brevipennis* Walker, 1871; *Nomia eburneifrons* Walker, 1871; *Meliturgula arabica* Popov, 1951
Oman: Wadi Quryat: NHM
UAE: Abu Arish: NHM

***Melitturga (Melitturga) clavicornis* (Latreille, 1806)**
Synonyms: *Eucera clavicornis* Latreille, 1806; *Macrocera nasalis* Eversmann, 1852; *Melitturga clavicornis var thuringiaca* Friese, 1895
Iran: Saraain: AMNH

***Melitturga (Melitturga) syriaca* Friese, 1899**
Synonyms: *Meliturga_sic praestans var syriaca* Friese, 1899
Israel: Golan Heights: AMNH
Lebanon: Monteverde nr. Mansourieh: OUMNH

Family: Halictidae

Subfamily: Rophitinae

***Dufourea bytinskii* Ebmer, 1999**
Synonym: *Dufourea (Dentirophites) bytinskii* Ebmer, 1999
UAE: Sharjah Desert Park, Wadi Safad: CAvH

Dufourea exigua **Ebmer, 2008**
Synonym: *Dufourea (Cyprirophites) exigua* Ebmer, 2008
UAE: Nr. Al-Dhaid, Wadi Shawkah: CAWE, DEI, UAEIC

Dufourea **aff.** ***fortunata*** **Ebmer, 1993**
UAE: Wadi Shawkah: CAvH

Dufourea goeleti **Ebmer, 1999**
Synonyms: *Dufourea (Dufourea) goeleti* Ebmer, 1999
Israel: Ein Gedi: AMNH

Dufourea nodicornis **(Warncke, 1979)**
Synonyms: *Rophites (Dufourea) nodicornis* Warncke, 1979; *Dufourea (Dufourea) nodicornis* (Warncke, 1979)
Israel: Wadi Ramon: AMNH

Dufourea phoenix **Ebmer, 2008**
Synonym: *Dufourea (Dufourea) phoenix* Ebmer, 2008
UAE: Wadi Maidaq, Wadi Shawkah: CAvH

Dufourea trigonellae **Ebmer, 1999**
Synonyms: *Dufourea (Dufourea) trigonellae* Ebmer, 1999
Israel: Ein Gedi, nr. Shizzafon Junction: AMNH

Rophites (Rophites) nigripes **Friese, 1902**
Israel: Tiberius: NHM

Systropha (Austrosystropha) aethiopica **Friese, 1911**
Oman: Dhofar (Wadi Sayq): NHM

Systropha (Systropha) androsthenes **Baker, 1996**
Saudi Arabia: Jeddah, Riyadh: NHM
UAE: Al Ain: NHM

Systropha (Systropha) diacantha **Baker, 1996**
Oman: Behla, Khasab, Rayy, Ruwi: NHM
UAE: Wadi Maidaq, Wadi Shawkah, Wadi Wurayah: NHM

Systropha (Systropha) hirsuta **Spinola, 1838**
Israel: Dimona, Palmachim: NHM

Systropha (Systropha) planidens **Giraud, 1861**
Synonyms: *Systropha planidens grandimargo* Pérez, 1905; *Systropha chrysura* Pérez, 1905; *Systropha planidens anatolica* Warncke, 1977
Iran: Saraain: AMNH

Subfamily: Nomiinae

Lipotriches (Armatriches) pallidicincta **(Cockerell, 1932)**
Synonym: *Nomia tricoloripes pallidicincta* Cockerell, 1932
Oman: Rayy: NHM

Lipotriches (Clavinomia) clavicornis **(Warncke, 1980)**
Synonym: *Nomia clavicornis* Warncke, 1980
Oman: Sayh Huwayyah: NHM
UAE: Asimah: NHM

Lipotriches (Rhopalomelissa) parca **(Kohl, 1906)**
Synonym: *Nomia parca* Kohl, 1906; *Nomia gracilipes_homonym* Perez, 1907; *Nomia pereziana* Cockerell, 1911; *Nomia karachiensis* Cockerell, 1911; *Nomia rubribasis* Cockerell, 1939; *Nomia gossypii* Cockerell, 1942; *Nomia villiersi* Benoist, 1950

UAE: Hatta: DEI & UAEIC
Yemen: El' Asr, Khormaskar: NHM

***Nomia (Crocisaspidia) forbesi* (W.F. Kirby, 1900)**
Synonym: *Crocisa forbesi* W.F. Kirby, 1900; *Crocisaspidia forbesii* (W.F. Kirby, 1900)
Oman: Khasab, Rayy, Rostaq: NHM
UAE: Asimah, Fagsha, Wadi Wurayah: NHM

***Nomia (Crocisaspidia) vespoides* Walker, 1871**
Synonym: *Nomia (Crocisaspidia) muscatensis* Cockerell, 1910; *Crocisaspidia vespoides* (Walker, 1871)
Oman: Dhofar (N. S. Road), Dhofar (Shisur), Masirah, Rumais, Ruwi: NHM
UAE: Dibba, Hatta, Lulayyah: NHM

***Nomia (Crocisaspidia) zonaria* Walker, 1871**
Synonym: *Crocisaspidia zonaria* (Walker, 1871); *Nomia lamellata* Smith, 1875; *Nomia superba* Friese, 1930
UAE: Wadi Shawkah: DEI

***Nomia (Leuconomia) lutea* Warncke, 1976**
Egypt: Faiyum: OUMNH
UAE: Khor al-Khwair: OUMNH

***Nomia (Leuconomia) omanica* (Pauly, 2000)**
Oman: Rostaq, Sohar: NHM
Yemen: Khormaskar: NHM

***Pseudapis (Nomiapis) bispinosa* (Brulle, 1832)**
Synonyms: *Nomia bispinosa* Brulle, 1832; *Nomia rufiventris* Spinola, 1838; *Nomia ruficornis* Spinola, 1838; *Nomia perforata* Lucas, 1849; *Nomia albocincta* Lucas, 1849; *Nomia aureocincta* Costa, 1861; *Nomia basalis_homonym* Smith, 1875; *Nomia albocincta var basirubra* Magretti, 1884; *Nomia aureocincta var turcomanica* Radoszkowski, 1893; *Nomia fletcheri* Cockerell, 1920
Egypt: Abo Aref nr. Suez, Assiut, Cairo, Etay El Baraud, Meadi: AMNH & NHM

***Pseudapis (Nomiapis) diversipes* (Latreille, 1806)**
Synonyms: *Nomia diversipes* Latreille, 1806; *Nomiapis diversipes* (Latreille, 1806); *Andrena humeralis* Jurine, 1807; *Nomia hungarica* Förster, 1853
Iran: Bandar Pahlavi: AMNH
Israel: nr. Bet Shean, Hula Reserve: AMNH

***Pseudapis (Nomiapis) edentata* (Morawitz, 1876)**
Synonym: *Nomia edentata* Morawitz, 1876; *Hoplonomia edentata* (Morawitz, 1876); *Nomia minor* Radoszkowski, 1893; *Nomia albifrons* Vachal, 1897; *Nomia albolobata* Cockerell, 1911
UAE: Abu Dhabi: CAVH

***Pseudapis (Nomiapis) equestris* (Gerstacker, 1872)**
Synonyms: *Nomia equestris* Gerstacker, 1872; *Nomiapis equestris* (Gerstacker, 1872); *Nomia caucasica* Friese, 1897; *Nomia equestris var smyrnensis* Strand, 1921

Lebanon: Deir Mar Maroun, Jdeide: OUMNH

Pseudapis (Nomiapis) fugax **(Morawitz, 1877)**

Synonyms: *Nomia fugax* Morawitz, 1877; *Nomiapis fugax* (Morawitz, 1877)
Iraq: Hinaidi: NHM

Pseudapis (Nomiapis) valga **(Gerstacker, 1872)**

Israel: Nr. Qumeran : AMNH

Pseudapis (Pseudapis) albolobata **(Cockerell, 1911)**
Synonym of *P. edentata*?

UAE: Asimah, Dibba

Pseudapis (Pseudapis) armata **(Olivier, 1812)**

Synonyms: *Nomia armata* Olivier, 1812
Egypt: Abo Aref (nr. Suez), Faiyum, nr. Suez City: AMNH

Pseudapis (Pseudapis) dixica **(Warncke, 1976)**

Synonyms: *Nomia (Lobonomia) dixica* Warncke, 1976
Egypt: Faiyum, Gara, Helwan, Khamissa Depression, Koreishid, Siwa, Wadi Digla, Wadi Quiseb: AMNH, NHM & OUMNH

Pseudapis (Pseudapis) flavolobata **(Cockerell, 1911)**

Synonym: *Nomia flavolobata* Cockerell, 1911; *Nomia iranica* Warncke, 1979
UAE: Al-Ajban: DEI & UAEIC

Pseudapis (Pseudapis) lobata **(Olivier, 1812)**

Synonyms: *Nomia lobata* Olivier, 1812
Iran: Karaj: AMNH

Pseudapis (Pseudapis) nilotica **(Smith, 1875)**

Synonym: *Nomia nilotica* Smith, 1875; *Nomia lucens* Vachal, 1897; *Nomia savignyi* Kohl, 1906
Bahrain: Manama: NHM
Egypt: Assiut, Faiyum, Siwa: NHM
Iran: Gilan (Lahijau): NHM
Israel: Ein Bokek: NHM
Jordan: Azrak Shishar: NHM
Oman: Adam, Masirah: NHM
Saudi Arabia: Abu Arish, Hofuf, Jeddah, Riyadh: NHM
UAE: Al Ain, Abu Dhabi, Bithnah, Dibba, Al-Ajban, Futaisi, Hatta, Jebel Ali Hotel, Jebel Hafit, Liwa, Sharjah Desert Park, Sweihan Road, Wadi Bih, Wadi Maidaq, Wadi Shawkah: NHM
Yemen: Khormaskar: NHM

Pseudapis (Pseudapis) patellata **(Magretti, 1884)**

Synonym: *Nomia patellata* Magretti, 1884; *Nomia chopardi* Benoist, 1950; *Nomia (Pseudapis) magretti_sic geddensis* Warncke, 1976; *Nomia (Pseudapis) patellata abassa* Warncke, 1980
Israel: Dead Sea En Zeelim: AMNH
Oman: Al Hamra, Bareimi, Dhofar (Salalah), Jebel Howrah, Nizwa, Sayh Huwayyah, Rayy: NHM
UAE: Dibba, Fagsha, Hatta, Khor Fakkan, Wadi Bih, Wadi Maidaq, Wadi Shawkah: NHM
Yemen: Usaifira, Wadi Hardaba: NHM

Pseudapis (Pseudapis) stenotarsus **Baker, 2002**
UAE: Bithnah, Wadi Maidaq, Wadi Shawkah: DEI & UAEIC
Pseudapis (Pseudapis) tadzhica **(Popov, 1956)**
Synonym: *Nomia tadzhica* Popov, 1956
Saudi Arabia: Qunfudha
UAE: Abu Dhabi, Futaisi, Hatta, Sweihan Road, Umm Al-Nar

Subfamily: Nomioidinae
Ceylalictus (Ceylalictus) punjabensis **(Cameron, 1907)**
Synonym: *Ceratina punjabensis* Cameron, 1907; *Nomioides excellens* Saunders, 1908; *Nomioides comberi* Cockerell, 1911
Egypt: Assiut, Kom Ushim, Siwa: NHM
Israel: Eiliat: NHM
Oman: Al Ghaftain: NHM
Saudi Arabia: Jeddah: NHM
UAE: Al-Ajban, Liwa, Sharjah Desert Park, Shuwaib: NHM
Ceylalictus (Ceylalictus) variegatus **(Olivier, 1789)**
Synonym: *Andrena variegata* Olivier, 1789; *Andrena pulchella* Jurine, 1807; *Allodape syrphoides* Walker, 1871; *Andrena flavopicta* Dours, 1873; *Nomioides jucunda* Morawitz, 1874; *Nomioides fasciatus var intermedius* Alfken, 1924; *Nomioides variegata var simplex* Bluthgen, 1925; *Nomioides variegata var unifasciata* Bluthgen, 1925; *Nomioides labiatarum* Cockerell, 1931; *Nomioides variegata var nigrita* Bluthgen, 1934; *Nomioides variegata var pseudocerea* Bluthgen, 1934; *Nomioides variegata var nigriventris* Bluthgen, 1934
Bahrain: Manama: NHM
Egypt: Abo Aref nr. Suez, Abu Rawash, 60 km S of Alexandria, Assiut, Aswan, Ein Khudra, Faiyum, Giza, Siwa: AMNH & NHM
Israel: Dimona, Eiliat, Ein Bokek, En Tamar, Shizzafon Junction, Tel Aviv: AMNH & NHM
Oman: Al Wafi, Dhofar (Salalah), Masirah, Muscat (Qurum), Rostaq, Rumais, Wadi Rafsah: NHM
Saudi Arabia: Jeddah, Qunfudha: NHM
Syria: Latakia, Palmyra: NHM
UAE: Abu Dhabi, Al Ain, Al-Ajban, Al-Jazirat al-Hamra, Hatta, Liwa, Shuwaib, Wadi Shawkah: NHM
Yemen: Khormaksar: NHM
Ceylalictus (Meganomioides) karachensis **(Cockerell, 1911)**
Synonym: *Nomioides karachensis* Cockerell, 1911
UAE: Al-Ajban, Wadi Maidaq: DEI & UAEIC
Nomioides abudhabiensis **Pesenko & Pauly, 2009**
UAE: Wadi Maidaq: DEI & UAEIC
Nomioides arabicus **Pesenko, 1983**
UAE: Asimah, Fagsha, Hayl, Wadi Maidaq, Wadi Wurayah: DEI & UAEIC
Nomioides chalybeatus **Bluthgen, 1934**
Synonyms: *Nomioides chalybeata* Bluthgen, 1934
Jordan: Azraq Shisan Marsh: OUMNH

Nomioides elbanus **Bluthgen, 1934**

Synonym: *Nomioides elbana* Bluthgen, 1934

UAE: Al-Ajban, Sharjah Desert Park, Wadi Shawkah: DEI & UAEIC

Nomioides facilis **(Smith, 1853)**

Synonym: *Halictus facilis* Smith, 1853; *Nomioides fallax_homonym* Handlirsch, 1888; *Nomioides callosus* Perez, 1895; *Halictus handlirschii* Dalla Torre & Friese, 1895; *Nomioides facilis var dusmeti* Bluthgen, 1925; *Nomioides facilis var bipunctata* Bluthgen, 1925; *Nomioides cruciferarum* Cockerell, 1931

Israel: Eiliat, Ein Bokek, Jericho (Wadi Qelt): NHM

Lebanon: Wadi Faria: OUMNH

Saudi Arabia: Abyan: NHM

Yemen: Jebel Jihaf, Socotra (Hadibo Plain): NHM

Nomioides klausi **Pesenko, 1983**

Synonym: *Nomioides (Nomioides) klausi* Pesenko, 1983: DEI & UAEIC

UAE: Al-Dhaid, Al-Jazirat Al-Hamra

Nomioides lahorensis **Bluthgen, 1934**

UAE: Hatta: NHM

Nomioides micheneri **Pesenko & Pauly, 2005**

UAE: Nr. Mahafiz: DEI

Nomioides minutissimus **(Rossi, 1790)**

Synonym: *Apis minutissima* Rossi, 1790; *Halictus pulchellus* Giraud, 1861; *Nomioides minutissima var schencki* Bluthgen, 1925; *Nomioides maurus* Bluthgen, 1925; *Nomioides minutissima var obscurata* Bluthgen, 1925; *Nomioides minutissima var versicolor* Bluthgen, 1925; *Nomioides minutissima var violascens* Bluthgen, 1925; *Nomioides campanulae* Cockerell, 1931; *Nomioides senscionis* Cockerell, 1931; *Nomioides maura var tingitana* Bluthgen, 1933; *Nomioides minutissima var fusca* Bluthgen, 1934; *Nomioides minutissima var tristis* Bluthgen, 1934

Egypt: Assiut: NHM

Israel: Jericho: NHM

Saudi Arabia: Medaen Salih: NHM

UAE: Abu Dhabi, Hatta, Shuwaib: NHM

Nomioides modestus **Pesenko, 1977**

Israel: Ein Sinya, Jerusalem, Rehovot: NHM

Nomioides punjabensis ???

UAE: Shuwaib: OUMNH

Nomioides rotundiceps **Handlirsch, 1888**

Synonym: *Nomioides rotundiceps var viridana* Bluthgen, 1925; *Nomioides persica* Bluthgen, 1933

Egypt: Faiyum: AMNH

Israel: Eiliat, Ein Bokek, Jericho: NHM

Oman: Muscat (Qurum), Sayh Huwayyah, Sohar: NHM

Saudi Arabia: Abu Arish, Jeddah, Riyadh, Wadi Majarish: NHM

    UAE: Abu Dhabi, Al Ain, Al Babha, Falaj Al Mualla, Futaisi, Hatta, Sweihan Road, Shuwaib: NHM

Nomioides squamiger **Saunders, 1908**
    Synonym: *Nomioides squamigera* Saunders, 1908
    Egypt: Qaliub: NHM
    Saudi Arabia: Jeddah: NHM

Nomioides turanicus **Morawitz, 1876**
    Egypt: Cairo: NHM
    Israel: Ashkelon, Ein Bokek, Ein Gedi, Zohar Junction: AMNH & NHM
    Oman: Dhofar (Salalah), Wadi Quryat: NHM
    Qatar: Al Shahaniyeh: NHM
    Saudi Arabia: Riyadh: NHM
    UAE: Abu Dhabi, Hatta, Lulayyah, Sharjah Desert Park, Shuwaib, Wadi Shawkah, Wadi Tarabat: NHM
    Yemen: Jebel Jihaf: NHM

Nomioides variegata ??
    Oman: Al Ghaftain: NHM & OUMNH
    Qatar: Al Shahaniyeh: NHM
    UAE: Abu Dhabi, Al Ain, Al Babha, Al Futaisi, Al Saad, Dhaid, Shuwaib, Wadi Uyaynah: OUMNH

Subfamily: Halictinae

Tribe: Halictini

Halictus (Acalcaripes) falcinellus **Warncke, 1982**
    Iran: Nr. Karaj: AMNH

Halictus (Argalictus) fatsensis **Bluthgen, 1936**
    Synonyms: *Halictus (Halictus) fatsensis* Blüthgen, 1936
    Israel: Jerusalem: AMNH

Halictus (Argalictus) humkalensis **Bluthgen, 1936**
    Synonyms: *Halictus (Halictus) humkalensis* Bluthgen, 1936
    UAE: Wadi Maidaq, Wadi Shawkah

Halictus (Argalictus) senilis **Eversmann, 1852**
    Synonyms: *Halictus (Halictus) senilis* (Eversmann, 1852); *Halictus albarius* Perez, 1895; *Halictus bivinctus* Vachal, 1902
    Egypt: Abo Aref nr. Suez, Faiyum: AMNH
    Israel: Dunes Nizzanim, Strand Nasholim, Wadi Qelt, Peza ‘el (Jordan Valley): AMNH
    Jordan: Amman: NHM

Halictus (Argalictus) subsenilis **Bluthgen, 1955**
    Synonyms: *Halictus (Halictus) subsenilis* Bluthgen, 1955
    Israel: Jericho: NHM

Halictus (Argalictus) tibialis **Walker, 1871**
    Synonym: *Halictus distinctus_homonym* Walker, 1871; *Halictus (Halictus) tibialis* Walker, 1871; *Halictus dampti* Alfken, 1926
    Egypt: St Katherine (Sinai): NHM
    Israel: Arava Valley, Ein Gedi, Qumeran: AMNH & NHM
    Oman: Behla, Muscat (Ruwi), Tinuf, Wadi Jizzi: NHM
    Saudi Arabia: Abha: NHM

UAE: Fagsha: NHM
Yemen: Ghaiman nr. Sana’a: NHM

Halictus (Hexataenites) berlandi **Bluthgen, 1936**
Israel: Nr. Zomet: AMNH

Halictus (Halictus) quadricinctus **(Fabricius, 1776)**
Synonyms; *Apis quadricincta* Fabricius, 1776; *Apis hortensis* Geoffroy, 1785; *Halictus quadristrigatus* Latreille, 1805; *Hylaeus grandis* Illiger, 1806; *Halictus chaharensis* Yasumatsu, 1940
Egypt: Meadi: NHM
Israel: Nr. Bet Shean, Daphne Oaks: NHM

Halictus (Hexataenites) resurgens **Nurse, 1903**
Synonyms: *Halictus turkomannus* Perez, 1903; *Halictus (Lucasius) holtzi* Schulz, 1906; *Halictus asiaeminoris* Strand, 1921
Iran: Hamadan, nr. Neishabour: AMNH & NHM
Israel: Har Gillo, Jerusalem, Mt. Carmel, Tiberius: AMNH & NHM
Lebanon: Anioune: NHM

Halictus (Hexataenites) sexcinctus **(Fabricius, 1775)**
Synonyms: *Apis sexcincta* Fabricius, 1775; *Hylaeus sexcinctus* Fabricius, 1793; *Hylaeus arbustorum* Panzer, 1797; *Andrena rufipes* Spinola, 1806; *Halictus sexcinctus var albohispidus* Blüthgen, 1923
Iran: Saraain: AMNH

Halictus (Monilapis) aegypticola **Strand, 1909**
Israel: Har Gillo: AMNH

Halictus (Monilapis) tetrazonianellus **Strand, 1909**
Israel: Nr. Bet Shean (Jordan Valley), Hula Reserve: AMNH

Halictus (Mucoreohalictus) pollinosus **Sichel, 1860**
Synonym: *Halictus pollinosus cariniventris* Morawitz, 1876; *Halictus balearicus* Perez, 1903; *Halictus thevestensis* Perez, 1903; *Halictus carinaeventris* Fahringer & Friese, 1921; *Halictus cariniventris var creticola* Strand, 1921; *Halictus cariniventris flavotectus* Cockerell, 1922; *Halictus pollinosus limissicus* Bluthgen, 1937
Egypt: Ismailia: SCU
Israel: Bet Oren, Jerusalem, Mt. Hermon, Tiberius: NHM
Yemen: Ghaiman nr. Sana’a, Sana’a, Ta’izz, Usaifira: NHM

Halictus (Platyhalictus) alfkenellus **Strand, 1909**
Synonyms: *Halictus posthumus_homonym* Blüthgen, 1925
Iran: Ramadan: AMNH

Halictus (Seladonia) cephalicus **Morawitz, 1873**
Synonyms: *Seladonia (Seladonia) cephalica* (Morawitz, 1874); *Halictus conjungens* Bluthgen, 1921; *Halictus neuter* Bluthgen, 1923
Iran: Bandar Pahlavi, Damavand: AMNH
Israel: Ein Sinya, Eshtaol, Jerusalem: NHM
Jordan: Amman: NHM

Halictus (Seladonia) lucidipennis **Smith, 1853**

Synonyms: *Halictus varipes* Morawitz, 1876; *Halictus niloticus* Smith, 1879; *Halictus varnalis* Smith, 1879; *Halictus magrettii* Vachal, 1892; *Halictus dives* Perez, 1895; *Halictus omanicus* Perez, 1907; *Halictus varipes var koptica* Bluthgen, 1933; *Halictus (Seladonia) sudanicus* Cockerell, 1945; *Halictus (Seladonia) tokarensis* Cockerell, 1945; *Halictus (Seladonia)*
Egypt: Abo Aref nr. Suez, 60 km S of Alexandria, Gara, Luxor, Siwa: AMNH & NHM
Qatar: Al Shahaniyeh: NHM
Saudi Arabia: Hofuf: NHM
UAE: Abu Dhabi, Al Ain, Al-Ajban, Al-Jazirat Al-Hamra, Al Saad, Bithnah, Dhaid, Jebel Ali Hotel, Hatta, Khor Fakkan, Nr. Mahafiz, Sharjah Desert Park, Umm Al Nar, Wadi Bih, Wadi Maidaq, Wadi Safad, Wadi Shawkah, Wadi Uyaynah: NHM
Yemen: Khormaksar: NHM

***Halictus (Seladonia) pici* Perez, 1895**
Egypt: Wadi Hof: NHM
Israel: Ein Bokek, nr. Yeroham: AMNH & NHM
Jordan: Azraq Shisan Marsh: NHM

***Halictus (Seladonia) phryganicus* (Devalez & Pauly, 2015)**
Synonyms: *Seladonia (Seladonia) phryganica* Devalez and Pauly, 2015
Israel: Nr. Qiryat Shemona Hermon Cableway, Tiberius: AMNH

***Halictus (Seladonia) seladonius* (Fabricius, 1794)**
Synonym: *Apis seladonia* Fabricius, 1794; *Halictus geminatus* Perez, 1903; *Seladonia (Seladonia) seladonia* (Fabricius, 1794)
Egypt: Meadi: NHM
Oman: Dhofar (Ayun Pools, Khadrafi, Salalah, Wadi Sayq), Khasab, Masirah, Rostaq, Wadi Quryat: NHM

***Halictus (Seladonia) semiticus* Bluthgen, 1955**
Israel: Wadi N'Aqev: AMNH
Jordan: Adjlun: NHM

***Halictus (Seladonia) smaragdulus* Vachal, 1895**
Synonyms: *Seladonia (Seladonia) smaragdulus* (Vachal, 1895); *Halictus barcelonicus* Perez, 1903; *Halictus smaragdulus form vinulus* Bluthgen, 1923
Israel: Banias, Deir al-Balah: NHM
Jordan: Adjlun: NHM
Lebanon: Tripoli: NHM

***Halictus (Seladonia) subauratus* (Rossi, 1792)**
Synonym: *Apis subaurata* Rossi, 1792; *Halictus virescens* Lepeletier, 1841; *Halictus gramineus* Smith, 1849; *Halictus meridionalis* Morawitz, 1874; *Halictus subauratus meridionalis* Morawitz, 1874; *Halictus subauratus syrius* Bluthgen, 1933; *Halictus subauratus var corsa* Bluthgen, 1933
Iran: Gilan: NHM
Israel: Jerusalem: NHM
Oman: Al Qabil, Wadi Jizzi: NHM

UAE: Abu Dhabi, Das Island, Hatta, Jebel Ali Hotel, Jebel Dhana, Wadi Bih: NHM

***Halictus (Tytthalictus) asperulus* Perez, 1895**

Synonyms: *Halictus rugulosus_homonym* Pérez, 1895

Israel: Nr. Bet Shean, Kefar Masaryik: AMNH

***Halictus (Tytthalictus) maculatus* Smith, 1848**

Synonyms: *Halictus interruptus_homonym* Lepeletier, 1841; *Halictus (Halictus) maculatus priesneri* Ebmer, 1975

Iran: Saraain: AMNH

Israel: Mt. Hermon: NHM

***Halictus (Vestitohalictus) cupidus* Vachal, 1902**

Synonyms: *Seladonia (Vestitohalictus) cupida* (Vachal, 1902)

Egypt: Wadi Digla: AMNH

Israel: Eiliat, Ein Bokek, Enot Zuqim Reserve, Jericho (Wadi Qelt), nr. Massada, Wadi N'Aqev: AMNH & NHM

***Halictus (Vestitohalictus) pici* Perez, 1895**

Egypt: Wadi Digla: AMNH

Oman: Dhofar (S. N. Road): NHM

UAE: Abu Dhabi, Al Ain: NHM

Yemen: El' Asr, Sana'a: NHM

***Halictus (Vestitohalictus) pici falx* ??**

UAE: Al-Ajban, Wadi Shawkah: CAWE, DEI, UAEIC

***Lasioglossum (Ctenonomia) denselineatum* (Cockerell, 1945)**

Synonym: *Halictus denselineatus* Cockerell, 1945

Yemen: Usaifira: NHM

***Lasioglossum (Ctenonomia) gibber* (Vachal, 1892)**

Synonym: *Halictus gibber* Vachal, 1892; *Halictus duplopunctatus* Cockerell, 1945; *Lasioglossum (Ctenonomia) duplopunctatum* (Cockerell, 1945)

Egypt: Aswan, Luxor: AMNH & NHM

Israel: Ein Gedi, En Tamar, En Zeelim, nr. Qumeran, Yotvata: AMNH & NHM

Oman: Rostaq, Sohar: NHM

Saudi Arabia: Riyadh: NHM

UAE: Al Ain, Al-Ajban, Asimah, Bithnah, Dhaid, Hatta, Khor Fakkan, Wadi Shawkah: NHM

***Lasioglossum (Ctenonomia) vagans* (Smith, 1857)**

Synonym: *Halictus vagans* Smith, 1857; *Halictus cattulus* Vachal, 1895; *Halictus cattulus var peguanus* Vachal, 1895; *Halictus buddha* Cameron, 1897; *Halictus vishnu* Cameron, 1897; *Halictus philippinensis* Ashmead, 1904; *Halictus matheranensis* Cameron, 1907; *Halictus emergendus* Cameron, 1908; *Halictus luteitarsellus* Strand, 1910; *Halictus micado* Strand, 1910; *Halictus nasicensis* Cockerell, 1911; *Halictus perhumilis* Cockerell, 1911; *Halictus statialis* Cockerell, 1911; *Halictus centrophorus* Strand, 1913; *Halictus nalandicus* Strand, 1913; *Halictus blepharophorus* Strand, 1913; *Halictus javanicus* Friese, 1914; *Halictus schmiedeknechti* Friese, 1914; *Halictus philippinensis var nigritarsellus* Cockerell, 1919; *Halictus*

chaldaeorum Morice, 1921; *Halictus (Evylaeus) semivagans* Cockerell, 1937; *Lasioglossum xerophilinum* Cockerell, 1945
Egypt: Abo Aref nr. Suez, 60 km S of Alexandria, Luxor, Siwa: AMNH & NHM
Oman: Rostaq: NHM
UAE: Al Ain, Hatta: NHM

Lasioglossum (Ctenonomia) vagans chalaeorum??
UAE: Sharjah Khor Kalba: CAWE, DEI & UAEIC

***Lasioglossum (Dialictus) chlorophaenum* Ebmer, 2008**
Synonym: *Lasioglossum (Evylaeus) chlorophaenum*
UAE: Sharjah Desert Park, Wadi Maidaq: CAWE, DEI, UAEIC

***Lasioglossum (Dialictus) enslini* Ebmer, 1972**
Synonyms: *Lasioglossum (Evylaeus) enslini* Ebmer, 1972
Israel: Hurfeish, Mt. Hermon, Zaura: AMNH & NHM

***Lasioglossum (Dialictus) ituraeum* Ebmer, 1972**
Israel: Hurfeish: AMNH

***Lasioglossum (Dialictus) leptocephalum* (Bluthgen, 1923)]**
Synonyms: *Halictus leptocephalus* Blüthgen, 1923; *Halictus kruegeri* Blüthgen, 1930; *Lasioglossum (Evylaeus) leptocephalum sinaiticum* Bytinski-Salz and Ebmer, 1974
Israel: Dunes Nizzanim: AMNH

***Lasioglossum (Dialictus) pseudolittorale* (Bluthgen, 1923)**
Israel: Netanya, Tel Aviv: AMNH

***Lasioglossum (Dialictus) soror* (Saunders, 1901)**
Synonyms: *Halictus soror* Saunders, 1901; *Halictus atrovirens* Pérez, 1903; *Halictus atrovirens livius* Warncke, 1982; *Halictus morio elatus* Warncke, 1975; *Lasioglossum (Evylaeus) morio elatum* (Warncke, 1975)
Israel: Hurfeish, Ramat Ha Nadiv: AMNH

***Lasioglossum (Dialictus_sensu_lato) kappadokium* Ebmer, 1974**
Yemen: Jebel Jihaf: NHM

***Lasioglossum (Evylaeus_sensu_lato) carneiventre* (Dours, 1872)**
Synonyms: *Halictus carnei-ventris* Dours, 1872; *Halictus carneiventris* Dours, 1872
Egypt: Abo Aref nr. Suez, Mariut: AMNH
Israel: Nr. Zohar Junction, Wadi En Agrabbim: AMNH

***Lasioglossum (Evylaeus_sensu_lato) dathei* Ebmer, 2008**
UAE: Wadi Maidaq, Wadi Safad, Wadi Wurayah: CAWE, DEI, NHML, UAEIC

***Lasioglossum (Evylaeus_sensu_lato) glabriusculum* (Morawitz, 1872)**
Synonyms: *Halictus glabriusculus* Morawitz, 1872; *Halictus leucopygus* Perez, 1903; *Halictus truncates_homonym* Alfken, 1905; *Halictus ultraparvus* Cockerell, 1938; *Lasioglossum (Evylaeus) politum aramaeum* Ebmer, 1974
Jordan: Amman: NHM

***Lasioglossum (Evylaeus_sensu_lato) mandibulare* Morawitz, 1866**

Synonyms: *Hylaeus mandibularis* Morawitz, 1866; *Halictus mandibularis* (Morawitz, 1866)
Egypt: Faiyum: NHM
Iran: Jajarm: NHM

***Lasioglossum (Evylaeus_sensu_lato) marginatum* (Brulle, 1832)**

Synonyms: *Halictus marginatus* Brullé, 1832; *Halictus fasciatellus* Schenck, 1869; *Halictus gribodoi* Kriechbaumer, 1873; *Halictus riparius* Morawitz, 1874; *Halictus vulgaris* Morawitz, 1876; *Halictus kervilleanus* Pérez, 1911
Israel: Daliyat El-Karmil, Mt. Carmel, Mt. Hermon: AMNH

***Lasioglossum (Evylaeus_sensu_lato) politum* (Schenck, 1853)**

Synonyms: *Hylaeus politus* Schenck, 1853; *Halictus politus* (Schenck, 1853); *Halictus atomarius* Morawitz, 1876; *Halictus pekingensis* Bluthgen, 1925; *Lasioglossum politum aramaeum* Ebmer, 1974
Israel: Bet Oren, Eshtaol, Jericho (Wadi Qelt), Jerusalem, nr. Modi'in, Peza' El, Rehovot, nr. Shoresh Junction, Tel Aviv, Tiberius: AMNH & NHM
Jordan: Adjlun, Amman: NHM

***Lasioglossum (Hemihalictus) ablenum* (Bluthgen, 1934)**

Oman: Rostaq
UAE: Asimah, Fagsha, Hatta, Khor Fakkan, Nr. Mahafiz, Sharjah Desert Park, Wadi Maidaq, Wadi Safad, Wadi Shawkah, Wadi Wurayah: CAWE, DEI, NHM, UAEIC
Yemen: El' Asr

***Lasioglossum (Hemihalictus) clypeiferellum* (Strand, 1909)**

Synonyms: *Halictus clypeiferellus* Strand, 1909; *Lasioglossum (Dialictus) clypeiferellum* (Strand, 1909); *Halictus testaceohirtulus* Blüthgen, 1929;
Israel: Daliyat El Karmil, Mt. Carmel: AMNH

***Lasioglossum (Hemihalictus) crassepunctatum* (Bluthgen, 1923)**

Synonyms: *Halictus crassepunctatus* Blüthgen, 1923; *Lasioglossum (Dialictus) crassepunctatum* (Blüthgen, 1923)
Israel: Nr. Zomet: AMNH

***Lasioglossum (Hemihalictus) diluculum* Ebmer, 2008**

Synonym: *Lasioglossum (Evylaeus) diluculum* Ebmer, 2008; *Lasioglossum (Dialictus) diluculum* Ebmer, 2008
UAE: Sharjah Desert Park: DEI

***Lasioglossum (Hemihalictus) flavoscapus* Ebmer, 2008**

Synonym: *Lasioglossum (Evylaeus) flavoscapus* Ebmer, 2008; *Lasioglossum (Dialictus) flavoscapus* Ebmer, 2008
UAE: Al-Ajban: CAWE, DEI, NHML

***Lasioglossum (Hemihalictus) griseolum* (Morawitz, 1872)**

Synonym: *Halictus griseolus* Morawitz, 1872; *Halictus labrosus_homonym* Vachal, 1895; *Halictus misellus* Perez, 1903; *Halictus dubitabilis* Saunders, 1904; *Halictus musculus* Bluthgen, 1924; *Halictus (Evylaeus) asnicus* Cockerell, 1937; *Lasioglossum (Dialictus) griseolum* (Morawitz, 1872)
Saudi Arabia: Taif: NHM
Yemen: El' Asr: NHM

***Lasioglossum (Hemihalictus) leptorhynchum* (Bluthgen, 1931)**
Synonym: *Halictus leptorhynchus* Bluthgen, 1931; *Lasioglossum (Dialictus) leptorhynchum* (Bluthgen, 1931)
UAE: Wadi Dibba, Wadi Maidaq, Wadi Safad, Wadi Shawkah, Wadi Wurayah

***Lasioglossum (Hemihalictus) limbellum* (Morawitz, 1876)**
Synonym: *Halictus limbellus* Morawitz, 1876; *Halictus ventralis* Perez, 1903; *Halictus gibbulus* Perez, 1903; *Halictus combinatus* Bluthgen, 1921; *Halictus limbellus var dongarica* Bluthgen, 1934; *Halictus (Evylaeus) rufulocinctus* Cockerell, 1937; *Halictus (Evylaeus) frigescens* Cockerell, 1938; *Lasioglossum (Dialictus) limbellum* (Morawitz, 1876)
Saudi Arabia: Riyadh: NHM

***Lasioglossum (Hemihalictus) mesosclerum* (Perez, 1903)**
Synonyms: *Halictus mesosclerus* Pérez, 1903; *Halictus rhodosianus* Strand, 1909; *Lasioglossum (Evylaeus) balneorum* Ebmer, 1974; *Halictus bubulcus* Warncke, 1982; *Lasioglossum (Dialictus) mesosclerum* (Pérez, 1903)
Egypt: Abo Aref nr. Suez: AMNH
Israel: Nr. Qumeran: AMNH

***Lasioglossum (Hemihalictus) minutissimum* (Kirby, 1802)**
Synonyms: *Melitta minutissima* Kirby, 1802; *Lasioglossum (Dialictus) minutissimum* (Kirby, 1802); *Halictus minutissimus* (Kirby, 1802); *Hylaeus exilis* Schenck, 1861; *Halictus hollandi* Saunders, 1904; *Halictus costiferellus* Strand, 1909; *Halictus kosensis* Strand, 1909; *Halictus xanthosensis* Strand, 1909; *Halictus arnoldi* Saunders, 1910; *Halictus (Evylaeus) lucidellus* Cockerell, 1937; *Halictus lilliput* Benoist, 1961;
Egypt: Mariut: AMNH
Israel: Tiberius: AMNH
Jordan: Amman: NHM
Yemen: El' Asr, Jebel Jihaf, Sana'a, Usaifira, Wadi Dhar: NHM

***Lasioglossum (Hemihalictus) nitidiusculum* (Kirby, 1802)**
Synonyms: *Evylaeus nitidiusculus* (Kirby, 1802); *Melitta nitidiuscula* Kirby, 1802; *Halictus nitidiusculus* (Kirby, 1802); *Lasioglossum (Dialictus) nitidiusculum* (Kirby, 1802); *Hylaeus rugulosus* Schenck, 1853; *Hylaeus pusillus* Schenck, 1853; *Halictus nitidulus_homonym* Pérez, 1903; *Halictus pseudocombinatus* Blüthgen, 1921; *Lasioglossum (Dialictus) nitidiusculum pseudocombinatum* (Blüthgen, 1921)
Iran: Hamadan: AMNH

***Lasioglossum (Hemihalictus) persicum* Cockerell, 1919**

Synonym: *Halictus persicus* Cockerell, 1919; *Lasioglossum (Dialictus) persicum* (Cockerell, 1919)
Yemen: Ghaiman nr. Sana'a: NHM

***Lasioglossum (Hemihalictus) sphecodimorphum* (Vachal, 1892)**

Synonyms: *Halictus sphecodimorphus* Vachal, 1892; *Lasioglossum (Dialictus) sphecodimorphum* (Vachal, 1892); *Halictus caelebs* Bluthgen, 1924; *Halictus coelebs* Bluthgen, 1924
Lebanon: Tripoli: NHM

***Lasioglossum (Hemihalictus) transitorium* (Schenck, 1870)**

Synonyms: *Halictus transitorius* Schenck, 1870; *Lasioglossum (Dialictus) transitorium* (Schenck, 1870) *Halictus planulus* Perez, 1903; *Lasioglossum (Evylaeus) transitorium planulum* (Perez, 1903); *Halictus uncinus* Vachal, 1905; *Lasioglossum (Evylaeus) transitorium uncium* (Vachal, 1905); *Halictus tunicol;a* Strand, 1909; *Halictus lentinicus* Strand, 1921
Israel: Ein Gedi, Haifa, Jericho (Hisham Palace), Peza' el, Shezaf Nature Preserve, Wadi Qelt, Zohar Junction: AMNH & NHM
Jordan: Amman: NHM

***Lasioglossum (Hemihalictus) truncaticolle* (Morawitz, 1877)**

Synonyms: *Halictus truncaticollis* Morawitz, 1877; *Lasioglossum (Dialictus) truncaticolle* (Morawitz, 1877); *Halictus brevithorax* Pérez, 1903; *Halictus blidahensis* Strand, 1909; *Halictus sudaghensis* Strand, 1909
Iran: Nr. Qazvin: AMNH

***Lasioglossum (Hemihalictus) villosulum* (Kirby, 1802)**

Synonym: *Melitta villosula* Kirby, 1802; *Melitta punctulata* Kirby, 1802; *Halictus villosulus* (Kirby, 1802); *Lasioglossum (Dialictus) villosulum* (Kirby, 1802); *Halictus hirtellus* Schenck, 1870; *Halictus medinai* Vachal, 1895; *Halictus pauperatulellus* Strand, 1909; *Halictus melanomitratus var mitratolus* Strand, 1914; *Halictus trichopsis* Strand, 1914; *Lasioglossum villosulum trichopse* (Strand, 1914); *Halictus barkensis* Bluthgen, 1930; *Halictus villosulopsis* Bluthgen, 1926; *Halictus pahanganus* Bluthgen, 1928; *Lasioglossum (Evylaeus) pahanganum* (Bluthgen, 1928); *Halictus villosulus perlautus* Cockerell, 1938; *Halictus (Evylaeus) rufotegularis* Cockerell, 1938; *Halictus villiersi* Benoist, 1941; *Halictus berberus* Benoist, 1941; *Lasioglossum (Evylaeus) villosulum arabicum* Ebmer, 2008
Jordan: Amman: NHM
Oman: Rostaq, Wadi Quryat: NHM
UAE: Al Ain, Asimah, Hatta, Sharjah Desert Park, Sharjah Khor Kalba, Wadi Maidaq, Wadi Shawkah
Yemen: Jebel Jihaf, Sana'a: NMM

***Lasioglossum (Lasioglossum) bicallosum* (Morawitz, 1874)**

Synonyms: *Halictus bicallosus* Morawitz, 1874; *Lasioglossum (Pallhalictus) bicallosum* (Morawitz, 1874); *Halictus dmitrijewi* Morawitz, 1891;
Israel: Hurfeish: AMNH

***Lasioglossum (Lasioglossum) caspicum* (Morawitz, 1874)**
Synonyms: *Halictus caspicus* Morawitz, 1874; *Lasioglossum (Pallhalictus) caspicum* (Morawitz, 1874); *Halictus emesianus* Pérez, 1911
Israel: Bet Oren, Daliyat El-Karmil, Har Gillo

***Lasioglossum (Lasioglossum) cribrum* Ebmer, 2008**
UAE: Wadi Wurayah: CAvH

***Lasioglossum (Lasioglossum) cristula* (Perez, 1895)**
Synonyms: *Halictus cristula* Pérez, 1895; *Lasioglossum (Pallhalictus) cristula* (Pérez, 1895); *Halictus mesoleus* Cockerell, 1938; *Halictus cristula donatus* Warncke, 1975
Israel: Nr. Zomet: AMNH

***Lasioglossum (Leuchalictus) callizonium* (Perez, 1895)**
Synonyms: *Halictus callizonius* Pérez, 1895; *Lasioglossum (Lasioglossum) callizonium* (Pérez, 1895); *Halictus (Curtisapis) mogadoricus* Cockerell, 1937;
Egypt: 60 km S of Alexandria, Luxor: AMNH

***Lasioglossum (Leuchalictus) discum* (Smith, 1853)**
Synonyms: *Halictus discus* Smith, 1853; *Lasioglossum (Lasioglossum) discum* (Smith, 1853); *Halictus morbillosus* Kriechbaumer, 1873; *Halictus fertoni* Vachal, 1895; *Lasioglossum discum fertoni* (Vachal, 1895); *Halictus morbillosus race glasunovi* Cockerell, 1924; *Lasioglossum pseudomorbillosum* Ebmer, 1970; *Lasioglossum aegyptiellum dalmaticum* Ebmer, 1970; *Lasioglossum (Leuchalictus) discum dalmaticum* Ebmer, 1970
Iran: Gilan, Sari: NHM

***Lasioglossum (Leuchalictus) leucozonium* (Schrank, 1781)**
Synonyms: *Lasioglossum (Lasioglossum) leucozonium* (Schrank, 1781); *Apis leucozonia* Schrank, 1781; *Apis leucostoma* Schrank, 1781; *Halictus similis* Smith, 1853; *Halictus bifasciatellus* Schenck, 1875; *Halictus leucozonius var nigrotibialis* Dalla Torre, 1877; *Halictus deiphobus* Bingham, 1908; *Halictus satschauensis* Blüthgen, 1934; *Lasioglossum (Lasioglossum) satschauense* (Blüthgen, 1934); *Halictus leucozonius clusium* Warncke, 1975; *Lasioglossum (Lasioglossum) leucozonium cedri* Ebmer, 1976; *Lasioglossum (Lasioglossum) satschauense mandschuricum* Ebmer, 1978
Iran: Hamadan: AMNH
Israel: Ma'agan Mikha'el, nr. Qumeran, Tel Aviv: AMNH

***Lasioglossum (Sphecodogastra) anellum* (Vachal, 1923)**
Synonyms: *Halictus anellus* Vachal, 1905; *Lasioglossum (Evylaeus) anellum* (Vachal, 1905); *Evylaeus anellus* (Vachal, 1905)

Israel: Nr. Bet Shean, Eshtaol, Hurfeish, Jericho (Wadi Qelt), Kefar Masaryik, Zomet: AMNH & NHM

***Lasioglossum (Sphecodogastra) articulare* (Perez, 1895)**

Synonym: *Halictus articularis* Perez, 1895; *Lasioglossum (Evylaeus) articulare* (Perez, 1895); *Evylaeus articulare* (Perez, 1895)

Israel: Elat: AMNH

UAE: Jebel Jibir, Wadi Wurayah: CAWE, DEI, NHML, UAEIC

***Lasioglossum (Sphecodogastra) damascenum* (Perez, 1911)**

Synonyms: *Halictus damascenus* Pérez, 1911; *Lasioglossum (Evylaeus) damascenum* (Pérez, 1911); *Evylaeus damascenus* (Pérez, 1911); *Halictus semitomentosus* Blüthgen, 1923

Iran: Kermanshahan: AMNH

Israel: Har Gillo: AMNH

***Lasioglossum (Sphecodogastra) elbanum* (Bluthgen, 1934)**

Synonym: *Halictus elbanus* Bluthgen, 1934; *Lasioglossum (Evylaeus) elbanum* (Bluthgen, 1934); *Evylaeus elbanus* (Bluthgen, 1934)

Oman: Rostaq: NHM

***Lasioglossum (Sphecodogastra) imbecillum* Ebmer, 1974**

Synonyms: *Lasioglossum (Evylaeus) imbecillum* Ebmer, 1974; *Halictus caprimulgus* Warncke, 1975

Israel: Peza ʻel (Jordan Valley): AMNH

Jordan: Amman: NHM

***Lasioglossum (Sphecodogastra) laticeps* (Schenck, 1870)**

Synonyms: *Hylaeus affinis_homonym* Schenck, 1853; *Hylaeus nigricornis* Schenck, 1853; *Evylaeus laticeps* (Schenck, 1870); *Halictus laticeps* Schenck, 1870; *Halictus hellenicus* Bluthgen, 1937; *Halictus laticeps atticus* Bluthgen, 1937; *Lasioglossum (Evylaeus) laticeps hellenicum* (Bluthgen, 1937)

Israel: Bet Oren, Eshtaol, Hula Reserve, Hurfeish, Maale Gilboa, Peza ʻel (Jordan Valley): AMNH & NHM

Lebanon: Baalbek: NHM

***Lasioglossum (Sphecodogastra) lineare* (Schenck, 1870)**

Synonyms: *Halictus linearis* Schenck, 1870; *Evylaeus linearis* (Schenck, 1870); *Lasioglossum (Evylaeus) lineare* (Schenck, 1870); *Halictus longuloides* Strand, 1909; *Halictus smyrnae* Strand, 1909; *Halictus aeginus* Strand, 1921

Iran: Kermanshahan: AMNH

Israel: Daliyat El-Karmil, Har Gillo, Hurfeish, Maale Gilboa, Peza ʻel (Jordan Valley): AMNH

***Lasioglossum (Sphecodogastra) malachurum* (Kirby, 1802)**

Synonyms: *Evylaeus malachurus* (Kirby, 1802); *Halictus malachurus* (Kirby, 1802); *Lasioglossum (Evylaeus) malachurum* (Kirby, 1802); *Melitta malachura* Kirby, 1802; *Halictus longulus* Smith, 1848; *Hylaeus apicalis* Schenck, 1853; *Hylaeus coriarius* Schenck, 1853; *Halictus malachuroides*

Strand, 1909; *Halictus malachurus sharificus* Cockerell, 1937; *Lasioglossum (Evylaeus) malachurum sharificum* (Cockerell, 1937)
Israel: Bat Shelomo, Bet Oren, Daliyat El-Karmil, Jerusalem, Ma'agan Mikha'el, Mt. Carmel, Strand Nasholim, Tel Aviv, Tiberius, Ze'elim: AMNH & NHM
Lebanon: Amioun: NHM

***Lasioglossum (Sphecodogastra) masculum* (Perez, 1895)**
Synonyms: *Halictus masculus* Pérez, 1895; *Halictus mozabensis* Pérez, 1895; *Lasioglossum (Evylaeus) masculum* (Pérez, 1895); *Evylaeus masculus* (Pérez, 1895); *Halictus leucopymatus var numidus* Blüthgen, 1924
Israel: Arava Valley, Wadi N'Aqev, nr. Yeroham: AMNH

***Lasioglossum (Sphecodogastra) mediterraneum* (Bluthgen, 1925)**
Iran: Gilan: NHM
Israel: Mt. Hermon, Tiberius: NHM

***Lasioglossum (Sphecodogastra) mose* Ebmer, 1974**
Synonyms: *Lasioglossum (Evylaeus) mose* Ebmer, 1974
Israel: Eiliat: AMNH
UAE: Hayl, Dibba, Nr. Al-Dhaid, Wadi Maidaq, Wadi Safad, Wadi Shawkah: NHM

***Lasioglossum (Sphecodogastra) nigripes* (Lepeletier, 1841)**
Synonyms: *Halictus nigripes* Lepeletier, 1841; *Lasioglossum (Evylaeus) nigripes* (Lepeletier, 1841); *Evylaeus nigripes* (Lepeletier, 1841); *Halictus cylindricus var orientalis_homonym* Magretti, 1890; *Lasioglossum (Evylaeus) nigripes pharaone* (Strand, 1909); *Halictus syriacus* Pérez, 1911
Israel: Har Gillo: AMNH
Iran: Karaj: AMNH

***Lasioglossum (Sphecodogastra) pauxillum* (Schenck, 1853)**
Hylaeus pauxillus Schenck, 1853; *Halictus pauxillus* (Schenck, 1853); *Lasioglossum (Evylaeus) pauxillum* (Schenck, 1853); *Evylaeus pauxillus* (Schenck, 1853)
Israel: Nr. Zomet: AMNH

***Lasioglossum (Sphecodogastra) pseudosphecodimorphum* (Bluthgen, 1923)**
Synonyms: *Evylaeus pseudosphecodimorphus* (Bluthgen, 1923); *Halictus pseudosphecodimorphus* Bluthgen, 1923; *Lasioglossum (Evylaeus) pseudosphecodimorphum* (Bluthgen, 1923)
Israel: Bet Oren, Har Gillo, Maale Gilboa, Mt. Carmel, Mt. Hermon: AMNH & NHM
Jordan: Amman

***Sphecodes albilabris* (Fabricius, 1793)**
Synonyms: *Nomada albilabris* Fabricius, 1793; *Dichroa fuscipennis* Germar, 1819; *Sphecodes latreillei* Wesmael, 1835; *Sphecodes rubripes* Spinola, 1838; *Sphecodes albilabris rubripes* Spinola, 1838; *Sphecodes africanus* Lepeletier, 1841; *Sphecodes nigripes* Lepeletier, 1841; *Sphecodes*

rugosus Smith, 1848; *Sphecodes nodicornis* Gistel, 1857; *Sphecodes fuscipennis var basalis* Dalla Torre, 1877; *Sabulicola cirsii* Verhoeff, 1890; *Sphecodes grandis* Meyer, 1922; *Sphecodes rufipennis* Cockerell, 1931; *Sphecodes atrescens* Cockerell, 1931
Etay El Baraud: AMNH

***Sphecodes dathei* Schwarz, 2010**
UAE: Wadi Shawkah

Sphecodes divieri
Qatar: Al Shahaniyeh: NHM

***Sphecodes* aff. *hirtellus* Bluthgen, 1923**
UAE: Bithnah: DEI

***Sphecodes longuloides* Bluthgen, 1923**
UAE: Khor Fakkan, Sharjah Desert Park: DEI, UAEIC

***Sphecodes marginatus* Hagens, 1882**
UAE: Dubai, Fagsha, Hatta: NHM

***Sphecodes miniatus* Hagens, 1882**
UAE: Hatta: NHM

***Sphecodes olivieri* Lepeletier & Audinet-Serville, 1825**
Synonym: *Sphecodes collaris* Spinola, 1843; *Sphecodes hispanicus var abyssinicus* Sichel, 1865; *Sphecodes ruficornis* Sichel, 1865; *Sphecodes punctulatus* Sichel, 1865; *Sphecodes subpunctulatus* Sichel, 1865; *Sphecodes rufithorax* Morawitz, 1876; *Sphecodes verticalis* Hagens, 1882; *Sphecodes desertus* Nurse, 1903; *Sphecodes chionospilus* Cockerell, 1911; *Sphecodes tenuis* Meyer, 1920
Egypt: Alexandra, Faiyum, Kom Ushim: AMNH
UAE: Abu Dhabi, Bithnah, Digdaga, Dubai, Hatta, Jebel Ali Hotel: NHM

***Sphecodes pinguiculus* Perez, 1903**
Synonym: *Sphecodes sareptensis* Meyer, 1922; *Sphecodes excellens* Meyer, 1922; *Sphecodes punctatissimus* Meyer, 1922; *Sphecodes coelebs* Bluthgen, 1923; *Sphecodes consobrinus* Bluthgen, 1923; *Sphecodes persicus* Bluthgen, 1925; *Sphecodes capverdensis* Pauly & LaRoche, 2002
UAE: Dubai:

***Sphecodes puncticeps* Thomson, 1870**
Synonym: *Sphecodes bituberculatus* Perez, 1903; *Sphecodes opacifrons* Perez, 1903; *Sphecodes puncticeps var cretanus* Strand, 1921
UAE: Abu Dhabi, Al Ain, Hatta, Jebel Ali Hotel, Remah: NHM

***Sphecodes ruficrus* (Erichson, 1835)**
Synonyms: *Dichroa ruficrus* Erichson, 1835; *Sphecodes hispanicus* Wesmael, 1835; *Sphecodes rufipes* Smith, 1853; *Sphecodes hispanicus_homonym* Hagens, 1882; *Sphecodes gibbus var tunetanus* Gribodo, 1894; *Sphecodes ruficrus piceohirtus* Blüthgen, 1958
Egypt: Between Ityai El-Barud and Shoprakhet: AMNH

***Sphecodes villosulus* Schwarz, 2010**

UAE: Dubai:

Family: Melittidae

Subfamily: Dasypodainae
Tribe: Dasypodaini
Dasypoda (Dasypoda) albipila **Spinola, 1838**
Oman: Dhofar (Qara Hills), Rostaq: NHM
Saudi Arabia: Riyadh: NHM
UAE: Al Ain: NHM
Dasypoda altercator **(Harris, 1780)**
Egypt: Wadi El Natrum: OUMNH
Dasypoda (Dasypoda) hirtipes **(Fabricius, 1793)**
Synonyms: *Andrena hirtipes* Fabricius, 1793; *Andrena hirta_homonym* Fabricius, 1793; *Podasys hirtipes* (Fabricius, 1793); *Dasypoda plumipes* Panzer, 1797; *Melitta swammerdamella* Kirby, 1802; *Dasypoda villosa* Lepeletier, 1841; *Dasypoda nemoralis* Bar, 1853; *Dasypoda palleola* Bar, 1853; *Dasypoda hirtipes var minor* Morawitz, 1874; *Dasypoda plumipes var nigrescens* Friese, 1901; *Dasypoda plumipes var flavescens* Friese, 1901
UAE: Sharjah Desert Park
Dasypoda sinuata **Perez, 1895**
Synonyms: *Dasypoda hirtipes canariensis* Warncke, 1973
Egypt: Ismailia: SCU
Eremaphanta iranica **Schwammberger, 1971**
Synonym: *Eremaphanta (Eremaphanta) iranica* Schwammberger, 1971
UAE: Nr. Al-Dhaid, Wadi Wurayah: CAWE, DEI, UAEIC
Tribe: Promelittini
Promelitta alboclypeata **(Friese, 1900)**
Synonym: *Dufourea alboclypeata* Friese, 1900; *Melitta (Promelitta) alboclypeata* (Warncke, 1977)
UAE: Wadi Maidaq, Wadi Shawkah
Subfamily: Melittinae
Melitta (Melitta) leporina **(Panzer, 1799)**
Synonyms: *Apis leporina* Panzer, 1799; *Andrena fortipes* Imhoff, 1832; *Cilissa ruthenica* Radoszkowski, 1891; *Melitta centaureae* Torka, 1922; *Melitta leporina var nigrinotum* Alfken, 1927; *Melitta sinkiangensis* Wu, 1978
Iran: Saraain: AMNH
Melitta (Melitta) schmiedeknechtii **Friese, 1898**
Synonyms: *Melitta schmiedeknechti tunensis* Warncke, 1973
Israel: Nr. Qumran, nr. Shizzafon Junction, Wadi Qelt: AMNH

Family: Megachilidae

Subfamily: Fideliinae
Tribe: Pararhophitini
Pararhophites quadratus **(Friese, 1898)**
Synonyms: *Rhophites (Pararhophites) quadratus* Friese, 1898

Egypt: Nr. Suez: AMNH

Subfamily: Megachilinae

Tribe: Lithurgini

***Lithurgus atratus* Smith, 1853**

Oman: Dhofar (Salalah): NHM

***Lithurgus chrysurus* Fonscolombe, 1834**

Synonyms: *Lithurgus analis* Lepeletier, 1841; *Lithurgus haemorrhoidalis* Lepeletier, 1841; *Lithurgus chrysurus var siculus* Pérez, 1897; *Lithurgus sublaevis* Pérez, 1897; *Lithurgus (Lithurgus) chrysurus siculus* Pérez, 1897

Egypt: Ityai El Barud: AMNH

***Lithurgus cornutus* (Fabricius, 1787)**

Synonyms: *Andrena cornuta* Fabricius, 1787; *Apis (Andrena) cornuta* (Fabricius, 1787); *Lasius cornuta* (Fabricius, 1787); *Lithurgus (Lithurgus) cornutus* (Fabricius, 1787); *Lithurgus umbraculatus* Lepeletier, 1841; *Lithurgus fuscipennis* Lepeletier, 1841; *Lithurgus (Lithurgus) cornutus fuscipennis* Lepeletier, 1841; *Lithurgus nasutus* Dufour, 1849; *Megachile monoceros* Eversmann, 1852; *Megachile dohrni* Radoszkowski, 1862; *Lithurgus maximus* Radoszkowski, 1871; *Lithurgus cornutus var obscurus* Cockerell, 1931

Iran: Bandar Pahlavi, Sarein: AMNH

***Lithurgus tibialis* Morawitz, 1875**

Pseudosmia tibiodentata Radoszkowski, 1888; *Lithurgus (Lithurgus) tibialis* Morawitz, 1875

UAE: Hatta, Masafi Village: NHM

Tribe: Osmiini

***Chelostoma (Foveosmia) bytinskii* (Mavromoustakis, 1948)**

Israel: Mt. Carmel, Upper Galilee (between Menara and Yitfah): AMNH & NHM

***Chelostoma (Foveosmia) isabellinum* (Warncke, 1991)**

Israel: Mt. Carmel: NHM

***Chelostoma (Foveosmia) schlettereri* (Friese, 1899)**

Synonyms: *Osmia schlettereri* Friese, 1899

Israel: Tiberius: NHM

***Chelostoma (Gyrodromella) rapunculi* (Lepeletier, 1841)**

Synonyms: *Apis fuliginosa_homonym* Panzer, 1798; *Heriades rapunculi* Lepeletier, 1841; *Heriades nigricornis* Nylander, 1848; *Chelostoma inerme* Eversmann, 1852; *Heriades casularum* Chevier, 1872; *Chelostoma proximum* Schletterer, 1889; *Eriades proximus* (Schletterer, 1889); *Chelostoma (Gyrodromella) proximum* Schletterer, 1889; *Osmia (Acanthosmia) archanensis* Cockerell, 1928; *Osmia (Acanthosmia) platyodonta* Cockerell, 1928; *Heriades confusa* Benoist, 1934; *Chelostoma (Gyrodromella) confusum* (Benoist, 1934)

Israel: Har Gillo: AMNH

***Haetosmia circumventa* (Peters, 1974)**

Synonyms: *Osmia (Haetosmia) circumventa* Peters, 1974
Egypt: Tel El Kebir: AMNH
UAE: Nr. Mahafiz, Sharjah Desert Park

Heriades (Heriades) crenulatus **Nylander, 1856**
Lebanon: Al Montazah nr. Mansourieh: OUMNH

Heriades (Heriades) rubicolus **Perez, 1890**
Lebanon: Al Montazah nr. Mansourieh, Deir Mar Maroun, Niha: OUMNH

Heriades (Heriades) truncorum **Linnaeus, 1758**
Synonyms: *Apis truncorum* Linnaeus, 1758; *Apis xanthogastria* Schrank, 1802; *Heriades sinuata* Spinola, 1808; *Osmia punctatissima* Lepeletier, 1841; *Heriades mordax* Schletterer, 1889
Israel: Jerusalem, Tel Aviv: AMNH & NHM
Lebanon: Deir Mar Maroun: NHM

Hoplitis (Alcidamea) acuticornis **(Dufour & Perris, 1840)**
Synonyms: *Osmia acuticornis* Dufour and Perris, 1840; *Osmia dentiventris* Morawitz, 1877; *Osmia (Acanthosmia) hispanica* Schmiedeknecht, 1885; *Osmia acuticornis brunneipes* Peters, 1975
Israel: Nr. Shoresh Junction: AMNH

Hoplitis (Alcidamea) alexandrina **(Warncke, 1991)**
UAE: Jebel Jibir, Wadi Maidaq: CAM, DEI, SEMC, UAEIC

Hoplitis (Alcidamea) hofferi **Tkalcu, 1977**
Israel: Wadi Amatzya: AMNH
Syria: Palmyra: NHM
UAE: Dibba, Jebel Hafit: NHM

Hoplitis (Alcidamea) limassolica **(Mavromoustakis, 1937)**
Oman: Rayy
UAE: Sweihan Road: NHM

Hoplitis (Annosmia) zonalis **(Perez, 1895)**
Israel: Ein Gedi, Nitzana: AMNH

Hoplitis (Anthocopa) bytinskii **(Mavromoustakis, 1948)**
Israel: Eshtaol, Wadi Qelt: NHM

Hoplitis (Anthocopa) batyamae **(van der Zanden, 1986)**
Egypt: Suez Canal University: AMNH
Israel: Nitzana: AMNH

Hoplitis (Anthocopa) cypriaca **(Mavromoustakis, 1938)**
Synonyms: *Osmia (Chalcosmia) cypriaca* Mavromoustakis, 1938
Israel: Modi'in: AMNH

Hoplitis (Anthocopa) daniana **(Mavromoustakis, 1949)**
Synonyms: *Osmia daniana* Mavromoustakis, 1949
Israel: Nr. Shoresh Junction: AMNH

Hoplitis (Anthocopa) hemisphaerica **(Alfken, 1935)**
Synonyms: *Osmia hemisphaerica* Alfken, 1935
Israel: Nr. Arad: AMNH

Hoplitis (Anthocopa) jerichoensis **(van der Zanden, 1996)**
Synonyms: *Anthocopa (Anthocopa) jerichoensis* van der Zanden, 1996

Israel: Wadi Qelt: NHM

***Hoplitis (Anthocopa) mocsaryi* (Friese, 1895)**

Synonyms: *Osmia moscaryi_sic* Friese, 1895; *Osmia mocsaryi* Friese, 1895

Israel: Belvoir Castle: AMNH

***Hoplitis (Anthocopa) wahrmani* (Mavromoustakis, 1948)**

Synonyms: *Osmia undulatum wahrmani* Mavromoustakis, 1948; *Anthocopa (Anthocopa) wahrmanni* (Mavromoustakis, 1948

Israel: Bat Yam, Rehovot: NHM

***Hoplitis (Hoplitis) adunca* (Panzer, 1798)**

Israel: Tiberius: NHM

***Hoplitis (Hoplitis) annulata* (Latreille, 1811)**

Synonyms: *Osmia annulata* Latreille, 1811; *Hoplitis (Annosmia) annulata* (Latreille, 1811); *Osmia crenulata_homonym* Morawitz, 1871; *Osmia (Annosmia) annulata crenulata* Morawitz, 1871; *Osmia pruinosa* De Stefani, 1887; *Osmia (Annosmia) annulata corsaria* Warncke, 1991;

Israel: Jericho (Hisham Palace), Tel Aviv: AMNH & NHM

***Hoplitis (Hoplitis) anthocopoides* (Schenck, 1853)**

Synonyms: *Osmia spinolae_homonym* Schenck, 1851; *Osmia anthocopoides* Schenck, 1853, replacement name; *Osmia caementaria* Gerstäcker, 1869; *Osmia clavipennis* Schenck, 1870; *Osmia hybrida* Pérez, 1879; *Osmia romana* Morice, 1901; *Fertonella algerica* Benoist, 1969; *Osmia anthocopoides perambigua* Peters, 1975

Jordan: Jerash: NHM

***Hoplitis (Hoplitis) carinata* Stanek, 1969**

Syria: Latakia: NHM

***Hoplitis (Hoplitis) christae* (Warncke, 1991)**

Synonyms: *Osmia (Annosmia) christae* Warncke, 1991; *Hoplitis (Annosmia) christae* (Warncke, 1991)

Israel: Wadi Sheizaf: AMNH

***Hoplitis (Hoplitis) erzurumensis* Tkalcu, 2000**

Israel: Har Gillo: AMNH

***Hoplitis (Hoplitis) fertoni* (Perez, 1891)**

Synonyms: *Osmia fertoni* Pérez, 1891; *Osmia albispina* Pérez, 1895; *Osmia mecheriana* Pérez, 1902

Israel: Nitzana: AMNH

***Hoplitis (Hoplitis) flabellifera* (Morice, 1901)**

Jordan: Below Salt, Jerash: NHM

***Hoplitis (Hoplitis) fortispina* (Perez, 1895)**

Synonyms: *Osmia fortispina* Pérez, 1895; *Osmia oreades* Benoist, 1934; *Osmia pectinifera* Benoist, 1934; *Hoplitis (Hoplitis) pectinifera* (Benoist, 1934); *Hoplitis (Hoplitis) oreades* (Benoist, 1934)

Jordan: Zai National Park: NHM

***Hoplitis (Hoplitis) hoggara* (Warncke, 1992)**

Synonyms: *Osmia (Hoplitis) hoggara* Warncke, 1992

Israel: Tiberius: NHM

***Hoplitis (Hoplitis) homalocera* Van der Zanden, 1991**

Israel: Jericho (Hisham Palace), Wadi Qelt: NHM

***Hoplitis (Hoplitis) improceros* van der Zanden, 1998**

Israel: Ein Gedi, Elat: AMNH

***Hoplitis (Hoplitis) jheringii* (Ducke, 1898)**

Synonyms: *Osmia jheringii* Ducke, 1898; *Osmia (Hoplitis) jheringii hirundo* Warncke, 1992; *Osmia (Hoplitis) jheringii urbica* Warncke, 1992

Israel: Tiberius: NHM

***Hoplitis (Hoplitis) mucida* (Dours, 1873)**

Synonyms: *Osmia mucida* Dours, 1873; *Osmia chobauti* Pérez, 1902; *Hoplitis (Hoplitis) mucida stecki* (Frey-Gessner, 1908); *Osmia mucida stecki* Frey-Gessner, 1908; *Osmia taorminaensis* Strand, 1917; *Osmia maroccana* Benoist, 1929;

Israel: Nitzana, Peza ‘el, Tiberius: AMNH & NHM

***Hoplitis (Hoplitis) pallicornis* (Friese, 1895)**

Israel: Daliyat El-Karmil, Eshtaol, Har Gillo, Merom Golan, Zaura: AMNH & NHM

Jordan: Jerash: NHM

***Hoplitis (Hoplitis) parana* (Warncke, 1991)**

Synonyms: *Osmia (Annosmia) parana* Warncke, 1991; *Hoplitis (Annosmia) parana* (Warncke, 1991)

Israel: Nr. Shizzafon Junction: AMNH

***Hoplitis (Hoplitis) ravouxi* (Perez, 1902)**

Israel: Tiberius: NHM

***Hoplitis (Pentadentosmia) helouanensis* (Friese, 1899)**

Synonyms: *Osmia helouanensis* Friese, 1899

Egypt: Cairo, Faiyum, Nuweiba, Suez, Wadi Digla, Wadi Rishrash, Wadi Watir: AMNH & OUMNH

Israel: Nr. Shizzafon Junction: AMNH

Saudi Arabia: Hadda Sham: NHM

UAE: Al Ain, Al Ajban, Al Saad, Jebel Ali Hotel, Sweihan Road: DEI, OUMNH, SEMC

***Hoplitis (Pentadentosmia) moricei* (Friese, 1899)**

UAE: Al Ain: SEMC

***Hoplitis (Pentadentosmia) ruficrus* (Morawitz, 1875)**

Israel: Nr. Shizzafon Junction: AMNH

***Hoplitis (Proteriades) semirubra* (Cockerell, 1898)**

Synonyms: *Heriades semirubra* Cockerell, 1898; *Proteriades (Proteriades) semirubra* (Cockerell, 1898)

Israel: Nr. Arad: AMNH

***Hoplitis (Stenosmia) flavicornis* (Morawitz, 1877)**

UAE: Liwa: NHM

***Hoplitis (Stenosmia) hartliebi* (Friese, 1899)**

Synonyms: *Osmia hartliebi* Friese, 1899; *Stenosmia hartliebi* (Friese, 1899)

Egypt: Suez: AMNH

***Hoplitis (Tkalcua) paralias* (Mavromoustakis, 1954)**

Synonyms: *Stenosmia paralias* (Mavromoustakis, 1954); Hoplitis (Microhoplitis_homonym) paralias (Mavromoustakis, 1954)
Israel: nr. Elat, nr. Zihor Junction: AMNH

***Ochreriades fasciata* (Friese, 1899)**
Synonyms: *Eriades fasciatus* Friese, 1899; *Ochreriades fasciatus* (Friese, 1899)
Jordan: Shuna: AMNH
Syria: Khabab, Umm es Charatite: AMNH & NHM

Osmia (Allosmia) lhotelleriei Perez, 1887
Synonyms: *Osmia fossoria* Perez, 1891; *Osmia (Allosmia) sybarita fossoria* Perez, 1891
Israel: Ashdod, Jerusalem, Netanya Iris Reserve, Nitzana, Peza 'el, Tel Aviv, Wadi Qelt: AMNH & NHM
Jordan: Below Salt: NHM
Syria: Latakia: NHM

***Osmia (Allosmia) rufohirta* Latreille, 1811**
Synonyms: *Osmia rufo-hirta* Latreille, 1811; *Osmia fulvo-hirta* Lepeletier, 1841; *Osmia fulvohirta* Lepeletier, 1841; *Osmia spiniventris* Giraud, 1857; *Osmia cognata_homonym* Pérez, 1895
Israel: Daliyat El Karmil, Mt Carmel: AMNH

***Osmia (Allosmia) rufotibialis* Friese, 1920**
Israel: Nr. Shoresh Junction: AMNH

***Osmia (Allosmia) sybarita* Smith, 1853**
Israel: Daliyat El-Karmil, Har Gillo, Wadi Loz: AMNH

***Osmia (Erythrosmia) andrenoides* Spinola, 1808**
Synonyms: *Pseudoosmia andrenoides* (Spinola*,* 1808)
Israel: Jerusalem: NHM

***Osmia (Hemiosmia) alfkenii* Ducke, 1899**
Synonyms: *Osmia (Melanosmia) alfkenii* Ducke, 1899; *Osmia niveibarbis* Pérez, 1902; *Osmia crinita* Alfken, 1942
Israel: Nr. Nitzana: AMNH
Jordan: Petra: NHM

***Osmia (Hemiosmia) balearica* Schmiedeknecht, 1885**
Synonyms: *Osmia (Helicosmia) balearica* Schmiedeknecht, 1886
Israel: Ashdod, nr. Haifa: AMNH & NHM

***Osmia (Helicosmia) alfkenii* Ducke, 1899**
Synonyms: *Osmia (Melanosmia) alfkenii* Ducke, 1899; *Osmia niveibarbis* Pérez, 1902; *Osmia crinita* Alfken, 1942
Israel: Ashdod, Ein Gedi: NHM

***Osmia (Helicosmia) dimidiata* Morawitz, 1870**
Iran: Bandar Pahlavi: AMNH

***Osmia (Helicosmia) dives* Mocsary, 1877**
Synonyms: *Osmia medanae* Magretti, 1890; *Osmia subintegra* Pérez, 1902; *Osmia (Helicosmia) sogdiana dives* Mocsáry, 1877; *Osmia hierosolomita* Benoist, 1934
Israel: nr. Haifa: AMNH

***Osmia (Helicosmia) fasciata* Latreille, 1811**

Israel: Arava Valley, nr. Nitzana, Qetura, nr. Shizzafon Junction: AMNH

Osmia (Helicosmia) frieseana **Ducke, 1899**

Israel: Jerusalem: NHM

Osmia (Helicosmia) latreillei **(Spinola, 1806)**

Synonyms: *Megachile latreillii_sic* Spinola, 1806; *Osmia nasidens* Latreille, 1811; *Osmia quadricornis* Kriechbaumer, 1869; *Osmia friesei* Verhoeff, 1892; *Osmia latreillei iberoafricana* Peters, 1975;

Egypt: Ismailia, Suez, Suez Canal University: AMNH & SCU

Israel: Ein Gedi, nr. Nitzana, Yeruham Reservoir: AMNH

Osmia (Helicosmia) melanogaster **Spinola, 1808**

Synonyms: *Osmia aterrima* Morawitz, 1872; *Osmia carniolica* Morawitz, 1872; *Osmia incerta* Radoszkowski, 1876; *Osmia subaenea* Pérez, 1895

Iran: Bandar Pahlavi, Saraain: AMNH

Israel: Jericho (Hisham Palace): NHM

Lebanon: Amioun: NHM

Osmia (Helicosmia) niveata **(Fabricius, 1804)**

Synonyms: *Apis fulviventris_homonym* Panzer, 1798; *Anthophora niveata* Fabricius, 1804; *Megachile niveata* (Fabricius, 1804); *Osmia minuta* Bramson, 1879; *Osmia sieversi* Morawitz, 1886; *Osmia carneiventris* Radoszkowski, 1887; *Osmia fulviventris var albiscopa_homonym* Alfken, 1914

Israel: Tiberius: NHM

Osmia (Helicosmia) notata **(Fabricius, 1804)**

Synonyms: *Anthophora notata* Fabricius, 1804; *Osmia decemsignata* Radoszkowski, 1874; *Osmia (Chalcosmia) laterefasciata* Costa, 1884

Egypt: Ismailia, Suez Canal University: AMNH & SCU

Osmia (Helicosmia) signata **Erichson, 1835**

Israel: Bet Oren, Eiliat, Jerusalem, Wadi Qelt, Zaura: AMNH & NHM

Jordan: Petra: NHM

Osmia (Hoplosmia) distinguenda **(Tkalcu, 1974)**

Israel: Bet Oren, Hurfeish: AMNH

Osmia (Hoplosmia) ligurica **Morawitz, 1868**

Synonyms: *Osmia ligurica* Morawitz, 1868; *Osmia detrita* Pérez, 1879

Israel: Tel Aviv: AMNH

Osmia (Hoplosmia) pinguis **Perez, 1895**

Synonyms: *Osmia pinguis* Pérez, 1895; *Osmia indivisa* Benoist, 1928; *Hoplosmia (Paranthocopa) pinguis carbo* van der Zanden, 1994

Israel: Netanya Iris Reserve, Nitzana, Peza ‘el, nr. Qumran, Sde Boker, Wadi Loz, nr. Yeroham: AMNH

Osmia (Hoplosmia) scutellaris **Morawitz, 1868**

Synonyms: *Osmia scutellaris* Morawitz, 1868; *Hoplosmia (Odontanthocopa) scutellaris* (Morawitz, 1868); *Heriades*

integra Benoist, 1934; *Stenoheriades integer* (Benoist, 1934); *Stenoheriades integra* (Benoist, 1934)
Israel: Nr. Shoresh Junction, Tel Aviv: AMNH

***Osmia (Hoplosmia) spinigera* Latreille, 1811**
Synonyms: *Osmia spinigera* Latreille, 1811; *Hoplosmia (Hoplosmia) spinigera* (Latreille, 1811); *Osmia clavicula* Gerstäcker, 1869
Israel: Bet Oren: AMNH

***Osmia (Melanosmia) melanota* Morawitz, 1888**
Egypt: Ein Khudra: NHM

***Osmia (Neosmia) gracilicornis* Perez, 1895**
Israel: Wadi Qelt: NHM

***Osmia (Neosmia) cinnabarina* Perez, 1895**
Israel: Nr. Nitzana: AMNH

***Osmia (Osmia) apicata* Smith, 1853**
Synonyms: *Osmia (Monosmia) apicata* Smith, 1853; *Osmia macroglossa* Gerstäcker, 1869
Israel: Jericho (Hisham Palace); Rosh ha'Ayin, Wadi Qelt: AMNH & NHM
Jordan: Jerash: NHM

***Osmia (Osmia) cornuta* (Latreille, 1805)**
Synonyms: *Megachile cornuta* Latreille, 1805; *Osmia divergens* Friese, 1920; *Osmia neoregaena* Mavromoustakis, 1938
Jordan: Petra: NHM

Osmia (Osmia) mustelina
Synonyms: *Osmia emarginata var griseohirta* Alfken, 1935; *Osmia mustelina umbrosa* Peters, 1978
Lebanon: Ain Zhalta: NHM

***Osmia (Pyrosmia) amathusica* Mavromoustakis, 1937**
Synonyms: *Osmia (Chalcosmia) amathusica* Mavromoustakis, 1937
Israel: Jericho (Hisham Palace), Nitzana, Wadi Qelt: AMNH & NHM
Syria: Latakia: NHM

***Osmia (Pyrosmia) avedata* Warncke, 1992**
Israel: Elat: AMNH

***Osmia (Pyrosmia) cephalotes* Morawitz, 1870**
Israel: Har Gillo, nr. Shoresh Junction, Tel Aviv: AMNH

***Osmia (Pyrosmia) cyanoxantha* Perez, 1879**
Synonyms: *Osmia cyanoxura* van der Zanden, 1991; *Osmia (Pyrosmia) elbaba* Warncke, 1992
Israel: Jerusalem, Shoresh Junction, Wadi Qelt: AMNH & NHM

***Osmia (Pyrosmia) ferruginea* Latreille, 1811**
Israel: Nr. Nitzana: AMNH

***Osmia (Pyrosmia) gallarum* Spinola, 1888**
Synonyms: *Osmia ruborum* Dufour and Perris, 1840; *Osmia lapidistructor* Ferton, 1921
Lebanon: Monteverde nr. Mansourieh: OUMNH

***Osmia (Pyrosmia) gemmea* Perez, 1895**

Synonyms: *Osmia purpurea_homonym* Pérez, 1895; *Osmia gemmea* Pérez, 1896

Israel: Nitzana: AMNH

***Osmia (Pyrosmia) laticella* Van der Zanden, 1986**

Egypt: Wadi Digla: OUMNH

Israel: Nr. Elat, Shezaf Nature Preserve, Wadi Shahak: AMNH

***Osmia (Pyrosmia) moreensis* van der Zanden, 1984**

Israel: Metulla, Tiberius: NHM

***Osmia (Pyrosmia) nana* Morawitz, 1874**

Synonyms: *Osmia tetrodonta* Benoist, 1934

Israel: Har Gillo, nr. Shoresh Junction, Tel Aviv: AMNH

***Osmia (Pyrosmia) saxicola* Warncke, 1988**

Synonyms: *Osmia caelestina* Benoist, 1934; *Osmia cypricola* Mavromoustakis, 1937; *Osmia (Chalcosmia) posti* Mavromoustakis, 1957

Israel: Mt. Hermon: AMNH

***Osmia (Pyrosmia) submicans* Morawitz, 1870**

Egypt: El Husseiniya, Gebel El Asfar, Ismailia, Suez Canal University, Tel El Kebir: AMNH & OUMNH

Israel: Ashdod, Ein Gedi, Jericho (Hisham Palace); Jerusalem, Tel Aviv: AMNH & NHM

***Osmia (Pyrosmia) versicolor* Latreille, 1811**

Synonyms: *Osmia corrusca* Erichson, 1835; *Megachile laeta_homonym* Gistel, 1857

Israel: Bet Oren: AMNH

***Osmia (Pyrosmia) viridana* Morawitz, 1874**

Synonyms: *Osmia rufispina* Morawitz, 1875; *Osmia angulata* Pérez, 1895; *Osmia (Chalcosmia) nicosiana* Mavromoustakis, 1939; *Osmia (Chalcosmia) viridana nicosiana* Mavromoustakis, 1939; *Osmia (Diceratosmia) viridana mulleolus* van der Zanden, 1984; *Osmia (Chalcosmia) viridana mulleolus* van der Zanden, 1984

Israel: Daliyat El-Karmil, Jerusalem, Eshtaol, Mt. Carmel, Upper Galilee (between Menara and Yiftah), Modi'in, Wadi Qelt: AMNH & NHM

***Protosmia (Chelostomopsis) longiceps* (Friese, 1899)**

Synonyms: *Eriades longiceps* Friese, 1899; *Heriades depauperata* Benoist, 1928

Israel: Mt. Carmel: NHM

***Protosmia (Protosmia) monstrosa* Perez, 1895**

Synonyms: *Osmia monstrosa* Pérez, 1895; *Osmia mirabilis* Friese, 1899; *Heriades limbata* Benoist, 1935; *Protosmia (Rhodosmia) limbata* (Benoist, 1935); *Protosmia (Protosmia) limbata* (Benoist, 1935); *Protosmia (Nanosmia) limbata* (Benoist, 1935)

Israel: Har Gillo, Jerusalem, Tiberius: AMNH & NHM

Jordan: Jerash: NHM

Lebanon: Amioun: NHM

Protosmia (Protosmia) paradoxa **(Friese, 1899)**
Synonyms: *Osmia paradoxa* Friese, 1899
Israel: nr. Shoresh Junction: AMNH
Jordan: Jerash, Zai National Park: NHM
Lebanon: Brummana, Nahr Al-Kalb: NHM

Protosmia (Protosmia) tiflensis **(Morawitz, 1876)**
Synonyms: *Osmia tiflensis* Morawitz, 1876; *Osmia (Acanthosmia) graeffei* Schmiedeknecht, 1890
Israel: Nr. Shoresh Junction: AMNH

Pseudoheriades grandiceps **Peters, 1988**
UAE: Al-Ajban, Wadi Safad: CAM, DEI, UAEIC

Pseudoheriades moricei **(Friese, 1897)**
Synonyms: *Eriades moricei* Friese, 1897
Israel: En Tamar: AMNH

Stenoheriades coelostoma **Benoist, 1935**
Israel: Mt. Carmel: NHM

Stenoheriades eingeddicus **Griswold, 1994**
Synonyms: *Stenoheriades eingeddicus* Griswold, 1994
Israel: Arava Valley: AMNH
Oman: Dhofar (Ayun Pools): NHM

Wainia (Caposmia) eremoplana **(Mavromoustakis, 1949)**
Synonyms: *Osmia eremoplana* Mavromoustakis, 1949; *Anthocopa (Anthocopa) eremoplana* (Mavromoustakis, 1949); *Anthocopa (Eremoplosmia) eremoplana* (Mavromoustakis, 1949)
Israel: Arava Valley, Nitzana: AMNH

Tribe: Anthidiini

Anthidium (Anthidium) bischoffi **Mavromoustakis, 1954**
Synonyms: *Anthidium bischoffi var hoggaricum* Mavromoustakis, 1954; *Anthidium bischoffi dzhachramicum* Popov, 1967
Israel: Nr. Qetura: AMNH
Egypt: Wadi Digla: AMNH

Anthidium (Anthidium) dalmaticum **Mocsary, 1884**
Israel: Har Meron: AMNH

Anthidium (Anthidium) echinatum **Klug, 1832**
Synonyms: *Anthidium (Echinanthidium) echinatum* Klug, 1832; *Anthidium rohlfsii* Friese, 1897
Egypt: Meadi, Serapeum: NHM

Anthidium (Anthidium) loti **Perris, 1852**
Synonyms: *Apis variegata_homonym* Fabricius, 1781; *Anthidium regulare* Eversmann, 1852; *Anthidium mosaicum* Costa, 1863; *Anthidium meridionale* Giraud, 1863; *Anthidium variegatum var meridionale* Giraud, 1863; *Anthidium (Anthidium) loti meridionale* Giraud, 1863; *Anthidium quadriseriatum* Kriechbaumer, 1873
Israel: Jerusalem: NHM

Anthidium (Anthidium) punctatum **Latreille, 1809**

Synonyms: *Anthidium minus* Nylander, 1848; *Anthidium senile* Eversmann, 1852; *Anthidium greyi* Radoszkowski, 1862; *Anthidium albidulum* Chevrier, 1872; *Anthidium nigrinum* Morawitz, 1875; *Anthidium nitidulum* Morawitz, 1893; *Anthidium mayeti* Pérez, 1895; *Anthidium punctatum var albofasciatum* Friese, 1897; *Anthidium punctatum var fulvipes_homonym* Friese, 1897; *Anthidium kohlii* Friese, 1897; *Anthidium punctatum var bequaerti* Alfken, 1914; *Anthidium punctatum bequaerti* Alfken, 1914; *Anthidium amanusense* Dusmet y Alonso, 1915; *Anthidium punctatum var ariasi* Dusmet y Alonso, 1915; *Anthidium kohli var nigritulum* Friese, 1917; *Anthidium punctatum var fulvipes_homonym* Kokujev, 1927; *Anthidium baicalense* Cockerell, 1928; *Anthidium punctatum zaidamense* Popov, 1948
Israel: Nr. Zomet: AMNH

***Anthidium (Anthidium) spiniventre* Friese, 1899**
Synonyms: *Anthidium spiniventris_sic* Friese, 1899; *Anthidium spiniventre var melanopygum* Friese, 1917
Israel: Nr. Jerusalem, Wadi Qelt: AMNH & NHM
Jordan: Below Salt, Wadi Shueib Dam: NHM

***Anthidium (Anthidium) taeniatum* Latreille, 1809**
Synonyms: *Anthidium fasciatum* Latreille, 1809; *Anthidium sulphureum* Lepeletier, 1841; *Anthidium affine* Morawitz, 1874; *Anthidium affine var monile* Friese, 1897; *Anthidium affine var nostrum* Radoszkowski, 1893; *Anthidium (Anthidium) frontevillosum* Pasteels, 1969
Iran: Divan Darreh: AMNH

***Anthidium (Anthidium) tesselatum* Klug, 1832**
Synonyms: *Anthidium helvolum* Klug, 1832; *Anthidium waltii* Spinola, 1838; *Anthidium villosulum* Smith, 1854; *Anthidium signiferum* Walker, 1871; *Anthidium tesselatum var aegyptiacum* Friese, 1897; *Anthidium lanitarse* Friese, 1917; *Anthidium lanitarse var lloydi* Mavromoustakis, 1936; *Anthidium lanitarse var zebra* Benoist, 1950
Egypt: Assiut, Wadi Hof: NHM
Israel: Wadi Qelt: NHM
Oman: Al Hamra, Behla, Dhofar (Ayun Pools), Masirah, Rostaq, Wadi Rafsah, Wadi Quryat: NHM
Saudi Arabia: Riyadh: NHM
UAE: Wadi Shawkah: NHM

***Anthidium (Gulanthidium) anguliventre* Morawitz, 1888**
Synonyms: *Anthidium (Gulanthidium) arabicum* Pasteels, 1969; *Anthidium (Gulanthidium) intermedium* Pasteels, 1969
Israel: Nr. Qetura: AMNH
Oman: Rostaq: NHM
Saudi Arabia: Riyadh: NHM

***Anthidium (Proanthidium) amabile* Alfken, 1932**
Synonyms: *Anthidium (Proanthidium) minimum* Pasteels, 1969

Egypt: Aswan: NHM
UAE: Fagsha, Wadi Madhah: NHM

***Anthidium (Proanthidium) undulatum* Dours, 1873**
Israel: Jerusalem: NHM
Lebanon: Deir Mar Maroun, Jdeide: OUMNH

***Eoanthidium (Eoanthidium) arabicum* Pasteels, 1980**
Oman: Rayy, Wadi Madha: NHM
UAE: Hatta, Wadi Bih: NHM

***Eoanthidium (Eoanthidium) bakerorum* Engel, 2004**
UAE: Al Hayl, Hatta: SEMC

***Eoanthidium (Eoanthidium) judaeense* (Mavromoustakis, 1945)**
Synonyms: *Dianthidium elongatum judaeense* Mavromoustakis, 1945; *Eoanthidium anale* Pasteels, 1969
Israel: Lubban: NHM

***Eoanthidium (Clistanthidium) nasicum* (Friese, 1917)**
Synonyms: *Anthidium nasicum* Friese, 1917; *Eoanthidium nasiculum* Pasteels, 1969
Israel: Arad: NHM

***Icteranthidium afrum* (Lepeletier, 1841)**
Oman: Ras al Khaimah: NHM
Saudi Arabia: Summan Plateau: NHM

***Icteranthidium decoloratum* Alfken, 1933**
Egypt: Faiyum: NHM

Icteranthidium discoidale
Synonym of I. ferrugineum?
UAE: Wadi Maidaq, Wadi Shawkah: DEI, UAEIC

***Icteranthidium ferrugineum* (Fabricius, 1787)**
Synonyms: *Apis ferruginea* Fabricius, 1787; *Anthidium ferrugineum* Fabricius, 1804; *Anthidium discoidale* Latreille, 1809; *Anthidium flavum* Latreille, 1809; *Anthidium thoracicum* Klug, 1832; *Anthidium cinctum* Klug, 1832; *Anthidium posticum* Klug, 1832; *Anthidium flavipes* Morawitz, 1895; *Anthidium ferrugineum var aegypticolum* Alfken, 1932; *Anthidium ferrugineum var subzonatum* Alfken, 1932; *Dianthidium ferrugineum subhyalinum* Mavromoustakis, 1948; *Icteranthidium bilobatum* Pasteels, 1969
Egypt: Faiyum, Gebel El Asfar, Giza, Meadi, Mersa Matruh, Minufiya: OUMNH & NHM
Oman: Al Wafi, Dhofar (Ayun Pools, S. N. Road), Khasab, Muscat (Seeb), Rayy, Tinaf, Wadi Quryat: NHM
Saudi Arabia: Asir Sabya, Jeddah, Riyadh: NHM
UAE: Al Ain, Fagsha, Hatta, Khor Fakkan, Wadi Bih, Wadi Uyaynah: OUMNH & NHM

***Icteranthidium grohmanni* (Spinola, 1838)**
Synonyms: *Anthidium numida* Lepeletier, 1841; *Anthidium latreillii* Lepeletier, 1841; *Anthidium provinciale* Lepeletier, 1841; *Anthidium rubiginosum* Lepeletier, 1841; *Anthidium comptum* Lepeletier, 1841; *Anthidium lepeletieri* Fonscolombe,

1846; *Anthidium coronatum_homonym* Smith, 1854; *Anthidium latreillei var obscurum* Dusmet y Alonso, 1908; *Icteranthidium tergale* Pasteels, 1969
Israel: Ein Gedi: AMNH

***Icteranthidium sinuatum* Pasteels, 1969 (invalid???)**
Oman: Rostaq, Wadi Quryat: NHM

***Pseudoanthidium (Exanthidium) enslini* (Alfken, 1928)**
Synonyms: *Anthidium enslini* Alfken, 1928
UAE: Fagsha: NHM

***Pseudoanthidium (Exanthidium) guichardi* (Pasteels, 1980)**
Oman: Dhofar (Qara Hills): NHM

***Pseudoanthidium (Pseudoanthidium) alpinum* (Morawitz, 1874)**
Synonyms: *Anthidium alpinum* Morawitz, 1874; *Anthidium barbatum* Mocsary, 1884; *Anthidium (Pseudoanthidium) alpinum* (Morawitz, 1874); *Anthidium serraticeps* Friese, 1917; *Pseudoanthidium alpinum gregoriense* Nobile, 1990
Israel: Palmachim: NHM

***Pseudoanthidium (Pseudoanthidium) ochrognathum* (Alfken, 1932)**
Synonyms: *Anthidium ochrognathum* Alfken, 1933; *Pseudoanthidium (Carinellum) ochrognathum* (Alfken, 1933); *Pseudoanthidium (Carinellium) rubellulum* Pasteels, 1969
Egypt: Gebel El Asfar: NHM
Israel: Hazeva, Palmachim: NHM
UAE: Abu Dhabi, Sharjah Desert Park, Sweihan Road: NHM

***Rhodanthidium (Rhodanthidium) septemdentatum* (Latreille, 1809)**
Lebanon: Monteverde nr. Mansourieh: OUMNH

***Stelis (Protostelis) signata* (Latreille, 1809)**
Synonyms: *Anthidium signatum* Latreille, 1809; *Anthidium parvulum* Lepeletier, 1841; *Stelis strigata* Kriechbaumer, 1874; *Stelis signata var flavescens* Friese, 1925; *Stelis signata eremica* Alfken, 1938; *Stelis (Pseudostelis) signata flavescens* (Friese, 1925)
Israel: Eshtaol, Lubban: NHM

***Stelis (Stelidomorpha) aegyptiaca* Radoszkowski, 1876**
Israel: Arad, Zihor Junction: AMNH & NHM
UAE: Wadi Maidaq: NHM

***Stelis (Stelidomorpha) nasuta* (Latreille, 1809)**
Synonyms: *Anthidium nasutum* Latreille, 1809; *Stelidomorpha nasuta* (Latreille, 1809)
Israel: Eiliat, Hula Reserve, Palmachim, Tiberius: AMNH
Oman: Tinaf: NHM

***Stelis (Stelis) murina* Perez, 1884**
Synonyms: *Stelis phaeoptera murina* Perez, 1884; *Stelis (Stelis) phaeoptera murina* Perez, 1884; *Stelis cassiopaea* Saunders, 1908; *Stelis murina cretica* Mavromoustakis, 1963
Egypt: Kom Oshim, Mariut: NHM

Tribe Dioxyini

***Dioxys cinctus* (Jurine, 1807)**

Synonyms: *Trachusa cincta* Jurine, 1807; *Dioxys cincta* (Jurine, 1807); *Dioxys pyrenaica* Lepeletier, 1841; *Dioxys maura* Lepeletier, 1841; *Dioxys cruenta* Gerstäcker, 1869; *Dioxys spinigera* Pérez, 1884; *Dioxys cincta var jucunda* Mocsáry, 1894; *Dioxys cincta ab friederikae* Mader, 1933

Israel: Peza ʻel (Jordan Valley): AMNH

***Ensliniana bidentata* (Friese, 1899)**

Synonyms: *Stelis bidentata* Friese, 1899; *Paradioxys pannonica var rufipes_homonym* Friese, 1899; *Dioxys richaensis* Friese, 1911; *Dioxys (Paradioxys) bidentata_homonym* Friese, 1924; *Ensliniana cuspidata* Alfken, 1938

Israel: Wadi Qelt: NHM

***Paradioxys pannonicus* (Mocsary, 1877)**

Synonyms: *Dioxys pannonica* Mocsáry, 1877; *Paradioxys pannonica* (Mocsáry, 1877)

Israel: Nr. Hazeva: AMNH

***Prodioxys carneus* (Gribodo, 1894)**

Synonyms: *Dioxys carnea* Gribodo, 1894; *Prodioxys carnea* (Gribodo, 1894); *Dioxys boghariensis* Pérez, 1902; *Megachile pyrsa* Vachal, 1910; *Prodioxys richardsi* Mavromoustakis, 1954

Israel: Nr. Yeroham: AMNH

Tribe: Megachilini

***Coelioxys (Allocoelioxys) afra* Lepeletier, 1841**

Israel: Eshtaol, Jerusalem, Lubban: NHM
Oman: Khasab, Sohar: NHM
Saudi Arabia: Hofuf: NHM

***Coelioxys (Allocoelioxys) coturnix* Perez, 1884**

Egypt: Suez Canal University, Tel El Kebir: AMNH
Saudi Arabia: Bahra: NHM

***Coelioxys (Allocoelioxys) emarginatellus* Pasteels, 1982**

Synonyms: *Coelioxys (Allocoelioxys) emarginatella* Pasteels, 1982

Israel: Iddan: AMNH
UAE: Al Ain, Bithnah, Hatta, Jebel Ali Hotel, Sweihan Road: DEI, UAEIC

***Coelioxys (Allocoelioxys) haemorrhoa* Forster, 1853**

Synonyms: *Coelioxys pulchella* Morawitz, 1874; *Coelioxys rhodacantha* Cockerell, 1931; *Coelioxys (Allocoelioxys) haemorrhoa rhodacantha* Cockerell, 1931

Iraq: Umm An-Ni'ajj: INHRCM

***Coelioxys (Liothyrapis) decipiens* Spinola, 1838**

Egypt: Dakhla Oasis, Faiyum, Minia, Tel El Kebir: AMNH & OUMNH

***Coelioxys (Rozeniana) rufescens* Lepeletier & Audinet-Serville, 1825**

Synonyms: *Coelioxys (Boreocoelioxys) rufescens* Lepeletier and Audinet-Serville, 1825; *Coelioxys umbrina* Smith, 1843; *Coelioxys hebescens* Nylander, 1848; *Coelioxys apiculata* Nylander, 1848; *Coelioxys trinacria* Förster, 1853; *Coelioxys diglypha* Förster, 1853; *Coelioxys carinata_homonym* Schenck, 1855; *Coelioxys longiuscula* Schenck, 1855; *Coelioxys obtusata_homonym* Schenck, 1855; *Coelioxys parvula* Schenck, 1855; *Coelioxys fallax* Mocsáry, 1881; *Coelioxys rufescens var agona* Alfken, 1912; *Coelioxys rufescens nigrescens* Cockerell, 1924; *Coelioxys rufescens var gigantea_homonym* Friese, 1925; *Coelioxys rufescens anatolica* Warncke, 1992
Iran: Saraain: AMNH

Coelioxys obtusa
Egypt: Gebel El Asfar
Saudi Arabia: Abu Arish

***Coelioxys indica* Friese, 1925**
UAE: Al-Ajban: DEI

***Coelioxys pruinosa* Smith, 1854**
Saudi Arabia: Taif: NHM

***Coelioxys puncticollissima* Friese, 1921**
Saudi Arabia: Abha: NHM
Yemen: Wadi Natid: NHM

***Megachile (Callomegachile) cephalotes* Smith, 1853**
UAE: Abu Dhabi, Jebel Ali Hotel: NHM

***Megachile (Callomegachile) simonyi* Friese, 1903**
Saudi Arabia: Abha, Wadi Majarish: NHM
Yemen: Ta'izz, Usaifira, Wadi Natid: NHM

***Megachile (Chalicodoma) albocristata* Smith, 1853**
Synonyms: *Megachile albo-cristata* Smith, 1853; *Chalicodoma (Allochalicodoma) albocristata* (Smith, 1853); *Megachile serrata* Smith, 1853; *Chalicodoma luctuosa* Dours, 1873; *Megachile luctuosa_homonym* (Dours, 1873); *Megachile lefeburei var tristis* Friese, 1898; *Chalicodoma (Chalicodoma) lefebvrei var* tristis (Friese, 1898)
Iran: Saraain: AMNH

***Megachile (Chalicodoma) atrocastanea* (Alfken, 1933)**
Israel: Hazeva: NHM

***Megachile (Chalicodoma) incerta* Radoszkowski, 1876**
Synonyms: *Megachile branicki* Radoszkowski, 1876
Egypt: Ein Khudra, Wadi Saal: NHM
Israel: Arava Valley, Eiliat, Ein Gedi, Shizzafon Junction, Wadi Ramon, Zafit Junction, Zihor Junction: AMNH & NHM
Bahrain: Manama: NHM

***Megachile (Chalicodoma) monstrifica* Morawitz, 1877**
Synonyms: *Chalicodoma (Chalicodoma) monstrifica* (Morawitz, 1877); *Megachile (Chalicodoma) monstrifica var* lebanotica Mavromoustakis, 1957
Israel: Bet Oren: AMNH

***Megachile (Chalicodoma) montenegrensis* Dours, 1873**
Synonyms: *Chalicodoma (Chalicodoma) montenegrense* (Dours, 1873); *Chalicodoma (Euchalicodoma) montenegrense* (Dours, 1873); *Megachile syraensis* Radoszkowski, 1874; *Chalicodoma (Euchalicodoma) asiatica* (Morawitz, 1875); *Megachile (Allomegachile) asiatica* Morawitz, 1875; *Chalicodoma ponticum* Alfken, 1933; *Megachile asiatica levantina* Hedicke, 1938; ; *Megachile (Chalicodoma) asiatica levantina* Hedicke, 1938
Israel: Nr. Telamim: AMNH

***Megachile (Chalicodoma) nigrita* Radoszkowski, 1876**
Synonyms: *Megachile aterrima_homonym* Pérez, 1895
Israel: Shizzafon Junction, Zihor Junction: AMNH

***Megachile (Chalicodoma) parietina* (Geoffroy, 1785)**
Israel: Nr. Shizzafon Junction, nr. Telamim: AMNH

***Megachile (Chalicodoma) sicula* (Rossi, 1792)**
Egypt: Alexandria Montaza, Ein Khudra, Meadi, Nawa: NHM
Israel: Ashdod, Eiliat, Jaffa, Shizzafon Junction, nr. Telamim: NHM
Jordan: Petra, Wadi Rum: NHM
Oman: Masirah: NHM

***Megachile (Creightonella) albisecta* (Klug, 1817)**
Synonyms: *Anthophora albisecta* Klug, 1817; *Creightonella (Metamegachile) albisecta* (Klug, 1817); *Megachile (Metamegachile) albisecta* (Klug, 1817); *Megachile sericans* Fonscolombe, 1832; *Megachile caucasica* Lepeletier, 1841; *Megachile dufourii* Lepeletier, 1841; *Megachile dufouri* Lepeletier, 1841, emend; *Megachile odontura* Smith, 1849; *Megachile carinulata* Costa, 1882; *Megachile sericans cyprica* Cockerell, 1931; *Megachile albisecta adlerbergi* Popov, 1936; *Megachile albisecta rufocincta* Hedicke, 1938; *Megachile cypricola* Mavromoustakis, 1938
Israel: Jaffa: NHM
Lebanon: Monteverde nr. Mansourieh: OUMNH

***Megachile (Creightonella) amabilis* Cockerell, 1933**
UAE: Hatta, Khor Fakkan: NHM, SEMC

***Megachile (Creightonella) arabica* Friese, 1901**
Oman: Dhofar (Ayun Pools): NHM
Saudi Arabia: Fayfa, Taif: NHM

***Megachile (Creightonella) felix* (Pasteels, 1979)**
Oman: Dhofar (S.N. Road): NHM

***Megachile (Eurymella) patellimana* Spinola, 1838**
Synonyms: *Megachile xanthopus* Gerstacker, 1857; *Megachile albescens* Smith, 1879; *Megachile (Eutricharaea) patellimana* Spinola, 1838
Egypt: Aswan: NHM
Israel: Jaffa: NHM
Oman: Sayh Huwayyah: NHM
Saudi Arabia: Abu Arish, Wadi Jowra: NHM

UAE: Abu Dhabi, Al-Ajban, Futaisi, Jebel Ali Hotel, Wadi Maidaq: NHM

***Megachile (Eutricharaea) anatolica* Rebmann, 1968**

Iran: Saraain: AMNH

***Megachile (Eutricharaea) apicalis* Spinola, 1808**

Synonyms: *Megachile mixta* Costa, 1863; *Megachile dimidiativentris* Dours, 1873; *Megachile massiliensis* Pérez, 1902; *Megachile virginiana* Mitchell, 1926
Iran: Bandar Pahlavi: AMNH
Lebanon: Jdeide, Monteverde nr. Mansourieh: OUMNH

***Megachile (Eutricharaea) concinna* Smith, 1879**

Synonyms: *Megachile multidens*
Egypt: Daqahlia, Ismailia, Kharga Oasis: OUMNH & SCU
Lebanon: Al Montazah nr. Mansourieh: OUMNH
UAE: Abu Dhabi, Al Ain, Hatta: OUMNH

***Megachile (Eutricharaea) deceptoria* Perez, 1890**

Oman: Sohar: NHM

***Megachile (Eutricharaea) inexspectata* Rebmann, 1968**

Lebanon: Al Montazah nr. Mansourieh: OUMNH

***Megachile (Eutricharaea) leachella* Curtis, 1828**

Synonyms: *Megachile dorsalis* Pérez, 1879; *Megachile (Eutricharaea) leachella dorsalis* Pérez, 1879; *Megachile argentata var fossoria_homonym* Ferton, 1909
Iran: Sarein: AMNH

***Megachile (Eutricharaea) leucostoma* Perez, 1907**

UAE: Bithnah, Hatta

***Megachile (Eutricharaea) levistriga* Alfken, 1934**

Israel: Ein Gedi: AMNH

***Megachile (Eutricharaea) malangensis* Friese, 1904**

Oman: Tinaf, Wadi Quryat: NHM

***Megachile (Eutricharaea) marginata* Smith, 1853**

Lebanon: Jdeide: OUMNH

***Megachile (Eutricharaea) minutissima* Radoszkowski, 1876**

Egypt: Assiut, Faiyum, Ismailia, Kharga Oasis, Luxor, Siwa, Suez Canal University, Tel El Kebir: AMNH, NHM & OUMNH
Israel: Nr. Zihor Junction: AMNH
Saudi Arabia: Qatif Oasis: NHM
UAE: Abu Dhabi, Dubai, Hatta, Jebel Ali Hotel, Shuwaib: NHM

***Megachile (Eutricharaea) rotundata* (Fabricius, 1787)**

Synonyms: *Apis rotundata* Fabricius, 1787
Lebanon: Deir Mar Maroun, Monteverde nr. Mansourieh: OUMNH

***Megachile (Eutricharaea) schmiedeknechti* Costa, 1884**

Lebanon: Monteverde nr. Mansourieh: OUMNH

***Megachile (Eutricharaea) striatella* Rebmann, 1968**

Iran: Bandar Pahlavi, Saraain: AMNH

***Megachile (Eutricharaea) submucida* Alfken, 1926**

Egypt: Siwa, Suez Canal University: AMNH

UAE: Abu Dhabi, Das Island, Dubai, Futaisi, Hatta, Jebel Ali Hotel, Khor Fakkan, Lulayyah, Remah: CAvH

***Megachile (Eutricharaea) ventrisi* Engel, 2008**

Yemen: Jebel Jihaf: NHM

***Megachile (Eutricharaea) walkeri* Dalla Torre, 1896**

Synonyms: *Megachile fulvescens_homonym* Walker, 1871; *Megachile walkeri* Dalla Torre, 1896; *Megachile argentata var moricei* Friese, 1899; *Megachile (Eutricharaea) blanda_homonym* Rebmann, 1968

UAE: Abu Dhabi, Al-Ajban, Bithnah, Wadi Maidaq, Wadi Shawkah, Wadi Wurayah: OUMNH

***Megachile (Megachile) centuncularis* (Linnaeus, 1758)**

Synonyms: *Apis centuncularis* Linnaeus, 1758; *Anthemois centuncularis* (Linnaeus, 1758); *Megalochila centuncularis* (Linnaeus, 1758); *Megachile parvula* Lepeletier, 1841; *Megachile infragilis* Cresson, 1878; *Anthemois infragilis* (Cresson, 1878); *Megachile appia* Nurse, 1903; *Megachile leoni* Titus, 1906; Perezia_homonym maura_homonym Ferton, 1914; *Fertonella maura_homonym* Ferton, 1914; *Megachile centuncularis nesiotica* Mavromoustakis, 1953

Iran: Bandar Pahlavi: AMNH

***Megachile (Megachile) pilicrus* Morawitz, 1877**

Iran: Bandar Pahlavi: AMNH

***Megachile (Pseudomegachile) cinnamomea* Alfken, 1926**

Synonyms: *Chalicodoma (Pseudomegachile) cinnamomeum* (Alfken, 1926)

Egypt: Tel El Kebir: AMNH

***Megachile (Pseudomegachile) flavipes* Spinola, 1838**

Synonyms: *Megachile (Archimegachile) flavipes* Spinola, 1838; *Megachile conficita* Walker, 1871; *Megachile despecta* Walker, 1871; *Megachile inficita* Walker, 1871; *Megachile squamigera* Mocsáry, 1879; *Megachile flavipes turcestanica* Friese, 1898; *Megachile flavipes var fasciata* Friese, 1898; *Chalicodoma (Pseudomegachile) flavipes* (Spinola, 1838); *Chalicodoma (Pseudomegachile) flavipes meridionalis* Pasteels, 1970

Egypt: Abo Aref nr. Suez, Cairo, Dakhla Oasis, Faiyum, Gebel El Asfar, Giza, Kharga Oasis, Minia, Suez Canal University, Tel El Kebir, Wadi Digla, Wadi Rishrash: AMNH & OUMNH

***Megachile (Pseudomegachile) incana* Friese, 1898**

Synonyms: *Megachile arlei* Benoist, 1943; *Chalicodoma (Parachalicodoma) incana* (Friese, 1898); *Megachile (Parachalicodoma) incana* Friese, 1898

Egypt: El Amarna: AMNH

***Megachile (Pseudomegachile) nigripes* Spinola, 1838**

Synonyms: *Chalicodoma (Pseudomegachile) nigripes* (Spinola, 1838); *Megachile nilotica* Perez, 1897; *Megachile mucorea* Friese, 1898

Egypt: Faiyum, Tel El Kebir: AMNH & OUMNH

Megachile (Pseudomegachile) rubripes **Morawitz, 1875**

Oman: Al Qabil, Rayy, Tinaf: NHM
Saudi Arabia: Riyadh: NHM
UAE: Abu Dhabi, Hatta: NHM

Megachile (Pseudomegachile) sanguinipes **Morawitz, 1875**

Lebanon: Deir Mar Maroun: OUMNH

Megachile (Pseudomegachile) transgrediens **Rebmann, 1970**

Lebanon: Wadi El Harir: NHM

Megachile (Xanthosarus) circumcincta **(Kirby, 1802)**

Iran: Saraain: AMNH

Megachile (Xanthosarus) fulvescens **Smith, 1853**

Egypt: St Katherine (Sinai): NHM

Megachile (Xanthosarus) maritima **(Kirby, 1802)**

Synonyms: *Apis maritima* Kirby, 1802; *Megachile flaviventris* Schenck, 1853; *Megachile kashgarensis* Cockerell, 1913; *Megachile maritima continentalis* Hedicke, 1938; *Megachile maritima yamadai* Yasumatsu, 1938
Iran: Saraain: AMNH

Megachile (Xanthosarus) willughbiella **(Kirby, 1802)**

Israel: Bet Oren: AMNH

Radoszkowskiana barrei **(Radoszkowski, 1893)**

Synonyms: *Paracoelioxys_homonym barrei* Radoszkowski, 1893; *Coelioxys barrei* (Radoszkowski, 1893); *Paracoelioxys rufiventris nursei* Cockerell, 1922
Iran: Rafsanjan: AMNH

Radoszkowskiana rufiventris **Spinola, 1838**

Synonyms: *Coelioxys rufiventris* Spinola, 1838; *Coelioxys (Radoszkowskiana) rufiventris* Spinola, 1838; *Megachile gymnopygia* Spinola, 1838; *Dioxys (Paradioxys) giovanelli* Biegeleben, 1932
Egypt: Assiut, Ezbet El Nakhl, Meadi, Tel El Kebir: AMNH & NHM

Family: Apidae

Subfamily: Xylocopinae

Tribe: Xylocopini

Xylocopa (Ctenoxylocopa) fenestrata **(Fabricius, 1798)**

Synonym: *Apis fenestrata* Fabricius, 1798; *Xylocopa lunata* Klug, 1807; *Xylocopa indica* Klug, 1807; *Xylocopa serripes* Burmeister, 1876; *Xylocopa gardineri* Cameron, 1902; *Xylocopa serripes_homonym* Hedicke, 1938; *Xylocopa hedickei* Maa, 1940, replacement name; *Xylocopa (Ctenoxylocopa) fenestrata mauritii* Maa, 1970
Iraq: Al Mada'in, Baghdad, Umm An-Ni'ajj: INHRCM
UAE: Al-Ajban, Sharjah-Khor Kalba: DEI, UAEIC

Xylocopa (Ctenoxylocopa) sulcatipes **Maa, 1970**

Israel: Jericho (Hisham Palace): NHM
UAE: Abu Dhabi, Al Ain: OUMNH

Xylocopa (Koptortosoma) aestuans **(Linnaeus, 1758)**
UAE: Nr. Mahafiz, Sharjah-Khor Kalba: DEI, UAEIC

Xylocopa (Koptortosoma) pubescens **Spinola, 1838**
Bahrain: Manama: NHM
Egypt: Abo Aref nr. Suez, Assiut, Aswan, Buhayrah, Faiyum, Suez Canal University, Suways: AMNH
Israel: Ma'agan Mikha'el: AMNH
Oman: Wadi Madbah: NHM
UAE: Abu Dhabi, Falaj al Mualla, Hatta, Lulayyah, Sweihan: NHM & OUMNH
Yemen: Sana'a: NHM

Xylocopa (Proxylocopa) olivieri **Lepeletier, 1841**
Synonyms: *Proxylocopa olivieri* (Lepeletier, 1841); *Xylocopa hellenica* Spinola, 1843; *Xylocopa fuscata* Smith, 1854; *Xylocopa lanata* Smith, 1854;
Iraq: Hinaidi: NHM
Israel: Har Gillo: AMNH
Jordan: Jerash: NHM
Lebanon: Ain Zhalta: NHM

Xylocopa (Xylocopa) valga **Gerstacker, 1872**
Synonyms: *Xylocopa ramulorum* Rondani, 1874; *Xylocopa convexa* Smith, 1878; *Xylocopa valga pyropyga* Friese, 1914
Iran: Saraain: AMNH

Xylocopa (Xylocopa) violacea **(Linnaeus, 1758)**
Synonyms: *Apis violacea* Linnaeus, 1758; *Apis insubrica* Müller, 1766, probable synonym; *Xylocopa femorata* Fabricius, 1804; *Xylocopa (Xylocopa) violacea ab* heteropennis Vicidomini, 2003
Iran: Bandar Pahlavi: AMNH
Israel: Har Gillo: AMNH

Tribe: Ceratinini

Ceratina (Ceratina) cucurbitina **(Rossi, 1792)**
Synonyms: *Apis cucurbitina* Rossi, 1792; *Hylaeus albilabris* Fabricius, 1793; *Ceratina decolorans* Brulle, 1832
Israel: Baram ruins, Bet Oren, Daliyat El-Karmil, Ein Sinya, Eshtaol, Har Gillo, Metula, Mt. Carmel: AMNH & NHM
Lebanon: Monteverde nr. Mansourieh, Tripoli: NHM & OUMNH

Ceratina (Dalyatina) aloes **Cockerell, 1932**
Egypt: Faiyum: AMNH

Ceratina (Dalyatina) parvula **Smith, 1854**
Synonyms: *Ceratina pygmaea* Lichtenstein, 1872; *Ceratina scintilla* Cockerell, 1931
Egypt: nr. Maadi, Wadi Digla: OUMNH
Israel: Ein Gedi, En Zeelim, Mezad Aqrabbim, nr. Qetura: AMNH
Lebanon: Ain Es Sayde: OUMNH
UAE: Wadi Shawkah: OUMNH

Ceratina (Euceratina) acuta **Friese, 1896**
Israel: Mt. Hermon: NHM

Ceratina (Euceratina) bifida **Friese, 1900**

Israel: Eshtaol, Lubban, Mt. Carmel, Rehovot: NHM

***Ceratina (Euceratina) chalcites* Germar, 1839**

Israel: Baram ruins, Lubban: NHM

***Ceratina (Euceratina) loewi* Gerstacker, 1869**

Israel: Wadi Qelt: NHM

***Ceratina (Euceratina) mandibularis* Friese, 1896**

Israel: Ein Sinya, Jerusalem, Jericho (Hisham Palace), Tiberius, Wadi Qelt: NHM
Lebanon: Ain Es Sayde, Monteverde nr. Mansourieh, Tripoli: NHM & OUMNH
Syria: Latakia: NHM

***Ceratina (Euceratina) moricei* Friese, 1899**

Synonyms: *Ceratina laevifrons var moricei* Friese, 1899
Israel: Jerusalem, Wadi Qelt: NHM

***Ceratina (Euceratina) neocallosa* Daly, 1983**

Egypt: Al Qasr, Faiyum, Gebel El Asfar, Kharga Oasis, Minia: OUMNH
Israel: Arad, Wadi Qelt: OUMNH

***Ceratina (Euceratina) tibialis* Morawitz, 1894**

Iran: Karaj: NHM

***Ceratina (Neoceratina) bispinosa* Handlirsch, 1889**

Egypt: Faiyum: NHM
Israel: Ashkelon, Bet Oren, Ein Sinya, Jericho, Jerusalem, Lubban, Ramat Gan, Rehovot, Rishon, Wadi Qelt: AMNH & NHM
Lebanon: Ain Es Sayde, Al Montazah nr. Mansourieh, Deir Mar Maroun, Monteverde nr. Mansourieh: NHM

***Ceratina (Neoceratina) nigra* Handlirsch, 1889**

Lebanon: Al Montazah nr. Mansourieh, Monteverde nr. Mansourieh: OUMNH

***Ceratina (Pithitis) arabiae* (Daly, 1983)**

Yemen: Sana’a: NHM

***Ceratina (Pithitis) citriphila* Cockerell, 1935**

Egypt: Abo Aref nr. Suez, Cairo, El Minya, Faiyum, Gebel El Asfar, Helwan, Luxor, Suez Canal University: AMNH, NHM & OUMNH
Saudi Arabia: Riyadh: NHM
Yemen: Sana’a, Ta’izz, Usaifira: NHM

***Ceratina (Pithitis) tarsata* Morawitz, 1872**

Synonyms: *Ceratina savignyi* Radoszkowski, 1876; *Ceratina caesia* Vachal, 1903
Egypt: Abo Aref nr. Suez, Cairo, El Ferdan, Faiyum, Gebel El Asfar, Giza, Helwan, Kharga Oasis, Minufiya, Qasr Qarum, Wadi El Natrum: AMNH, NHM & OUMNH
Oman: Al Qabil, Rostaq, Wadi Jizzi: NHM
Saudi Arabia: Abyan: NHM
UAE: Dibba, Fagsha, Hatta, Hayl, Jebel Ali Hotel, Khor Fakkan, Lulayyah, Masafi Village, Sharjah Desert Park, Wadi Madhah, Wadi Shawkah: NHM & OUMNH
Yemen: El’ Asr, Marib, Musaybir, Museimir, Usaifira: NHM

- **Tribe: Allodapini**
  - ***Exoneuridia (Exoneuridia) libanensis* (Friese, 1899)**
    - Synonyms: *Exoneura libanensis* Friese, 1899
    - Lebanon: Deir Mar Maroun: OUMNH

- **Subfamily: Nomadinae**
  - **Tribe: Nomadini**
    - ***Nomada agrestis* Fabricius, 1787**
      - Egypt: Etay El Baraud: AMNH
      - Iraq: Hinaidi: NHM
      - Israel: Daliyat El Karmil, Mt. Carmel, Tel Aviv, Wadi Qelt, Yeroham: AMNH & NHM
    - ***Nomada amabilis* Radoszkowski, 1876**
      - Israel: Jerusalem, Wadi Qelt: NHM
    - ***Nomada basalis* Herrich-Schaffer, 1839**
      - Israel: Daliyat El-Karmil: AMNH
    - ***Nomada bifasciata* Olivier, 1812**
      - Synonyms: *Nomada zonata_homonym* Lepeletier, 1841; *Nomada lepeletieri* Pérez, 1884; *Nomada pusilla_homonym* Pérez, 1884; *Nomada planiscuta* Saunders, 1908; *Nomada navasi* Dusmet y Alonso, 1913; *Nomada scutellata_homonym* Friese, 1921
      - Israel: Ashdod: NHM
    - ***Nomada caspia* Morawitz, 1894**
      - Synonyms: *Nomada graeca* Schwarz, 1967
      - Israel: Mt. Carmel: AMNH
    - ***Nomada cherkesiana* Mavromoustakis, 1955**
      - Israel: Tiberius: NHM
    - ***Nomada chrysopyga* Morawitz, 1871**
      - Synonyms: *Nomada mauritanica chrysopyga* Morawitz, 1871; *Nomada chrysopyga pyrosoma* Dours, 1873; *Nomada obburdinensis* Morawitz, 1875; *Nomada speciosissima* Schmiedeknecht, 1882; *Nomada nigrita_homonym* Pérez, 1895; *Nomada mamillaris* Pérez, 1895; *Nomada superba_homonym* Pérez, 1902; *Nomada scutellata_homonym* Saunders, 1908; *Nomada syriaca_homonym* Friese, 1921; *Nomada chrysopyga var pharaonis* Friese, 1921; *Nomada chrysopyga forma* umbripennis Alfken, 1924
      - Egypt: Meadi: NHM
    - ***Nomada cleopatra* Schwarz, 1989**
      - Synonyms: *Nomada (Nomadita) cleopatra* Schwarz, 1989
      - Egypt: Faiyum, Wadi Rishrash: NHM
    - ***Nomada distinguenda* Morawitz, 1874**
      - Synonyms: *Nomada rugithorax* Perez, 1902
      - Israel: Jericho (Hisham Palace), Wadi Qelt: NHM
      - Syria: Palmyra: NHM
    - ***Nomada eos* Schmiedeknecht, 1882**
      - Israel: Daliyat El-Karmil: AMNH

Nomada femoralis **Morawitz, 1869**
Israel: Daliyat El-Karmil: AMNH
Nomada fenestrata **Lepeletier, 1841**
Synonyms: *Nomada faventiana* Pérez, 1902; *Nomada ceballosi* Dusmet y Alonso, 1915; *Nomada affinis_homonym* Dusmet y Alonso, 1932; *Nomada rufopleurae* Schwarz, 1964
Egypt: Meadi: NHM
Israel: Shezaf Nature Preserve, Shizzafon Junction, nr. Yeroham: AMNH
Saudi Arabia: Riyadh: NHM
UAE: Ras al-Khaimah , Wadi Maidaq: NHM
Nomada flavinervis **Brulle, 1832**
Israel: Netanya: AMNH
Nomada flavoguttata **(Kirby, 1802)**
Synonyms: *Apis flavoguttata* Kirby, 1802; *Apis rufo-cincta* Kirby, 1802; *Apis rufocincta* Kirby, 1802; *Nomada minuta_homonym* Fabricius, 1804; *Nomada nana* Schenck, 1874; *Nomada pygmaea_homonym* Schenck, 1874; *Nomada flavoguttata var serotina* Schmiedeknecht, 1882; *Nomada flavoguttata var h*öppneri Alfken, 1898; *Nomada annexa* Nurse, 1904; *Nomada kurilensis* Yasumatsu, 1939; *Nomada flavoguttata japonensis* Tsuneki, 1973; *Nomada tridentata* Tsuneki, 1986
Israel: Mt. Carmel, Tiberius, Wadi Qelt: AMNH & NHM
Nomada fulvicornis **Fabricius, 1793**
UAE: Jebel Jibir: UAEIC
Nomada gribodoi **Schmiedeknecht, 1882**
Israel: Eshtaol, Jericho (Hisham Palace), Tiberius: NHM
Syria Latakia, Ugarit: NHM
Nomada guichardi **Schwarz, 1981**
Israel: Tiberius: NHM
Nomada guttulata **Schenck, 1861**
Israel: Daliyat El Karmil: AMNH
Nomada insignipes **Schmiedeknecht, 1882**
Israel: Tiberius: NHM
Nomada integra **Brulle, 1832**
Synonyms: *Nomada germanica_homonym* Fabricius, 1804; *Nomada ferruginata var cinctiventris* Friese, 1921; *Nomada cinctiventris nigra* Schwarz, 1967
Israel: Wadi Qelt: NHM
Nomada keroanensis **Perez, 1895**
Israel: Tiberius: NHM
Nomada limassolica **Mavromoustakis, 1955**
Synonyms: *Nomada flavinervis var limassolica* Mavromoustakis, 1955
Israel: Jerusalem: NHM
Nomada mandibularis **Schwarz & Gusenleitner, 2013**
Israel: Tiberius: NHM

Nomada mauritanica **Lepeletier, 1841**
Syonyms: *Nomada mephisto* Schmiedeknecht, 1882; *Nomada poultoni* Saunders, 1901; *Nomada beata* Nurse, 1903; *Nomada lynesi* Cockerell, 1933
Israel: Deir Al-Balah: NHM
UAE: Ras al-Khaimah: NHM

Nomada rhenana **Morawitz, 1872**
Synonyms: *Nomada rufipes_homonym* Schenck, 1870
Israel: Jericho (Hisham Palace), Wadi Qelt: NHM

Nomada rubiginosa **Perez, 1884**
Israel: Nr. Yeroham: AMNH

Nomada rubricollis **Schwarz, 1967**
Israel: Eshtaol, Jerusalem, Tiberius, Wadi Qelt: AMNH & NHM

Nomada sexfasciata **Panzer, 1799**
Synonyms: *Apis connexa* Kirby, 1802; *Apis schaefferella* Kirby, 1802: AMNH

Nomada zonata **Panzer, 1798**
Synonyms: *Nomada bofillana* Perez, 1913; *Nomada banatica* Zilahi-Kiss, 1915
Israel: Mt. Hermon: NHM

Tribe: Epeolini

Epeolus flavociliatus **Friese, 1899**
UAE: Sweihan: DEI

Tribe: Ammobatoidini

Ammobatoides abdominalis **(Eversmann, 1852)**
Synonyms: *Phileremus abdominalis* Eversmann, 1852; *Phileremus hirsutulus* Eversmann, 1852; *Phiarus abdominalis* (Eversmann, 1852); *Ammobates extraneus* Förster, 1855; *Ammobates rufitarsis* Smith, 1879; *Ammobatoides rufitarsis* (Smith, 1879); *Phiarus abdominalis var sanguinea* Friese, 1911; *Phiarus abdominalis var rufa* Friese, 1911; *Phiarus angarensis* Cockerell, 1928; *Ammobatoides abdominalis marchicus* Bischoff, 1952; *Ammobatoides lebanensis* Mavromoustakis, 1959
Israel: Merom Golan: AMNH

Tribe: Ammobatini

Ammobates (Ammobates) dubius **Benoist, 1961**
Synonyms: *Phileremus niveatus* Spinola, 1838; *Biastes niveatus* (Spinola, 1838)
Egypt: nr. Wadi El Natrum: OUMNH
Israel: Nr. Shizzafon Junction: NHM

Ammobates (Euphileremus) latitarsis **Friese, 1899**
Israel: Daliyat El-Karmil, Ein Sinya: AMNH & NHM
Jordan: Zai National Park: NHM

Ammobates (Euphileremus) oraniensis **(Lepeletier, 1841)**
Synonyms: *Pasites (Euphileremus) oraniensis melectoides* (Smith, 1854); *Phileremus melectoides* Smith, 1854; *Ammobates oraniensis var manni* Friese, 1895; *Ammobates oraniensis tenuicornis* Popov, 1951; *Pasites*

(Euphileremus) oraniensis tenuicornis (Popov, 1951); *Pasites (Euphileremus) oraniensis anatolicus* Warncke, 1983
Israel: Wadi Qelt: NHM

***Parammobatodes maroccanus* (Warncke, 1983)**
UAE: Shuwaib: SEMC, UAEIC

***Parammobatodes nuristanus* (Warncke, 1983)**
Israel: Nr. Shizzafon Junction: AMNH

***Pasites maculatus* Jurine, 1807**
Synonyms: *Nomada albomaculata* Lucas, 1849; *Pasites schottii* Eversmann, 1852; *Ammobates variegatus* Smith, 1854; *Phileremus rufiventris_homonym* Förster, 1855; *Phiarus maculatus var pusillus* Radoszkowski, 1872; *Pasites maculatus var aschabadensis* Radoszkowski, 1893; *Pasites maculatus var brunneus* Friese, 1895; *Pasites comptus* Alfken, 1929
Egypt: Between Ityai El-Barud and Shoprakhet: AMNH

Subfamily: Apinae

Tribe: Ancylini

***Ancyla orientalica* Warncke, 1979**
Israel: nr. Bet Shean: AMNH

***Tarsalia persica* (Warncke, 1979)**
Synonyms: *Ancyla (Tarsalia) persica* Warncke, 1979
Iran: Haft Tepe: NHM

Tribe: Eucerni

***Eucera (Eucera) thoracica* Spinola, 1838**
Israel: Nr. Kzi'ot: AMNH

***Eucera (Hetereucera) atricornis* Fabricius, 1793**
Iran: Gilan: NHM

***Eucera (Hetereucera) caerulescens* Friese, 1899**
Israel: Hurfeish: AMNH
Lebanon: Monteverde nr. Mansourieh, Salima (Mt. Lebanon): OUMNH

***Eucera (Hetereucera) clypeata* Erichson, 1835**
Synonyms: *Eucera (Stilbeucera) clypeata* Erichson, 1835; *Eucera punctilabris* Lepeletier, 1841; *Eucera coarctata* Eversmann, 1852; *Eucera medusa* Nurse, 1904
Israel: Mt. Carmel: NHM

***Eucera (Hetereucera) decipiens* Alfken, 1935**
Synonyms: *Eucera (Atopeucera) decipiens* Alfken, 1935
Israel: Eshtaol, nr. Haifa, Mt. Carmel: AMNH & NHM

***Eucera (Hetereucera) gaullei* Vachal, 1907**
Israel: Nr. Haifa: AMNH
Lebanon: Deir El Harf: OUMNH

***Eucera (Hetereucera) helvola* Klug, 1845**
Israel: Nr. Zomet: AMNH

***Eucera (Hetereucera) laxiscopa* Alfken, 1935**
Israel: Mt. Carmel, Zomet: AMNH & NHM
Lebanon: Al Montazah nr. Mansourieh, Mt. Lebanon Salima: OUMNH

Eucera (Hetereucera) moricei **Alfken, 1935**
Syria: Banias: OUMNH
Eucera (Hetereucera) nigripes **Klug, 1845**
Israel: Golan Heights: AMNH
Eucera (Hetereucera) nigrita **Friese, 1895**
Synonyms; *Eucera caspica var nigrita* Friese, 1895; *Eucera albofasciata* Friese, 1895; *Eucera (Pareucera) nigrita* Friese, 1895; *Eucera albofasciata var piceitricha* Strand, 1915
Jordan: Petra, Zai National Park: NHM
Eucera (Hetereucera) spatulata **Gribodo, 1894**
Synonyms: *Eucera (Atopeucera) spatulata* Gribodo, 1894
Jordan: Amman: NHM
Eucera (Hetereucera) squamosa **Lepeletier, 1841**
Synonyms: *Eucera rutila* Perez, 1895
Israel: Hurfeish: AMNH
Eucera (Hetereucera) sulamita **Vachal, 1907**
Jordan: Wadi El Mujib: NHM
Eucera (Hetereucera) vulpes **Brulle, 1832**
Synonyms: *Eucera parvula* Friese, 1896
Lebanon: Monteverde nr. Mansourieh, Salima (Mt. Lebanon): OUMNH
Eucera (Pteneucera) nigrifacies **Lepeletier, 1841**
Israel: Hurfeish: AMNH
Eucera (Synhalonia) hungarica **Friese, 1895**
Synonyms: *Eucera (Macrocera) hungarica* Friese, 1895
Jordan: Kerak, Petra: NHM
Syria: Aleppo: NHM
Eucera (Synhalonia) plumigera **Kohl, 1905**
Israel: Eshtaol: NHM
Lebanon: Nr. Cedar's Hotel: NHM
Eucera (Synhalonia) spectabilis **(Morawitz, 1875)**
Synonyms: *Tetralonia spectabilis* Morawitz, 1875; *Macrocera spectabilis* (Morawitz, 1875)
Israel: Jaffa, Mt. of Olives: NHM
Eucera (Synhalonia) velutina **(Morawitz, 1874)**
Synonyms: *Macrocera velutina* Morawitz, 1874
Iran: Gilan: NHM
Israel: Jericho (Hisham Palace), Sea of Galilee: AMNH & NHM
Jordan: Amman, Mt. Nebo, Petra: NHM
Eucera (Synhalonia) vernalis **(Morawitz, 1875)**
Synonyms: *Tetralonia vernalis* Morawitz, 1875
Iran: nr. Borujerd: AMNH
Eucera (Synhalonia) zeta **Torre, 1896**
Jordan: Kerak: NHM
Tetraloniella (Tetraloniella) blanda **(Walker, 1871)**
Saudi Arabia: Haddat ash Sham, Jeddah: NHM
Tetraloniella (Tetraloniella) decora **(Walker, 1871)**
Saudi Arabia: Abu Arish, Baish, Haddat ash Sham: NHM

Tribe: Anthophorini

Anthophora (Anthophora) aegyptiaca **(Dalla Torre & Friese, 1895)**

Synonyms: *Megilla aegyptiaca* Dalla Torre & Friese, 1895; *Podalirius aegyptiacus* (Dalla Torre & Friese, 1895)
Egypt: Nawa: NHM
Iraq: Baghdad: NHM
Israel: Wadi Qelt: NHM

Anthophora (Anthophora) biciliata **Lepeletier, 1841**

Israel: Jerusalem: NHM
Lebanon: Ain Zhalta, Mt. Lebanon Hazerta: NHM & OUMNH

Anthophora (Anthophora) canescens **Brullé, 1832**

Synonyms: *Anthophora canescens* Brullé,1832; *Anthophora nigro-cincta* Lepeletier,1841; *Anthophora nigrocincta* Lepeletier,1841; *Megilla lanata* Klug, 1845; *Podalirius lanatus* (Klug, 1845); *Anthophora senescens canescens_homonym* Dours, 1870; *Anthophora lati-cincta* Dours, 1870; *Anthophora laticincta* Dours, 1870; *Anthophora procera* Costa, 1883; *Anthophora subterranea procera* Costa, 1883; *Anthophora nigrocincta var procera* Costa, 1883; *Anthophora nigrocincta var flavescens_homonym* Gribodo, 1893; *Anthophora venerabilis* Cockerell, 1911;
Israel: Mt. of Olives: NHM

Anthophora (Anthophora) caroli **Perez, 1895**

Israel: Peza ‘el: AMNH

Anthophora (Anthophora) crinipes **Smith, 1854**

Israel: Ein Gedi, Har Gillo, Wadi Qelt: AMNH & NHM

Anthophora (Anthophora) fulvitarsis **Brulle, 1832**

Synonyms: *Megilla personata* Erichson, 1835; *Anthophora nasuta* Lepeletier, 1841; *Anthophora personata var euris* Dours, 1870; *Anthophora arietina* Dours, 1870
Israel: Arava Valley, Wadi Qelt: AMNH

Anthophora (Anthophora) plumipes **(Pallas, 1772)**

Israel: Ein Ha Shofet, Wadi Qelt: AMNH

Anthophora (Anthophora) senescens **Lepeletier, 1841**

Egypt: Meadi, Nawa: NHM
Israel: Ma’ale Aqrabbim, Ein Gedi, nr. Nitzana, Wadi Ramon: AMNH
Lebanon: Nr. Cedar’s Hotel: NHM

Anthophora (Caranthophora) dufourii **Lepeletier, 1841**

Iraq: Haj Omran: NHM
Israel: Eshtaol, Har Gillo, Ramat Hanadiv, Tiberius, Wadi Qelt: AMNH & NHM
Jordan: Jerash: NHM

Anthophora (Heliophila) fayoumensis **Priesner, 1957**

UAE: Wadi Maidaq: UAEIC

Anthophora (Lophanthophora) affinis **Brulle, 1832**

Synonyms: *Anthophora biciliata* Lepeletier, 1841; *Anthophora liturata* Lepeletier, 1841; *Anthophora asiatica var*

lusitanica Friese, 1919; *Anthophora morawitzi_homonym* Alfken, 1937
Israel: Bet Oren: AMNH

***Anthophora (Lophanthophora) agama* Radoszkowski, 1869**
Synonyms: *Anthophora stschurovskyi* Fedtschenko, 1875; *Anthophora kessleri* Fedtschenko, 1875
Israel: Jerusalem: NHM
Jordan: Amman: NHM
Lebanon: Ain Zhalta, Deir El Harf: NHM & OUMNH

***Anthophora (Lophanthophora) caelebs* Gribodo, 1924**
Israel: Ein Gedi, nr Zihor Junction: AMNH

***Anthophora (Lophanthophora) dispar* Lepeletier, 1841**
Synonyms: *Anthophora dispar var speciosa* Friese, 1919; *Anthophora dispar var niveohirta* Friese, 1922
Egypt: Mariut: NHM
Israel: Nr. Telamim: AMNH

***Anthophora (Lophanthophora) hispanica* (Fabricius, 1787)**
Synonyms: *Apis hispanica* Fabricius, 1787; *Anthophora grandis* Lepeletier, 1841; *Anthophora hispanica candidata* Gribodo, 1893; *Anthophora hispanica cyrenaica* Gribodo, 1924
Egypt: Mariut: NHM
Israel: Shizzafon Junction: AMNH
Jordan: Petra: NHM

***Anthophora (Lophanthophora) robusta* (Klug, 1845)**
Synonyms: *Megilla robusta* Klug, 1845; *Megilla caliginosa* Klug, 1845; *Anthophora nigromaculata* Lucas, 1849; *Anthophora oxygona* Dours, 1870; *Anthophora atro-ferruginea* Dours, 1870; *Anthophora atroferruginea* Dours, 1870; *Anthophora robusta var atra* Friese, 1919; *Anthophora robusta var atratula* Friese, 1919; *Anthophora robusta var atroscopacea* Friese, 1919; *Anthophora fuliginosa pamirica* Hedicke, 1931
Iran: Mt. Damavand: NHM
Lebanon: Nr. Cedar's Hotel: NHM

***Anthophora (Lophanthophora) rutilans* Dours, 1870**
Synonyms: *Anthophora moderna* Morawitz, 1877
Israel: Daliyat El Karmil, University of Galilee: AMNH

***Anthophora (Melea) plagiata* (Illiger, 1806)**
Synonyms: *Apis parietina_homonym* Fabricius, 1793; *Megilla plagiata* Illiger, 1806; *Anthophora parietina var fulvo-cinerea* Dours, 1870; *Anthophora parietina var fulvocinerea* Dours, 1870; *Anthophora turanica* Fedtschenko, 1875; *Anthophora parietina var schenkii* Dalla Torre, 1877; *Anthophora simplicipes* Morawitz, 1880; *Anthophora mlokosewitzi* Radoszkowski, 1884; *Anthophora nigripes_homonym* Morawitz, 1887; *Podalirius simplicipes var semiater* Friese, 1896; *Anthophora pulcherrima* Bingham, 1897; *Podalirius parietinus var nigrescens* Friese,

1897; *Anthophora filchnerae* Friese, 1908; *Anthophora khambana* Cockerell, 1910; *Anthophora khambana var atramentata* Cockerell, 1911; *Anthophora pilosella* Friese, 1919; *Anthophora semenovi* Kuznetzov-Ugamsky, 1927; *Anthophora parietina pamiricola* Hedicke, 1931; *Anthophora khambana f chodjana* Hedicke, 1938; *Anthophora parietina baltistanica* Hedicke, 1940; *Anthophora parietina ladakhana* Hedicke, 1940; *Anthophora pulcherrima himalayaensis* Wu, 1982
Iran: Saraain: AMNH

***Anthophora (Paramegilla) armata* Friese, 1905**
Yemen: Dhala: NHM

***Anthophora (Paramegilla) erubescens* Morawitz, 1880**
Synonyms: *Anthophora carnea* Gribodo, 1894
Egypt: Meadi: NHM

***Anthophora (Paramegilla) semirufa* (Friese, 1898)**
Synonyms: *Podalirius semirufus* Friese, 1898; *Anthophora fulviscopa* Alfken, 1930
Israel: Ein Bokek: NHM
Oman: Muscat (Ruwi), Wadi Rafsah: NHM
Saudi Arabia: Riyadh: NHM
UAE: Dibba: NHM
Yemen: Aden: NHM

***Anthophora (Paramegilla) valga* (Klug, 1845)**
Saudi Arabia: Jeddah: NHM

***Anthophora (Paramegilla) vidua* (Klug, 1845)**
Synonyms: *Megilla vidua* Klug, 1845; *Anthophora boops* Alfken, 1926; *Anthophora fumipennis_homonym* Alfken, 1926
Egypt: Cairo, Gebel El Asfar: NHM
Saudi Arabia: Summan Plateau: NHM

***Anthophora (Petalosternon) extricata* Priesner, 1957**
UAE: Hatta: NHM

***Anthophora (Petalosternon) priesneri* Alfken, 1932**
Oman: Dhofar (Qara Hills), Rostaq: NHM
Saudi Arabia: Abha, Taif: NHM
UAE: Asimah, Dibba, Fagsha, Hatta, Khor Fakkan, Wadi Bih, Wadi Sidr: NHM
Yemen: Aden, Sana'a: NHM

***Anthophora (Petalosternon) rivolleti* Perez, 1895**
Synonyms: *Anthophora ambigua* Pérez, 1895; *Anthophora guigliae* Dusmet y Alonso, 1929
Egypt: El Amarna: AMNH

***Anthophora (Petalosternon) wegelini* Friese, 1914**
Egypt: Meadi: NHM

***Anthophora (Pyganthophora) aestivalis* Panzer, 1801**
Synonyms: *Apis aestivalis* Panzer, 1801; *Anthophora intermedia* Lepeletier, 1841
Lebanon: Nr. Cedar's Hotel: NHM

***Anthophora (Pyganthophora) albosignata* Friese, 1896**

Synonyms: *Podalirius albosignatus* Friese, 1896; *Anthophora fastuosa* Gribodo, 1924; *Anthophora tenuiciliata* Alfken, 1926; *Anthophora pedata var nigroscopacea* Friese, 1919
Israel: Jericho (Hisham Palace): NHM

***Anthophora (Pyganthophora) arida* Brooks, 1988**
UAE: Jebel Jibir: CAvH

***Anthophora (Pyganthophora) atriceps* Perez, 1879**
Israel: Ein Gedi, Peza ʻel, nr. Qumran, nr. Shizzafon Junction, nr. Telamim, nr. Yeroham: AMNH

***Anthophora (Pyganthophora) atroalba* Lepeletier, 1841**
Synonyms: *Anthophora atro-alba* Lepeletier, 1841; *Anthophora liturata* Lepeletier, 1841; *Anthophora antiope* Bingham, 1898; *Podalirius vedettus* Nurse, 1904
Israel: Jerusalem: NHM

***Anthophora (Pyganthophora) libyphaenica* Gribodo, 1893**
Israel: Nr. Telamim, nr. Yeroham: AMNH

***Anthophora (Pyganthophora) nigriceps* Morawitz, 1886**
Synonyms: *Podalirius nigriceps* (Morawitz, 1886)
Lebanon: Mt. Lebanon Hazerta: OUMNH

***Anthophora (Pyganthophora) orientalis* Morawitz, 1877**
Synonyms: *Podalirius orientalis* (Morawitz, 1877)
Israel: Har Gillo, Ma'agan Mikha'el: AMNH
Lebanon: Deir El Harf: OUMNH

***Anthophora (Pyganthophora) retusa* (Linnaeus, 1758)**
Synonyms: *Apis retusa* Linnaeus, 1758; *Apis haworthana* Kirby, 1802; *Apis pennipes* Kirby, 1802; *Anthophora intermedia* Lepeletier, 1841, partim; *Megilla monacha* Erichson, 1849; *Anthophora ruthenica* Morawitz, 1870; *Anthophora retusa var meridionalis* Pérez, 1879; *Anthophora retusiformis* Cockerell, 1911; *Anthophora retusa var fasciata* Alfken, 1913; *Anthophora aestivalis baicalensis* Hedicke, 1929; *Anthophora retusa baicalensis* Hedicke, 1929; *Anthophora retusa var seminigra* Benoist, 1930; *Anthophora aestivalis alaica* Hedicke, 1931; *Anthophora monacha tschelcarica* Ponomareva, 1967; *Anthophora (Pyganthophora) rudolphae* Romankova, 2003
Lebanon: Ain Zhalta: NHM

***Anthophora (Pyganthophora) rogenhoferi* Morawitz, 1871**
Iran: Nr. Borujerd: AMNH
Israel: Har Gillo, Mt. Hermon, Zaura: AMNH

***Anthophora (Pyganthophora) romandii* Lepeletier, 1841**
Israel: Halamish Dunes, Wadi Qelt: AMNH

***Anthophora (Pyganthophora) scopipes* Spinola, 1838**
Synonyms: *Anthophora spinolana* Priesner, 1957
Israel: Nr. Shizzafon Junction, nr. Zihor Junction: AMNH

***Anthophora (Pyganthophora) sergia* (Nurse, 1904)**
Israel: Nr. Elat, Ma'ale Aqrabbim, Nitzana, Shizzafon Junction, Wadi Qelt, Zihor Junction: AMNH

Anthophora (Pyganthophora) vernalis **Morawitz, 1877**
Synonyms: *Podalirius vernalis* (Morawitz, 1877)
Israel: Yeroham: AMNH

Amegilla (Amegilla) garrula **(Rossi, 1790)**
Synonyms: *Apis garrula* Rossi, 1790; *Anthophora garrula* (Rossi, 1790); *Podalirius garrulus* (Rossi, 1790); *Anthophora bombylans* Mocsáry, 1881
Iran: Bandar Pahlavi, nr. Hashtpar: AMNH & NHM

Amegilla (Amegilla) incana **(Klug, 1845)**
Saudi Arabia: Jeddah: NHM
UAE: Hatta: NHM

Amegilla (Amegilla) quadrifasciata **(de Villers, 1789)**
Synonyms: *Apis quadrifasciata* de Villers, 1789; *Anthophora quadrifasciata var albescens* Dours, 1870; *Anthophora maderae* Sichel, 1868; *Anthophora mervensis* Radoszkowski, 1893; *Anthophora mediterranea* Alfken, 1927; *Anthophora quadrifasciata var tenereffensis* Cockerell, 1930; *Anthophora klugi* Priesner, 1957; *Anthophora litorana* Priesner, 1957
Iraq: Baghdad, Kut: INHRCM

Amegilla (Megamegilla) acraensis **(Fabricius, 1793)**
Yemen: Jebel Jihaf, Usaifira: NHM

Amegilla (Micramegilla) byssina **(Klug, 1845)**
Egypt: Assiut, Giza: NHM
Israel: Deir Al-Balah: NHM
UAE: Abu Dhabi, Al-Ajban, Dubai, Hatta, Remah, Sharjah Desert Park, Shuwaib: NHM

Amegilla (Micramegilla) latizona **(Spinola, 1838)**
Synonyms: *Saropoda latizona* Spinola, 1838; *Podalirius latizonus* (Spinola, 1838)
Iran: Ahwaz: AMNH

Amegilla (Micramegilla) mucorea **(Klug, 1845)**
Synonyms: *Megilla mucorea* Klug, 1845; *Anthophora liriope* Bingham, 1898; *Anthophora delicata* Cockerell, 1911
Egypt: Assiut, Cairo, Minufiya: NHM & OUMNH
Saudi Arabia: Riyadh: NHM
UAE: Al Ain, Falaj al Mualla, Hatta, Madam, Mileiha, Sharjah Desert Park, Shuwaib, Wadi Bih, Wadi Shawkah: NHM

Amegilla (Zebramegilla) albigena **(Lepeletier, 1841)**
Synonyms: *Anthophora albigena* Lepeletier, 1841; *Anthophora binotata* Lepeletier, 1841; *Anthophora quadrifasciata var nana* Radoszkowski, 1869; *Anthophora albigena var albida* Sichel, 1870; *Podalirius albigena var nigrithorax* Dalla Torre, 1877; *Anthophora talaris* Pérez, 1895; *Anthophora graeca* Alfken, 1942; *Anthophora albigena afra* Priesner, 1957
Egypt: Cairo: AMNH
Iran: Hamadan, Saraain: AMNH

Amegilla (Zebramegilla) cognata **(Smith, 1854)**

Synonyms: *Anthophora cognata* Smith, 1854; *Anthophora salviae* Morawitz, 1876; *Amegilla (Zebramegilla) salviae* (Morawitz, 1876); *Anthophora pipiens* Mocsáry, 1881
Iran: Bandar: AMNH

***Amegilla (Zebramegilla) crocea* (Klug, 1845)**
Synonyms: *Megilla crocea* Klug, 1845
Egypt: Aswan: AMNH
Oman: Behla, Dhofar (Raysut), Muscat, Wadi Quryat: NHM
Saudi Arabia: Abyan, Jeddah: NHM
UAE: Bithnah, Hatta, Khor Fakkan, Munai, Sharjah-Khor Kalba: NHM

***Amegilla (Zebramegilla) punctifrons* (Walker, 1871)**
Egypt: 60 km S of Alexandria, Faiyum: AMNH
UAE: Wadi Maidaq, Wadi Shawkah : CMS, DEI, UAEIC

***Amegilla (Zebramegilla) savignyi* (Lepeletier, 1841)**
UAE: Wadi Maidaq, Wadi Safad, Wadi Shawkah: CAvH

***Amegilla* (Uncertain) *lutulenta* (Klug, 1845)**
UAE: Wadi Shawkah: CMH, UAEIC

Tribe: Melectini

***Melecta (Melecta) aegyptiaca* Radoszkowski, 1876**
Synonyms: *Melecta lindbergi* Lieftinck, 1958
Egypt: Etay El Baraud: AMNH

***Melecta (Melecta) albifrons* (Forster, 1771)**
Synonyms: *Apis albifrons* Forster, 1771; *Apis punctata* Fabricius, 1775; *Andrena armata* Panzer, 1799; *Melecta nigra* Spinola, 1806; *Melecta albifrons nigra* Spinola, 1806; *Melecta fasciculata* Spinola, 1806; *Crocisa atra* Jurine, 1807; *Melecta tisiphone* Newman, 1835; *Melecta alecto* Newman, 1835; *Melecta clotho* Newman, 1835; *Melecta megaera* Newman, 1835; *Melecta albifrons albovaria* Erichson, 1840; *Melecta albovaria* Erichson, 1841; *Melecta bipunctata* Lepeletier, 1841; *Melecta aterrima* Lepeletier, 1841; *Melecta calabrina* Radoszkowski, 1876; *Melecta pseudoarmata* Radoszkowski, 1893; *Melecta armata var mediterranea* Gribodo, 1894; *Melecta novellai* Dusmet y Alonso, 1915; *Melecta armata var gigantea* Friese, 1925; *Melecta luctuosa var minima* Friese, 1925
Israel: Jericho (Hisham Palace), Mt. Hermon, nr. Qumeran, nr. Telamim: AMNH & NHM

***Melecta (Melecta) angustilabris* Lieftinck, 1980**
Egypt: Meadi: NHM
Israel: Shezaf Nature Preserve: AMNH

***Melecta (Melecta) festiva* Lieftinck, 1980**
Israel: Bet Oren, Eshtaol, Har Gillo, nr. Telamim: AMNH & NHM

***Melecta (Melecta) fulgida* Lieftinck, 1980**
Israel: Jericho (Hisham Palace): NHM
Jordan: Jerash: NHM

***Melecta (Melecta) italica* Radoszkowski, 1876**
Israel: Bet Oren, nr. Telamim: AMNH

Melecta (Paracrocisa) sinaitica (Alfken, 1937)
Oman: Muscat (Ruwi): NHM

Thyreus elegans (Morawitz, 1878)
Synonyms: *Crocisa elegans* Morawitz, 1877; *Crocisa quadridentata* Saunders, 1908; *Crocisa brezzii* Guiglia, 1933
Egypt: Assiut, Faiyum: NHM
Saudi Arabia: Summan Plateau: NHM
UAE: Abu Dhabi, Liwa, Wadi Shawkah: NHM

Thyreus histrionicus (Illiger, 1806)
Synonyms: *Melecta histrionica* Illiger, 1806; *Crocisa major* Morawitz, 1875; *Crocisa divisa* Pérez, 1905; *Crocisa major var alboscutellata* Meyer, 1921; *Crocisa rimosiscutum* Alfken, 1927
Iran: Lahijau: NHM
Yemen: Socotra (Hadibo Plain): NHM

Thyreus hyalinatus (Vachal, 1903)
Egypt: Giza, Suez: NHM
Israel: En Hazeva: AMNH
Oman: Dhofar (Wadi Sayq): NHM
Saudi Arabia: Abu Arish, Jeddah: NHM
UAE: Asimah, Shuwaib: NHM

Thyreus ramosus (Lepeletier, 1841)
Synonyms: *Crocisa ramosa* Lepeletier, 1841; *Crocisa rufa* Radoszkowski, 1886; *Crocisa ashabadensis* Radoszkowski, 1893; *Crocisa caucasica* Radoszkowski, 1893; *Crocisa ramosa var albociliata* Meyer, 1921; *Crocisa affinis var minor* Friese, 1925; *Crocisa circulata* Alfken, 1927; *Thyreus ashabadensis* (Radoszkowski, 1893)
Egypt: Faiyum, Kom Oshim: AMNH & NHM
Israel: Banias, Wadi Qelt: NHM
Jordan: Wadi Shueib Dam: NHM
Oman: Al Awabi, Dhofar (Ayun Pools, Wadi Sayq), Khasab, Musah, Rostaq, Tinaf, Wadi Quryat: NHM
Saudi Arabia: Abha, Nr. Bisha: NHM
UAE: Fagsha, Hatta, Khor Kalba, Wadi Maidaq, Wadi Safad: NHM
Yemen: Sana'a: NHM

Tribe: Bombini

Bombus (Pyrobombus) haematurus Kriechbaumer, 1870
Iran: Bandar Pahlavi: AMNH

Bombus (Thoracobombus) armeniacus Radoszkowski, 1877
Synonyms: *Bombus pomorum var armeniacus* Radoszkowski, 1877; *Bombus pallasi* Vogt, 1909; *Fervidobombus scythes* Skorikov, 1926
Iran: Saraain: AMNH

Chapter 6.

General discussion

General discussion

In the last three years, two well-publicised papers have reported severe declines in insect abundance in Germany (Hallman et al., 2017) and Puerto Rico (Lister & Garcia, 2018). In the case of the German study, Hallman et al. (2017) report an alarming decline of 76% of aerial insect biomass over 27 years of monitoring. The Puerto Rico work notes an even greater estimated loss of 78-98% of terrestrial and canopy arthropod biomass over 36 years (Lister & Garcia, 2018; Sánchez-Bayo & Wyckhuys, 2019). These two papers draw attention to the fact that there is currently a global decline in insect abundance and diversity across a wide range of habitat types. Sánchez-Bayo & Wyckhuys (2019) list several causes for this decline, such as climate change and the overuse of pesticides. However, they emphasise that habitat loss through the conversion of natural habitats to agricultural monocultures is the main driver of this reported decline.

The results from Puerto Rico (Lister & Garcia, 2018) are especially alarming because the authors draw a link between the declines of insects with a decline in vertebrate numbers, a cascade effect through the food web. While this type of threat to biodiversity has long been recognized, conservation to date has tended to focus on protecting individual species and habitats, rather than trying to conserve networks (Tylianakis et al., 2010). Lister & Garcia (2018) demonstrate the importance of understanding network structure, both in terms of its components and links, but also how the network changes temporally and spatially, because this may affect stability to perturbation. It is only in the last few decades that steps have been taken to comprehend how networks operate. First, the structure of pollination networks has been studied at the community level, demonstrating that plants often receive visits from multiple types of pollinator (Waser et al., 1996; Waser & Ollerton, 2006). Secondly, there is now an appreciation that networks are dynamic structures changing through time (Ponisio et al., 2019). Finally, the most recent insight is that turnover does not simply mean a straightforward loss of species. Within networks, interaction turnover occurs, with pollinators swapping the plants they visit (Poisot et al., 2015). The combination of these three elements creates a more detailed view of the complexity and dynamism within networks, but in turn challenges the conventional view that specialisation moulds floral phenotypes.

To advance the understanding of how pollination networks operate in xeric habitats, and thus how this relates to network analyses globally, the overall purpose of this study has been to understand the degree to which specialisation operates at the species level. This is still contentious, and as I have argued, the generalities are based mainly on studies done in temperate regions. This justifies the need for network analyses in different regions.

Summary of findings

In Chapter 2, I investigated the structure of a visitation network from the lowlands of the Hajar Mountains in Oman. Transects were set up in 13 sites across three areas of the range, with every flowering plant observed in order to record all visitors. The results showed the network was 'typical', in the sense of being dominated by bees (33% of all visitors), asymmetric in interactions, and nested. Modularity was limited, with only two compartments at the overall network level, suggesting that unlike nestedness (Bascompte et al., 2003) the occurrence of modularity is not as common. What was unexpected were the high levels of specialisation (mean no. of links per insect species) of not just bees, but all insect taxa. There was no significant correlation between the abundance of individual species and increased generalisation in visit patterns. Therefore it appears that specialisation in this system is not purely a reflection of the low numbers of individuals, since the more common taxa were also highly specialised. Behavioural studies are needed to test whether the observed levels of specialisation result from high levels of floral constancy across the network. Survey areas were widely separated, and high levels of visitor specialisation occurred in all areas, implying a general rather than local constancy.

The third chapter looked at visitors to the *Euphorbia larica*, the commonest plant in the area, studying temporal and spatial variation. This approach facilitated a discussion of how changes to the pollinator spectrum can influence the evolution of floral phenotypes. As predicted, there were many species of Diptera visiting early in the flowering season, but, based purely on the abundance of flies, these did not appear to be the primary pollinators of *E. larica* at any time during the study. Instead numerous species of ant and beetles may play a greater role in pollination than expected, because of their high abundance throughout the study. There was no evidence for functional group specialisation, an indication of the existence of a particular floral syndrome. Instead, the behavioural trait of 'secondary pollinators' was the most common trait. Taxonomic distinctness within sites was high throughout the whole study, and there was no evidence for any convergence of pollinator communities to one dominant type with increasing altitude (typically Diptera: Lefebvre et al., 2018). As in Chapter 4, from temporal changes in the visitor spectra (i.e. turnover), species replacement was found to be high and was the primary type of turnover. *E. larica* is clearly a generalist, with visitor assemblages changing geographically and temporally. Increased floral display led to greater abundance up to an asymptote, possibly a reflection of pollinator limitation in the environment as a whole.

In Chapter 4, I explored whether bee populations in xeric habitats are influenced over time by rainfall events stimulating emergence from diapause. Running for almost two years at a single locality, my study found no significant evidence of spikes of abundance after the 18 rainfall events. This appears to falsify the proposition (Danforth, 1999; Minckley et al., 2000; Danforth et al., 2003) that rainfall is a trigger for bee emergence.

However, I caution this may be due to the fact rainfall was limited during each event, and therefore it might never have met the putative threshold to break dormancy. This highlights the need for further recording of the bee population in years when rainfall is greater. Abundance among species was low throughout almost all of the study, with only three trapping dates showing surges of abundance of particular species (though not linked to rainfall). A major finding was that species replacement was high between the two years of the study, demonstrating that two different communities of bees existed within the site. The assemblage changed from halictid-dominated (2017) to megachilid-dominated (2018). Minckley (2013) suggests drought can impact levels of generalist and specialist species in a desert habitat. Further much more long-term work is needed to understand the turnover and potential changes in levels of specialisation.

The final chapter looked as trends in distributions across the whole Middle East using species distribution modelling (MaxEnt) of data from museum specimens of bees to predict their possible responses to climate change. This has been done only once before for bees of xeric environments (Silva et al., 2018). The climate scenario used was a relatively negative one (the HadGEM2-CC Representative Concentration Pathway 8.5 for 2070). The results suggested that all but four of the 45 modelled species showed little evidence of isolated or endemic ranges. They instead predicted relatively continuous distributions across the region. 82% of species were predicted to show declines in distributions with climate change, with the southern half of the Arabian Peninsula worst affected. There was a moderate to high environmental niche overlap for most species. This implies that while climate change will negatively affect bee distributions, this effect will not be catastrophic. However, depending on levels of specialisation or generalisation, the effect at a local level for pollination network stability could still be severe. However, the SDM's did not take into account biotic interactions. Therefore, as specialism amongst plant-insect interactions appeared to be key at a local level in the Hajar Mountains, this would suggest declines in certain plant species with climate change would cause serious declines in individual insect species that specialise on them. Consequently, these models should not be taken to mean climate change may not seriously impact pollination networks in the region.

Homogenisation of the Middle Eastern bee fauna

This study of community composition at a local and regional level suggests that communities appear to be spatially similar but had high species replacement over time. Thus the visitation networks of the three sections of the lowland Hajar Mountains (chapter 2) showed no significant difference in composition. Likewise at the regional scale from SDMs (chapter 5), the patterns of bee species richness were highest in the same areas of the Middle East. This was particularly evident in the Nile and Jordan river valleys, and in northern UAE, with the majority of species showing similar abiotic niches. The results of these two chapters suggest that there is relative spatial homogeneity of the pollinator community within the Middle East. This type of homogenisation has been reported for the pollinator communities of Europe, but the evidence there suggests that the cause is habitat loss since the 1950s (Carvalheiro et al., 2013). We have no previous baseline datasets to say whether the observed Middle Eastern homogeneity is a reflection of losses of rare and/or endemic species from man-made causes. Although habitat loss is a worldwide issue, the conversion of land to agriculture in the Arabian Peninsula is in no way comparable to Europe. Thus the community similarity of bees may be a natural response to relatively low levels of plant diversity, believed to encourage generalisation of feeding behaviour (Olesen et al., 2002). If generalisation is common amongst pollinators in the Arabian Peninsula, then this might explain their relative homogeneity. Although bees in xeric habitats are generally regarded as being oligolectic, this inference appears to be based mainly on North American xeric habitats (Minckley, 2008; Minckley et al., 2013). Prior to my own study, the only published visitation network from Arabia was carried out in the UAE (Gess & Roosenschoon, 2016). This study found that out of 23 species of bee, only 39% were specialists. My own data (chapter 2) suggest that specialisation may be common amongst all visitors in the Hajar Mountains, not just the bees. However, the spatial and temporal turnover in the visitors to *E. larica* was extremely high. This suggests that the overall network may reflect floral constancy at particular times within the flowering season, rather than true specialisation.

Although homogeneity of the pollinator community within the study region was indicated, when temporal changes were studied (chapters 3 and 4), high levels of turnover and specifically species replacement were observed. The two communities of the first and second year of the study (chapter 4) were almost completely different, with first more Halictidae (44%) than Megachilidae (22%), and then many more Megachilidae (59%) than Halictidae (29%). This highlights how populations at a single site can change dramatically through time. Studying the site during only one year would have given a totally false impression of the local species assemblage. The same was true of the visitors to *E. larica*: only 7% of the species were recorded in all three-study periods.

There are, therefore, two contrasting patterns from my work: spatial homogeneity of pollinators at both a relatively local level (the Hajar Mountains) and more widely (Arabia); and intense turnover of species through time. It would be very interesting to know (but challenging to study) whether this turnover affects communities at the same rate and in the same way over broad spatial scales. Although the species composition may change, at particular times the same communities may occur across the Arabian Peninsula, causing spatial but not temporal homogeneity.

Future steps: an approach for addressing the Linnean shortfall in the Middle East

One of the fundamental foundations too much of biological research, including this study, is the ability to identify and describe the species present in an environment (Hajibabaei et al., 2006). Nevertheless, for much of the world these primary data remain out of reach because of the complexity of taxonomy, the lack of identification keys, and the paucity of trained taxonomists (Weeks et al., 1999; Sheffield et al., 2009). This is particularly true for the Middle East, for which the insect fauna is rich but remains comparatively unknown. This problem was encountered multiple times throughout this study, often resorting identifications to morpho-species or even simply to the subfamily level (e.g. Eumeninae).

Mayer et al (2011) lists the key topics that require further attention in order to make progress in pollination biology, and improving the taxonomy of pollinators is emphasised as an area of importance. As the authors stress, taxonomy is not simply describing species, although separating individuals into manageable units is a first step in creating order when trying to understand a system. Instead it allows more detailed questions to be asked regarding biogeography, or how morphology influences functional group specialisation and hence evidence for or against floral syndromes, topics explored in this thesis. This shortage of keys for most floral visitors within the region means that pollination networks cannot be fully described. When generalisations are made, therefore, they are often based on networks described from temperate habitats where the identification of pollinators is better understood. This is potentially dangerous because temperate networks differ greatly from those of the xeric conditions found throughout most of the Middle East. For instance, bumblebees (*Bombus* spp) are a key component of European networks and, like many eusocial species are generalists (Michener, 2007). In contrast, a high proportion of Oman's pollinator community is composed of *Megachile* species, most of which are probably oligolectic. This makes it risky to make comparisons between these very different networks.

Sheffield & Westby (2007) state that 30% of *Megachile* species in North America, a country with a long history of entomological research, are known from only one sex, let alone any details regarding their ecology (Sheffield et al., 2009). In regions such as the Middle East, a known hotspot for bee diversity (Patiny & Michez, 2007), this type of problem is undoubtedly much greater. While recent efforts in the UAE (Dathe, 2009) and Saudi Arabia (Engel et al., 2013) have started to give a clearer picture of bee diversity, a considerable amount of work remains. With insects believed to be declining worldwide, this is clearly a problem (Delabye et al., 2018).

DNA barcoding is a technique that can contribute to integrative taxonomy (Kipling et al., 2005). Along with more traditional taxonomic approaches it provides an additional tool for identifying species, as well as helping to deduce their evolutionary relationships (Gill et al., 2019). It can be particularly useful in determining species in groups that have few obvious morphological characters (Nicholls et al., 2012). First developed in 2003 (Hebert et al., 2003), the technique in animals uses a 658-base-pair section of the COI or *cox1* mitochondrial gene (cytochrome *c* oxidase I) (Sheffield et al., 2009; Delabye et al., 2018) as a 'fingerprint' to discriminate species much more quickly. The process is now recognised as a vital tool in rapidly assessing faunas, especially where diversity is hyperdiverse and under threat (Smith et al., 2005).

While the number of studies using barcoding has proliferated over the last two decades, the methodology is not without issues. For instance, the use of a single section of mitochondrial DNA to determine a new species identity has led critics to suggest this returns taxonomy to typology i.e. the overreliance of a single defining character to separate species (Kipling et al., 2005; Meyer & Paulay, 2005). Some authors DeSalle (2006) have argued barcoding rather than being used for species discovery should primarily be used for species identification. Databases such as GenBank and Barcode of Life Data System (BOLD) store sequences after correctly identified species are barcoded and the sequence is added to the reference database. The Fish Barcode of Life campaign (www.fishbol.org) returned a 98% success rate in recognising known fish species using the CO1 gene (Krück et al., 2013), demonstrating barcoding's success in recognising well-established species. Where issues with the use of a single gene may arise is with hybrids, sibling species, or groups of species that have undergone recent adaptive radiation (Krück et al., 2013) where the barcode gap to separate species is not reliable. Hybridization events can result in inter-specific swapping of genes and therefore gene trees are attempting to record the speciation events of multiple species (Petri et al., 2013; Naciri & Linder, 2015). Other issues relate to species concepts. Recent work has led to species being considered as independently evolving metapopulations (De Queiroz, 2007; Naciri & Linder, 2015). This would imply the populations that form a species share a common history but are distinct to some degree phenotypically and ecologically (Naciri & Linder, 2015). Therefore, genetic diversity varies in different populations and will impact tree reconstructions depending on the individuals sampled (Naciri & Linder, 2015).

To attempt to overcome this issue when barcoding, samples of individuals within several populations that varies geographically should be made. Another way to improve success with species that are morphologically similar and prone to hybridise is through the use of more than one barcoding gene (Qu et al., 2018). For example, both CO1 and NADH dehydrogenase subunit 2 (ND2) were used to successfully identify Grouper (Epinephelidae) fish that lack significant morphological characters that make alternative taxonomic methods unsuitable. Public databases, such as GenBank and BOLD are also in need of careful curation as noted by Piemontese et al (2020) in their study of Miridae bugs. Here the authors found that these databases often mismatched a molecular sequence with a taxonomic name. Without improvement and careful input of data, these databases can be a hindrance rather than helping identifying cryptic species.

Nevertheless, when applied carefully and with sufficient recognition of the issues around using a single locus, barcoding can be an additional implement to help with taxonomy. Using this technique with other methods that provide multiple species characters can allay the initial fears of a return to typology.

Though initially used only for taxonomic purposes, barcoding is now being used in more ecologically based projects, such as investigating insect-plant host relationships (Jurado-Rivera et al., 2009), revealing the links within food webs (Pompanon et al., 2012), and recording spatial and temporal turnover of species richness between different sites (Delabye et al., 2018). In addition, it provides information on another level of diversity, phylogenetic diversity, an important but sometimes overlooked element of biodiversity (Swenson, 2012). Another use of barcoding beyond purely taxonomic applications has been to understand plant-pollinator interactions. By sequencing both bee specimens and pollen collected from the bee specimens themselves, a detailed picture of the topology of pollination networks can be created (Gous et al., 2018).

A major development to the understanding of the diversity of insects in Arabia has been the publication of the Arthropod Fauna of the UAE series (van Harten 2008, 2009, 2010, 2011, 2014 & 2017). This hugely successful project has documented more than 6000 arthropod species (Monks et al., 2019) and allowed the first detailed assessments to be made of insect diversity in eastern Arabia. While these publications are rightly recognised as keystone studies of Middle Eastern insect biodiversity, they have taken more than a decade to complete, and relied on the expertise of more than 150 specialists. For a country such as Oman, more than three times the size of the UAE, and containing a much wider range of habitats including the floristically unique Dhofar Mountains (Patzelt, 2015), the challenge of recording the insect biodiversity is much higher. Deploying the techniques of DNA barcoding offers a way of potentially speeding up this process.

DNA barcoding of the bee specimens collected during this study has now begun, although the results were not ready in time to be included in this thesis. A further step will be to barcode their pollen loads for comparison with the visitation networks of Chapter 2.

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