Contrasting patterns of turnover between plants and pollinators in an arid landscape

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Abstract

Aim

We propose two contrasting models explaining how beta diversity can be maintained across a landscape and test these models on a plant-pollinator system in arid South Sinai. The region is known for its irrigated agricultural gardens, which appear as high diversity islands in the arid mountainous habitat. We aim to establish how these gardens are influencing patterns of landscape scale diversity and whether plants and pollinators are responding in contrasting ways.

Location

South Sinai, Egypt

Methods

Plant-pollinator interactions were surveyed in agricultural gardens and unmanaged habitat in the high mountains and the low mountains. Patterns of alpha-diversity and species turnover were quantified using three measures (Hill’s numbers) and compared between the two levels of the interaction networks.

Results

In the high mountains, gardens supported an equally abundant and more diverse ($D_0$, $D_1$, $D_2$) plant community than the unmanaged habitat, but had no impact upon the complexity of the interaction networks or the abundance or diversity of pollinators. In the low mountains, gardens supported a more abundant and more diverse ($D_0$, $D_1$, $D_2$) plant community than the unmanaged habitat and actively increased the complexity of the interaction networks and the abundance and diversity ($D_0$, $D_1$) of pollinators.

In accordance with Model One, plants exhibited high levels of species turnover across the landscape, with gardens increasing overall heterogeneity. In accordance with Model Two, pollinators exhibited extremely low levels of turnover across the landscape, with gardens in
the low mountains increasing local diversity by supporting species that were shared with the natural species pool.

**Main conclusions**

Plants and pollinators exhibited highly contrasting patterns of species turnover across a landscape. Gardens supported a novel floral community, but pollinators exhibited the flexibility to forage on cultivated species and maintained extremely low levels of turnover. The landscape context had a strong influence upon the abundance and diversity of plant-pollinator interactions, with gardens in the low mountains receiving inflated numbers of pollinators due to crowding effects.

1. **Introduction**

Predicting patterns of species diversity on a landscape scale is an important challenge for conservation biogeography, one that can inform decisions on which land management strategies are most beneficial for the conservation of targeted taxa. Here we propose two contrasting conceptual models explaining how beta diversity can be maintained across a landscape and test these models on a plant-pollinator system in arid South Sinai. Model One predicts that landscape scale diversity will be maintained as distinct assemblages across the habitat with each assemblage supporting novel species (Fig 1 A). In this model you would expect to find high levels of species turnover across the habitat, resulting in high levels of landscape heterogeneity. Model Two predicts that less diverse assemblages of species will form a nested subset of those present in the entire species pool (Fig 1 B). This model predicts low levels of species turnover across the landscape, with a high overlap in the species found between assemblages. Communities of species following the two models would require contrasting conservation strategies; in Model One it would be essential to conserve habitat heterogeneity if you were to benefit all species in the community, but in Model Two the improvement of single patches of habitat could benefit all species within the community and increase levels of local diversity.

The unusual distribution of resources associated with our study site in South Sinai makes it an ideal location to test these two conceptual models. It is an arid mountainous region, but the presence of rainwater harvesting allows the cultivation of agricultural gardens with a higher potential for plant growth than the unmanaged habitat (Norfolk et al., 2013). These gardens appear as high diversity islands in an arid landscape and have been shown to support a higher diversity of wild plants that the surrounding habitat (Norfolk et al 2013) which receive higher rates of floral-visitation (Norfolk & Gilbert, in review). Here we are
interested in how these gardens are affecting landscape scale patterns of diversity and whether they are; a) increasing landscape heterogeneity by supporting a novel community of species (Model One), or b) increasingly levels of local diversity by supporting the same species as those found in the unmanaged habitat (Model Two).

Different taxa are known to display varying patterns of beta diversity across a shared landscape, with organisms with higher dispersal abilities tending to show lower rates of turnover (Soininen et al., 2007). Herbivorous insects have also been shown to show extremely low levels of species turnover in heterogeneous tropical forests habitat, due to their ability to adapt their foraging preferences (Novotny et al., 2007). Here, we contrast the patterns of diversity in plants and their interacting pollinators, to see whether they follow the same models. As pollinators are more mobile than plants and known to exhibit generalised foraging behaviour (Bjerknes et al., 2007; Graves & Shapiro, 2003; Williams et al., 2011) we expected them to exhibit much lower levels of species turnover than plants.

Landscape context is known to have a strong influence on the composition of pollinator communities (Holzschuh et al., 2007), with the species richness of crop pollinators declining with distance from natural or semi-natural habitat (Ricketts et al., 2008) and increasing with the quality of the surrounding habitat (Kennedy et al., 2013). We predicted that impact of the gardens upon pollinators would differ in accordance to the quality of the surrounding habitat, so have selected gardens from two altitudinal categories with distinct environmental properties; a) the high mountains (isolated, cooler temperatures, higher water availability) and b) the low mountains (close proximity to villages, more disturbed, greater water limitation).

In this study we used utilise a network approach, combined with new techniques in similarity analyses (Gotelli & Chao, 2013) to determine which model best described the observed patterns of diversity for plants and pollinators in the high and low mountains. Specifically we hypothesised that:

1) Irrigated gardens would increase the abundance and diversity of plants and pollinators above that found in the unmanaged habitat, with a differential effect in the high and low mountains.

2) Plants would follow Model One, with gardens increasing the landscape heterogeneity by supporting species that were not present in the unmanaged habitat.

3) Pollinators would follow Model Two, with gardens increasing local levels of diversity by supporting species that were shared with the unmanaged species pool.
We found that plants and pollinators exhibited highly contrasting patterns of turnover across the agricultural landscape and that patterns of diversity were strongly influenced by the landscape context.

2. Methods

2.1 Study area

This study was conducted in the St Katherine Protectorate (28°33'N, 33°56'E) in South Sinai, Egypt. It is an arid, mountainous region with altitudes of 1200-2624 m a.s.l.. The landscape is typified by rugged mountains, interspersed with steep-sided valleys known as wadis. The region has a hyper-arid climate, experiencing extremely dry, hot summers and cold winters. Average annual rainfall ranges from 10 mm per year in low coastal areas to 50 mm per year in the high mountains, but this entire annual rainfall can fall within the space of a single day as unpredictable flash floods (Cools et al., 2012). The local Bedouin traditionally farm orchard gardens at the base of the wadis that depend on the runoff rainwater to facilitate the growth of a variety of orchard products as well as vegetables and herbs (Norfolk et al., 2012; Zalat et al., 2008). The gardens are primarily used for subsistence, but also contain ornamental flowers and have been shown to provide important habitat for rare wild native plants (Norfolk et al., 2013). From satellite imaging we have estimated that there are between 500-600 gardens in the St Katherine Protectorate, which form a dense network of walled gardens that run along the base of mountain wadis. The average size of the gardens was 2000m², with areas ranging from 500m² to >6000m².

Gardens were selected at random from the two altitudinal categories, (a) high mountains, 1800-1850 m a.s.l. (N = 9), and (b) low mountains, 1300-1550 m a.s.l. (N = 10). An equal number of unmanaged plots were sampled at the base of the selected wadis, in areas where slope and soil type resembled those found in the neighbouring gardens (Fig. 2). We refer to these plots as unmanaged plots, because they have no active management and represent the habitat that would be present in the absence of agriculture. Five 10 x 10 m² quadrats were measured out in each garden and unmanaged plot for repeat surveys across the season. Gardens ranged from 600 - 2800 m² in size, so between 20 % - 80% of each garden was surveyed.

2.2. Flower-visitor surveys

In order to contrast patterns of diversity in plants and pollinators we conducted monthly plant-pollinator surveys in the selected gardens and unmanaged plots throughout April to July 2013. The total number of fresh flowers (ie. petals and anthers intact and not dried) was recorded to allow calculation of floral abundance and species richness. For clustered,
umbelled or spiked inflorescences the average number of flowers per inflorescence was calculated from three flower heads in the field, with floral abundance calculated as the total number of inflorescences multiplied by the average number of flowers per inflorescence.

Surveys were always carried out during sunny, non-windy days between 9am and 4pm. During sampling, a single collector thoroughly searched each 10 x 10 m² quadrat in turn and examined all flowering-plants. All observed flower-visiting insects were net-collected directly from the plants, unless confident identification was possible in the field (honeybees and certain butterflies), and the identity of the plant species was recorded to establish the interaction. The collector walked at a steady pace around the quadrat searching each flowering plant once; if there were no visitors then the collector continued the walk and moved on to the next plant. When multiple visitors were observed simultaneously on one plant, the collector spent no more than five minutes (excluding handling time) catching insects from that particular plant.

Plants were identified in the field where possible or collected for identification using Boulos (1999-2005). Plants were classified as either wild or cultivated, with cultivated defined as any plant actively tended for consumption, household use or ornamental purposes. All captured insects were pinned and identified to species level for orders Hymenoptera and Lepidoptera and family Syrphidae by taxonomists. Coleoptera and non-syrphid Diptera were identified to family level and have been grouped into morphospecies based on visual characteristics to allow network analyses. Capture rates were 92 %; visitors that evaded capture were still recorded, but since species level identification was not possible they were excluded from further analyses.

2.3. Data analyses

Spatial patterns in alpha diversity were explored using Hill’s numbers (species richness [\(^q\)D], the exponential of Shannon entropy [\(^1\)D] and the inverse Simpson index [\(^2\)D]) (Hill, 1973) in accordance with current consensus (Chao et al., 2012; Jost, 2006; Leinster & Cobbold, 2011). Hill’s numbers are defined to the order of q (\(^q\)D), whereby parameter q indicates the weight given towards rare or common species. \(^0\)D is insensitive to relative frequencies, and is therefore weighted towards rare species. \(^1\)D is weighted towards common species, and \(^2\)D is weighted towards abundant species. Diversity measures were calculated in package vegan in R (Oksanen et al., 2012). Data from the four-month sampling period were pooled for each garden and unmanaged plot. Pollinator abundance was quantified as the total number of insects recorded visiting flowers in each plot.
Plant and pollinator abundance and diversity were compared between the gardens and unmanaged habitats using linear-mixed effect models (lme4 package) (Bolker et al., 2009). Abundance and all three measures of diversity were included as response variables, with habitat (garden/natural) as the fixed variable and wadi as a random variable to account for spatial differences. Model simplifications followed Zuur et al. (2009).

**Visitation network analyses**

To visualise the interactions between plants and flower-visitors at a community level we created cumulative visitation networks for gardens and unmanaged plots in the high and low mountains using R package `bipartite` (Dormann et al., 2009). These visitation networks were derived from quantitative interaction matrices with n rows (representing plant species) and m columns (representing insect species), with the value at the intersect representing the number of interactions observed between flower and insect. In order to compare interaction diversity between habitats we then created individual visitation webs for each plot (38 in total) and calculated interaction diversity for each network using the `networklevel` function. Interaction diversity was defined as the exponential of the Shannon diversity of interactions. Interaction diversity was compared between the gardens and unmanaged habitat using a linear-mixed effect model and the previously described method.

**Similarity analyses**

In order to evaluate whether landscape scale species turnover followed Model One or Model Two we compared the similarity of species and interactions in the gardens and unmanaged habitats using three measures of beta diversity, derived from the $C_{qn}$ measure (Gotelli & Chao, 2013). As with the previously described Hill’s numbers, $q$ is a parameter to that determines the measures’ sensitivity to species’ relative abundances and N is the number of assemblages (in this case $N = 2$ for the high and low mountains respectively). For $q=0$, $C_{0N}$ is the Sorenson similarity index; for $q=1$, $C_{1N}$ is the Horn overlap index; and for $q=2$, $C_{2N}$ is the Morisita-Horn similarity index. These three similarity indices were calculated for flower-visitors, flowers and their interactions in SPADE using 200 iterations (Chao & Shen, 2010). $C_{qn}$ ranges between unity (when communities are identical) and zero (when communities are completely different). Higher similarity means more species shared between gardens and unmanaged plots and would indicate the potential to increase local diversity. Lower similarity means fewer shared species and would indicate that the gardens are supporting a distinct community of species thus increasing landscape heterogeneity. In order to assess the proportion of shared species in gardens and natural plots we then estimated the total relative abundance of shared species and interactions in (a) gardens and (b) natural plots, using an adjusted Sorenson’s similarity index.
3. Results

Plant-pollinator interactions in the gardens and unmanaged habitat

In the high mountains, the gardens had no significant effect upon the abundance of plants or pollinators (Table 1). Plant diversity ($^{0}D$, $^{1}D$ and $^{2}D$) was significantly higher within the gardens, but there was no significant difference in the diversity of pollinators. The cumulative visitation networks were of a similar size in the gardens and unmanaged plots, with a total of 478 interactions (between 80 insect and 40 plant species) in the garden network (Fig 3 A), and 365 interactions (between 77 insect and 27 plant species) in the unmanaged network (Fig 3 B). There was no difference in the average diversity of interactions (Table 1).

In the low mountains, the gardens had a much stronger positive effect upon the abundance and diversity of plants and pollinators. Plant and pollinator abundance were significantly higher within the gardens than the unmanaged habitat, as were plant diversity ($^{0}D$, $^{1}D$ and $^{2}D$) and pollinator diversity ($^{0}D$ and $^{1}D$) (Table 1.) In the low mountain gardens the cumulative visitation network (Fig 3 C) consisted of 1389 interactions (between 111 insect and 53 plant species) and was almost eight times larger than the unmanaged network (Fig 3 D) which consisted of 178 interactions (between 53 insect and 25 plant species). The average diversity of interactions was significantly higher within the garden networks (Table 1).

The ten most abundant pollinator species for each habitat are shown in Appendix A2. In the high mountains, seven of these ten species occurred in gardens and unmanaged habitats, with *Megachille walkerii* the dominant species in both. In the low mountains, six of these ten species occurred in gardens and unmanaged habitats and *Syritta fasciata* and *Apis mellifera* were the dominant species in both. In accordance with the Hill's diversity estimates (Table 1), there tended to be one or two highly abundant flower-visitors in each habitat followed by many rarer species.

Species similarity of plants and pollinators

In accordance with Model One, plants exhibited low levels of similarity between gardens and unmanaged plots in both the high and low mountains, with the similarity of interactions lower still (Fig 4). The similarity of plants and interactions decreased steeply to the order of $q$, suggesting that a high proportion of species and interactions were shared, but that the identities of abundant species and interactions tended to differ. In accordance with Model Two, pollinators exhibited high levels of similarity between gardens and unmanaged plots in both the high and low mountains (Fig 4). As with the flowers and interactions, similarity
decreased to the order of \( q \) again suggesting that rare species were more likely to be shared between the two habitats than common or abundant species.

The vast majority of plants and pollinators observed within the unmanaged plots were shared with the gardens with approximately 90% of the species and interactions from the natural habitat also found within the gardens (Fig 5). Within the gardens, the majority of pollinators were shared with the natural habitat, but the proportion of shared plants and interactions was considerably lower with approximately half of all plants and interactions unique to the gardens. This suggests that the dissimilarities in community structure are primarily due to the presence of novel plant species and interactions within the gardens and not due to a loss of species or interactions in either habitat.

4. Discussion

Patterns of landscape scale diversity differed between the two levels of the interaction network, with plants and pollinators exhibiting contrasting patterns of species turnover. As predicted, plants followed Model One (Fig 1 A), with gardens increasing the overall landscape heterogeneity by supporting a distinct assemblage of species that was highly dissimilar to that in the unmanaged habitat. Pollinators followed Model Two (Fig 1 B) and showed extremely low levels of turnover across the landscape, with gardens increasing local diversity (in the low mountains) by supporting species that were already present in the natural species pool. This is consistent with the idea that better dispersers (in this case the pollinators) tend to have lower levels of beta diversity (Soininen, Lennon & Hillebrand 2007) and demonstrates that pollinators have the capacity to modify the floral resources that they forage upon.

The impact of the gardens and the importance of landscape context

The quality of the surrounding habitat affected how the pollinator community responded to the presence of the agricultural gardens. At higher altitudes the natural habitat is relatively water-rich and undisturbed, containing a high abundance and diversity of wild flora (Ayyad et al., 2000). In this high quality habitat, gardens supported an equally abundant and more diverse plant community than the unmanaged habitat, but had no impact upon the complexity of the interaction networks or the abundance of dependent pollinator. Conversely, in the low mountains where natural floral resources were scarce, the gardens actively increased the complexity of interaction networks and the abundance and diversity of pollinators. Both ornamental and agricultural gardens have been known to boost pollinator abundances in other resource-limited habitats, such as desert environments (Gotlieb et al., 2011), heavily developed cities (Matteson et al., 2008) and intensively managed farmlands.
(Samnegård et al., 2011) and these agricultural gardens seem to have a similar positive effect upon pollinator abundances in the low mountains where the surrounding environment is particularly sparse.

Gardens in the poorer-quality landscape received twice as many pollinators as those in the high mountain gardens, despite gardens supporting an equal abundance and species richness of flora. These inflated abundances could be indicative of a “crowding effect” in the low mountains, with gardens acting as florally-rich islands that collect species from the surrounding sparse habitat. The crowding effect has been documented for arthropods in highly fragmented habitats (Collinge & Forman, 1998; Debinski, 2000; Zhao et al., 2011), and predicts that when habitat is removed from a landscape, surviving individuals in the disturbed matrix will move into the remaining habitat fragments leading to elevated densities (Grez et al., 2004). In a reversal of typical habitat fragmentation, the human-modified gardens may be acting as resource-rich islands in the low quality desert habitat, resulting in elevated densities of pollinators within the gardens. In recently fragmented habitats, crowding effects tend to be transient, with inflated densities adjusting to a lower equilibrium within a matter of months (Debinski, 2000; Grez et al., 2004), though abundances can be maintained through sustained immigration from neighbouring populations (Bowman et al., 2002). The gardens in the low mountains all date back 50 years or more (Gilbert, 2011), so the high abundances of pollinators are unlikely to be transient, but it is possible they are being maintained through sustained immigration from the high mountains.

**Contrasting turnover between plants and pollinators**

Plants exhibited high levels of landscape level turnover, with distinct communities of species in the gardens and the unmanaged habitat. This was primarily due to the additional presence of cultivated species within the gardens and was not a reflection of a loss of wild plant species, with gardens supporting the vast majority of wild flowers (95 %) and interactions (85 %) that were present in the unmanaged habitat. Other studies in the region have shown that the gardens contain a higher diversity of wild plants than the natural habitat (Norfolk et al., 2013), suggesting that these rain-water irrigated gardens are having a positive role in the conservation of native flora in this region.

The presence of cultivated flora led a major restructuring of the plant-pollinator interaction networks. Despite this, pollinators maintained an extremely similar community of species in the gardens and unmanaged habitat. Pollinators were able to adapt to the novel floral resources within the gardens, with interactions with cultivated flora augmenting those with wild species. Such generalised foraging behaviour has been observed in other systems, with many alien flowers receiving substantial levels of visitation from native pollinators (Bjerknes
et al., 2007; Graves & Shapiro, 2003; Williams et al., 2011). Alien flora can become well integrated in visitation networks (Memmott & Waser, 2002; Vilà, Bartomeus, Dietzsch, Petanidou, Steffan-Dewenter et al., 2009) to such an extent that the simulated removal of alien plants can lead to species extinctions when flower-visitors fail to reorganise their interactions (Valdovinos et al., 2009). In accordance with other studies, cultivated flora (some of which were alien to the region) were deeply integrated into visitation networks within the gardens and provided important resources for native pollinators.

Using three measures of alpha and beta diversity allowed us to establish the relative abundance of rare, common and abundance species within the two habitats; flower-visitors showed unusual patterns of alpha diversity in both habitats, with a higher diversity of hyper-abundant species than of common species. The distribution was highly uneven, with several highly-abundant dominant species and numerous rare species. The dominance of one or two pollinator species has been in observed in other desert systems (Gotlieb et al., 2011) and may be a reflection of the unusual distributions of floral resources associated with this arid environment. Levels of species similarity also differed for rare, common and abundant species, with rare species more likely to be shared between the two habitats than common or abundant species. This pattern is expected for the plants, because the highly abundant species tended to be cultivated species that only existed within the gardens, with the rarer wild native species most likely to be found in both habitats.

**Conclusions**

This study highlights the positive potential of arid land agriculture for pollinator conservation, showing that rainwater-fed gardens can maintain and in cases actively enhance pollinator abundance and diversity. The high species similarity of pollinators in the gardens and the surrounding unmanaged habitat suggests that the benefits of agriculture are being experienced by the whole community and not just by common, generalist pollinators. The vast majority of work on pollinators comes from temperate and tropical regions, where agricultural conversion typically results in a reduction in bee abundance and diversity (Ferreira et al., 2013). We demonstrate that the situation is very different in arid environments like South Sinai, where these irrigated agricultural gardens are maintaining pollinator abundance and diversity, and in some cases actively increasing it.
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References


Gilbert, H. (2011) 'This is Not Our Life, It's Just a Copy of Other People's': Bedu and the Price of 'Development' in South Sinai. Nomadic Peoples, 15, 7-32.


Norfolk, O, Gilbert, F (In review) Insect visitation rates to wild flowers increase in the presence of arid agriculture in South Sinai, Egypt. Journal of Arid Environments.


Table 1. Mean abundance and diversity of plants, pollinators and their interactions in the gardens and unmanaged plots (± Standard Error of the Mean) and the results of linear mixed-effect models comparing the two habitats. Models contained abundance/diversity as the response variable, habitat (gardens/unmanaged) as the fixed effect and wadi a random effect.

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Fig 1. Two conceptual models describing patterns of diversity between gardens and unmanaged habitat. (A) Model One predicts that diversity is maintained in distinct assemblages that contain novel species (B) Model Two predicts that diversity is maintained in overlapping assemblages that form a nested subset of the entire species pool.

Fig 2. Map of study site, with locations of gardens and unmanaged plots.

Fig 3. Quantitative bipartite networks of the interactions between flowers and insect-visitors in gardens and unmanaged habitats. In each network the rectangles represent plants (bottom row) and insects (top row) and the connecting lines represent links between species. The width of the rectangle represents the total number of interactions, and the widths of the connecting lines represent the number of interactions observed for that link. The insects in the top row are grouped by taxonomic groups. The plants in the bottom rows represent species, with species names listed in Appendix A3.

Fig 4. The similarity profile $C_{qN}$ of species and interactions in gardens and unmanaged plots for A) high mountains and B) low mountains, for $q = 0, 1, 2$. $C_{qN}$ ranges between unity (when communities are identical) and zero (when communities are completely different).

Fig 5. The relative abundance of shared species and interactions in the all gardens and natural plots, estimated using an adjusted Sorenson’s similarity index with 200 iterations, error bars represent standard errors.
Fig 1

(A) Model One

(B) Model Two
FIG 2

- **High mountain gardens** >1800 m. asl.
- **Low mountain gardens** 1300-1550m asl.
- **Unmanaged plots**

High mountain gardens are indicated by black circles, low mountain gardens by gray circles, and unmanaged plots by open circles.
FIG 3

SYR= Syrphidae, DP = true flies, BOM = Bombylidae, APIS= *Apis mellifera*, APID= other Apidae, HAL= Halictidae, MEG= Megachillidae, CRAB= Crabonidae, VESP= Vespidae, LEP= Lepidoptera, COL= Coleoptera

SYR DIP BOM APIS APID COLLET HAL MEG SOL_WASP PARASITIC LEP COL
AC AK
AM
AO
AS
AS1
BB
BO BU BV
CG
CH...
FIG 4

(A) High mountains

(B) Low mountains

Similarity ($C_{qN}$)

- Pollinators
- Plants
- Interactions
Fig 5

Relative abundance of shared species/interactions

- Pollinators
- Plants
- Interactions

Garden □ Unmanaged
### Plant species

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<td>DH</td>
<td>Diplotaxis harra</td>
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<td>HP</td>
<td>Hyosyarus pusillas</td>
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<td>IC</td>
<td>Ipomea cairica</td>
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<tr>
<td>LN</td>
<td>Launaea nudicaulis</td>
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<tr>
<td>LP</td>
<td>Lavandula pubescens</td>
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<td><em>Matthiola arabica</em></td>
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<tr>
<td>ML</td>
<td><em>Matthiola longipetala</em> (sub sp livida)</td>
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<tr>
<td>OS</td>
<td><em>Origanum syriacum</em></td>
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<tr>
<td>P</td>
<td><em>Papaver sp</em></td>
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<td>PA</td>
<td><em>Phlomis aurea</em></td>
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<td><em>Petroselinum crispum</em></td>
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<td><em>Prunus dulcis</em></td>
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<td>PG</td>
<td><em>Punica granatum</em></td>
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<td><em>Peganum harmala</em></td>
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<td>PO</td>
<td><em>Portulaca oleracea</em></td>
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<tr>
<td>PR</td>
<td><em>Paracaryus rugulosum</em></td>
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<tr>
<td>PV</td>
<td><em>Phaseolus vulgaris</em></td>
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<tr>
<td>R</td>
<td><em>Rosa sp</em></td>
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<td><em>Rosa canina</em></td>
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<td><em>Rosmarinus officinalis</em></td>
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<td><em>Stachys aegyptiaca</em></td>
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<td><em>Salvia multicaulis</em></td>
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<td>SN</td>
<td><em>Solanum nigrum</em></td>
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<td>SX</td>
<td><em>Scrophularia xanthoglossa</em></td>
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<td>TS</td>
<td><em>Tanacetum santolinoides</em></td>
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<tr>
<td>UK1</td>
<td><em>Asteraceae unknown sp.</em></td>
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<tr>
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<td><em>Asteraceae unknown sp.</em></td>
</tr>
<tr>
<td>VS</td>
<td><em>Verbascum sinaiticum</em></td>
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<tr>
<td>VV</td>
<td><em>Vitis vinifera</em></td>
</tr>
<tr>
<td>ZS</td>
<td><em>Zilla spinosa</em></td>
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Appendix A2. The most common flower-visitors observed in gardens and control plots

<table>
<thead>
<tr>
<th>Garden</th>
<th>High Mountain (&gt;1800m)</th>
<th>Low Mountain (1500m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N (% visits)</td>
<td>Unmanaged N (% visits)</td>
</tr>
<tr>
<td>Megachile (Eutricharea) walkeri</td>
<td>84 (17 %)</td>
<td>Megachile walkeri</td>
</tr>
<tr>
<td>Dalla Torre 1896</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hylaeus (Dentigera) sinaicicus</td>
<td>59 (12 %)</td>
<td>halicld 8</td>
</tr>
<tr>
<td>(Alffen 1938)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Omophlus sp. A</td>
<td>33 (6 %)</td>
<td>Anthophera pauperata</td>
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<tr>
<td></td>
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<tr>
<td>Seladonia smaragdula</td>
<td>25 (5 %)</td>
<td>Capitites augur</td>
</tr>
<tr>
<td>(Vachal 1895)</td>
<td></td>
<td>(Frauenfeld)</td>
</tr>
<tr>
<td>Lampides boeticus L.</td>
<td>23 (5%)</td>
<td>Hylaeus sinaicicus</td>
</tr>
<tr>
<td></td>
<td></td>
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</tr>
<tr>
<td>Euepodes corrolae (Fabricius 1794)</td>
<td>17 (5 %)</td>
<td>Seladonia smaragdula</td>
</tr>
<tr>
<td>Syritta fasciata (Wiedemann 1830)</td>
<td>15 (3 %)</td>
<td>Halictus tibialis</td>
</tr>
<tr>
<td>Coccinella septempunctata L.</td>
<td>13 (3 %)</td>
<td>Omophlus sp. A</td>
</tr>
<tr>
<td>Capitites augur (Frauenfeld)</td>
<td>13 (3 %)</td>
<td>Euepodes corrolae</td>
</tr>
<tr>
<td>Halictus tibialis Walker 1871</td>
<td>13 (3 %)</td>
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</table>