

Insights from measuring pollen deposition: quantifying the pre-eminence of bees as flower visitors and effective pollinators

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Abstract Using our accumulated datasets from Kenyan savanna, Mediterranean garigue, UK gardens and heathland, involving 76 plants from 30 families, we present detailed data to quantify the superiority of bees as pollinators of most flowering plants when compared with other flower visitors. Bees provided the majority of visits to study species at all sites, and 33 of the 76 plants received more than 90% of their visits from bees. Furthermore, pollen deposition onto stigmas from single-visit events (SVD, a measure of pollination effectiveness) was significantly higher for bees than non-bees at all the four sites where a major proportion of the flora was sampled. Solitary bees, and also bumblebees in temperate habitats, were the best potential pollinators for most plants in this respect, and significantly out-performed honeybees. Only a few plants were well served by bombyliid flies, and fewer again by larger hoverflies, butterflies, or solitary wasps. Bees also achieved better matches of their visit timing to peak pollen availability (measured indirectly as peak SVD), and made much shorter visits to flowers than did non-bees, permitting a substantially greater visit frequency. Additionally, they deposited significantly lower levels of potentially deleterious heterospecific pollen on stigmas in heathland and Mediterranean garigue, though not in the UK garden with

densely clustered high-diversity flowering, or in the Kenyan savanna site with particularly dispersed flowering patches and some specialist non-bee flowers. Our data provide a novel and quantified characterisation of the specific advantages of bees as flower visitors, and underline the need to conserve diverse bee communities.

Keywords Pollination · Pollen deposition · Bees · Flower visit duration · Visit timing · Heterospecific pollen

Introduction

There has been a long tradition of seeking to improve our understanding of pollinator effectiveness or importance when visiting flowers (e.g. Primack and Silander 1975; Wilson and Thomson 1991, 1996; Adler and Irwin 2006; Ne'eman et al. 2010), rather than just recording visitation frequencies. Achieving this improvement can have a substantial impact on our views of the broader issue of generalisation and specialisation in pollination (Ollerton et al. 2009; Willmer 2011; Armbruster 2017). For several years, we have therefore been using measurements of single-visit pollen deposition (SVD) onto previously unvisited stigmas, across four very different habitats, to compare the qualities of flower visitors as effective floral pollinators, with the aim of producing more realistic 'pollination networks' than those previously based on visitation alone. Our studies, at four sites, have used standard network metrics to highlight the increased specialisation revealed when pollinator performance measures are incorporated into network analyses (Ballantyne et al. 2015, in press and in prep). This exercise, with consistent methods of assessment across sites, has also allowed us to accumulate large pollinator visit datasets at a community level, and in this paper we specifically extract

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our information on ‘bees’ compared with ‘all other visitors present’, across four very different habitats, in the UK (heathland and gardens), Israel (Mediterranean garigue) (Potts et al. 2006) and Kenya (savanna). The dataset includes 76 flower species, and for the four key sites include examples of most of the common flowers and floral morphological types in bloom at the time of surveys, with representatives from 30 families. Earlier studies have commonly reported the better performance of bees on single plant species (e.g. Pellmyr and Thompson 1996; Sahli and Connor 2007) or on a few species that co-flower and may be competing for pollinators (Watts et al. 2012; cf Garibaldi et al. 2013); but no previous study has accumulated such detailed data for large parts of multiple flowering communities.

Our comparisons for each plant species concentrate on several key parameters to compare bees and other visitor types, on a quantified community scale. What proportions of all visits made, in the community and for individual plants, were from bees? How do mean pollen deposition levels per visit (SVD, pollination effectiveness) compare for bees and for other visitors, and how does pollen deposition vary with bee size/sociality (comparing *Apis*, *Bombus*, and three size groupings of solitary bees)? How well is peak visitation time matched to peak pollen availability through the day for the different visitors? How does visit length for different taxonomic groups relate to effective pollen deposition? And how do amounts of heterospecific pollen deposition vary between visitors?

From all these records, we strengthen and quantify the case for bees having key behavioural characteristics that make them by far the most effective and important pollinators for the great majority of all the plants included in these studies, and across a variety of habitat types. It should be noted that our study areas did not include bird- or bat-pollinated plants, where flower traits (advertisements and rewards) commonly match these larger flower visitors and where bees may be relatively ineffective (reviewed in Willmer 2011).

Methods

Sites and choice of flowers used

Dorset heath

Data were collected at Hyde Heath, Dorset (50°43.7′N 2°07.2′W) from late May to late August in 2013, and in early May 2014. This ancient heathland is dominated by the heathers *Erica tetralix*, *Erica cinerea* and *Calluna vulgaris* and the gorses *Ulex europaeus* and *Ulex minor*. All five plant species were used (Ballantyne et al. 2015).

Israel

Data were collected from early February to late April in 2014 and 2015, in a 0.35 km² area of sheep-grazed garigue habitat on Mount Carmel National Reserve, (32°729740′N, 35°010495′E). Data collection covered the Mediterranean ‘spring burst’ period (Pico and Retana 2001; Petanidou and Lamborn 2005), when Israeli flower visiting is dominated by bees and bee diversity (of species and genera) is particularly high. A total of 23 plant species were used, which represented a reasonable proportion of total species diversity (~35%).

Kenya

Data were collected within Mpala Research Centre, Laikipia Province (0°292244′N, 36°898045′E) from early July to early September 2014 and mid-May to early July 2015. A total of 19 plant species were used here, with a wide range of visitor groups, and including flowers mainly visited by flies, wasps or lepidopterans, with a lesser domination by bees.

UK Kent garden

Data were gathered across two summer seasons (May to August 2014, March to August 2015), from a garden in Dover College, (51°7′N, 1°18′E), with data from 26 species included here.

For these last three sites, where plant diversity was high, plant species were selected if they (i) were common in the environment, representing a high proportion of floral density at the time of study; (ii) had a high enough visitation rate to allow generation of a satisfactory sample size of flower visitors; and (iii) contributed towards a morphologically and taxonomically diverse dataset. A few common floriferous species were initially assessed but not included due to high levels of self-pollen contamination (particularly small Asteraceae and Apiaceae).

For the *UK Fife garden*, only three plants are included here, each specifically selected for high abundance and high visit frequency by bees, as part of other pollination studies. Data are included here only when additional insight into key issues can be gained.

A summary of the plants used at each site, with their family and key aspects of morphology, is given in Supplementary Material Table 1.

SVD and visitation records

To determine single-visit pollen deposition (SVD—our measure of pollinator effectiveness, PE), flowers or inflorescences were bagged in the evening, with fine mesh

sheeting or with more carefully constructed mesh pollination cages as appropriate. The following morning bags were carefully removed and, where whole plants had been bagged, flowers with virgin stigmas were identified using a hand lens. In many cases, stigma receptivity occurred on the first day following bagging, but a few species (usually long-lived and strongly protandrous) were unbagged two or three days later when stigmas did become receptive.

The unbagged flowers were then observed until their first visit. Where possible insect visitors to flowers were identified by eye to species or genus; if this was not possible, a visitor was either photographed or caught for later identification. The visitor identity, length of visit and behaviour at the flower were recorded. To acquire realistic pollen deposition values, insects were always allowed to complete their visit before being disturbed or captured, unless the visit exceeded 5 min. Recordings for SVD were partly weather-dependent but usually carried out throughout the morning and into the mid or late afternoon. Surveys continued on each day until there were no more bagged flowers to sample, and/or visitation rate had decreased to a very low level. (Note that in always taking the first visit to each unbagged flower, occasional types of visitors to particular plants were not recorded, so that our reports of (for example) ‘percentage of visits by bees’ to flowers may not always reflect the absolute ratios of visitor types; thus, for some species with ‘100% bee visitation’, we did in practice observe very occasional visits from other groups not supplying a SVD record).

Following a visit, the stigma of the target flower was removed with tweezers and dabbed several times onto a 1–2 mm³ cube of fuchsin gel, simultaneously removing and staining all pollen. The gel was then melted under a coverslip and the slide stored: all conspecific and heterospecific pollen grains deposited were later counted under a light microscope ($\times 400$). Pollen could be identified to species in most cases, with the exception of *Cistus* spp. and some Brassicaceae pollen in Israel, which had to be treated as conspecific pollen on these plants.

Control stigmas (11–34 per species, depending on variance) were also sampled, by removing stigmas from bagged flowers before a visit took place and assessing pollen presence microscopically in the same way, to account for pollen found on stigmas due to opening of the flower and/or handling and bagging procedures. Mean control SVD values per species were subsequently subtracted from individual SVD records.

All visitation and SVD data were organised in 1-h time bands, except for the UK garden where less precise timings were available. We assume that the hour of day at which peak SVD values were recorded is a reasonable proxy for the timing of peak pollen availability in the flowers of a given species; this is broadly supported by personal

observations (unpublished) on several species in our experimental laboratory work, and specifically for the Israel site (Ballantyne et al. in press). Methods for matching peak timing of visits to this peak pollen availability were problematic, with no appropriate statistical options. Instead, two methods of assessing a match were used: conservatively scoring a ‘yes’ where peak visiting hour coincided with single peak SVD hour, or with one of multiple peaks where these were within 10% of the maximum; or scoring a ‘yes’ where peak visiting hour was within one hour on either side of the maximum SVD (a less conservative criterion, especially as some flowers only offered pollen for 3–4 h daily).

Categorisation of solitary bee size groups (small, medium and large) was based on standard bee taxonomic sources and our own field observations at each site, and at the generic level (disregarding occasional outliers such as two rarer medium-sized species of *Andrena* amongst many species categorised as small).

Statistical methods

As all datasets used here included many zero values, invalidating parametric test assumptions, and simple and more conservative non-parametric approaches were preferred to identify large-scale patterns in the data. Mean values for plants within a site, and between totals or means for all sites, were compared using Mann–Whitney tests. Values in the Results are given as means ± 1 SE, where appropriate medians and statistical values (all given in a separate table) are also cited in the text.

More in-depth models of species-level analyses can be found in the single-site publications that underlie this overview paper (Ballantyne et al. 2015 (Dorset); Ballantyne et al., in press (Israel) and in prep (Kenya); Cunnold et al, in prep (Kent)).

Results

(A) What proportions of all visits made, in the community and for individual plants, were from bees?

For most sites, the proportions of flower visits during SVD recording that were performed by bees at the community level were above 75% (see Table 1). The highest level of 94.3% was recorded for the simplest habitat of UK heathland, which had only five flowering plants in the spring/summer months (3 heathers and 2 gorse), visited almost entirely by species of bumblebee and in the case of heathers also by *Apis* and some small solitary bees (*Andrena*, *Lasioglossum*, *Colletes*). The small percentage of

Table 1 Numbers of plant species studied by site, and proportions of visits to all those plants summed across each site, and mean SVD (\pm SE) for bees (*Apis*, *Bombus* and three size-categories of solitary bees) and for non-bees

No. of plant species	% visits by bees	Mean SVD	Main NON-BEE groups										ALL NON-BEES																																												
			Solitary bees			All bees			Beetles			Wasps			Leps			Ants																																							
			<i>Bombus</i>		Small	Medium	Large	Flies			Beetles			Wasps			Leps			Ants																																					
UK Dorset heath	5	94.3	18.9 \pm 1.5 (322) 4	28.6 \pm 1.4 (891) 5	35.7 \pm 6.1 (49) 5	26.4 \pm 1.2 (1262)	14.8 \pm 3.0 (60) 4	5.5 \pm 5.0 (14) 1	13.0 \pm 2.1 (75)	UK Kent garden	26	80.6	166.8 \pm 19.7 (284) 17	198.4 \pm 10.0 (1226) 22	92.7 \pm 10.6 (399) 21	244.7 \pm 23.8 (106) 11	165.2 \pm 7.5 (2223)	83.8 \pm 8.0 (549) 20	69.0 \pm 37.0 (25) 5	51.6 \pm 29.9 (18) 6	530.7 (59)	82.0 \pm 5.2 (599)	UK Fife garden	3	78.6	18.8 \pm 2.8 (61) 3	22.5 \pm 4.4 (513) 3	13.0 \pm 4.5 (15) 1	21.9 \pm 3.1 (589)	1.7 \pm 1.3 (156) 3	1.7 \pm 1.3 (156)	Israel	23	78.7	92.7 \pm 12.1 (483) 14	156.0 \pm 2.5 (1601) (1) 1	116.9 \pm 19.2 (403) 17	70.1 \pm 16.9 (290) 13	116.9 \pm 7.5 (1785)	70.5 \pm 18.7 (381) 18	106.8 \pm 13.5 (63) 14	37.4 \pm 25.2 (25) 2	72.9 \pm 7.5 (483)	Kenya	19	55.0	29.3 \pm 9.2 (180) 9	66.9 \pm 8.9 (284) 18	82.3 \pm 12.4 (243) 16	64.8 \pm 7.6 (384) 13	63.4 \pm 3.8 (1091)	56.3 \pm 7.1 (289) 15	34.6 \pm 15.1 (18) 8	44.4 \pm 11.1 (198) 14	29.6 \pm 3.6 (287) 15	61.4 \pm 8.6 (93) 8	44.4 \pm 1.4 (896)

Leps lepidopterans

Numbers in italics indicate the number of the studied plant species that were visited by that genus or group. For non-bees, only the main taxa are shown, omitting small numbers of visits by other groups (included in total non-bee means). For the Kent garden site, there was an anomaly of many high SVD visits by butterflies to just one plant (*Buddleja*) and these are omitted in calculating the non-bee mean SVD. For every site, the 'all bee' mean and the 'all non-bee' mean are significantly different (Table 2)

visits by other taxonomic groups mainly involved syrphid and muscid flies, especially to *Calluna vulgaris* flowers, and occasional visits by *Lasius* ants to *Erica tetralix*. Israeli and UK sites recorded about 80% bee visitation, across their wider floral diversities.

For one site, the Kenyan savanna, the overall percentage of flower visits made by bees was substantially lower at just 55.0%. This reflects the wider range of floral types occurring here and the presence of several plant species that were largely avoided by bees and instead visited mainly by wasps (*Achyranthes*, *Heliotropium*), various flies (*Acacia gerrardii*, *Balanites*), lepidopterans (*Barleria*) or a mixture of small bees, bombyliid flies and butterflies (*Pentanisia*).

Hence, at the level of individual plants, proportions of visits by bees were highly varied (Supplementary Material Table 2), with values from 0 to 100%. In

Dorset, all five plants received close to or above 90% bee visits. In Israel, 19 of the 23 plants had over 60% of their visits from bees (many of these bee-specialists with over 90% bee visits, and *Nonea*, *Phlomis* and *Prasium* with 100%), whilst *Convolvulus*, *Ornithogalum* and *Tordylium* received around 40% bee visits and *Linum* (a known bombyliid specialist (Johnson and Dafni 1998)) had none. In Kenya, 10 out of the 19 plants had over 60% bee visits (only three, *Chlorophytum*, *Commelina* and *Hypoestes*, recording over 90%), whilst seven received less than 20% bees. In the Kent garden, 20 of 26 plants had >60% bee visits (many being bee-specialists with over 90% bee visits, and *Cotoneaster*, *Crataegus*, *Digitalis*, *Geranium* and *Pentaglottis* with 100%). As an overview, of the 76 plants studied across all 5 sites, 60 had >50% bee visits and 33 received >90% bees.

Table 2 Mann–Whitney tests for significance, showing medians where (appropriate) and *p* values, for the main comparisons covered in the text

(a) SVD bee vs. SVD non-bee across sites.

	Median values		<i>p</i> value
	Bee	Non-bee	
Kenya	7	2	<i>p</i> < 0.01
Israel	10	1	<i>p</i> < 0.0001
Kent garden	24	4	<i>p</i> < 0.001
Dorset heath	12	1	<i>p</i> < 0.001

(b) SVD bee comparisons for individual groups in each site (*p* values)

	Kenya	Israel	UK Garden	UK Heath
ss vs. ms	0.019	0.032	0.006	–
ss vs. ls	NS	0.000	NS	–
ms vs. ls	0.007	NS	0.008	–
ss vs. <i>Apis</i>	0.000	0.0004	0.029	0.0079
ms vs. <i>Apis</i>	<0.001	NS	NS	–
ls vs. <i>Apis</i>	<0.001	NS	0.024	–
ss vs. <i>Bombus</i>	–	–	0.000	NS
ms vs. <i>Bombus</i>	–	–	NS	–
ls vs. <i>Bombus</i>	–	–	<0.001	–
<i>Bombus</i> vs. <i>Apis</i>	–	–	0.002	0.001

(c) Visit lengths (s)

	Median values		<i>p</i> value
	Bee	Non-bee	
Kenya	2	3	<i>p</i> < 0.0001
Israel	7	13	<i>p</i> < 0.0001

(d) % Heterospecific within sites (*p* values)

	Kenya	Israel	UK Garden	UK Heath
Bee vs. non-bee	<0.0001	0.0002	<0.0001	0.24

ss small solitary bees, ms medium, ls large

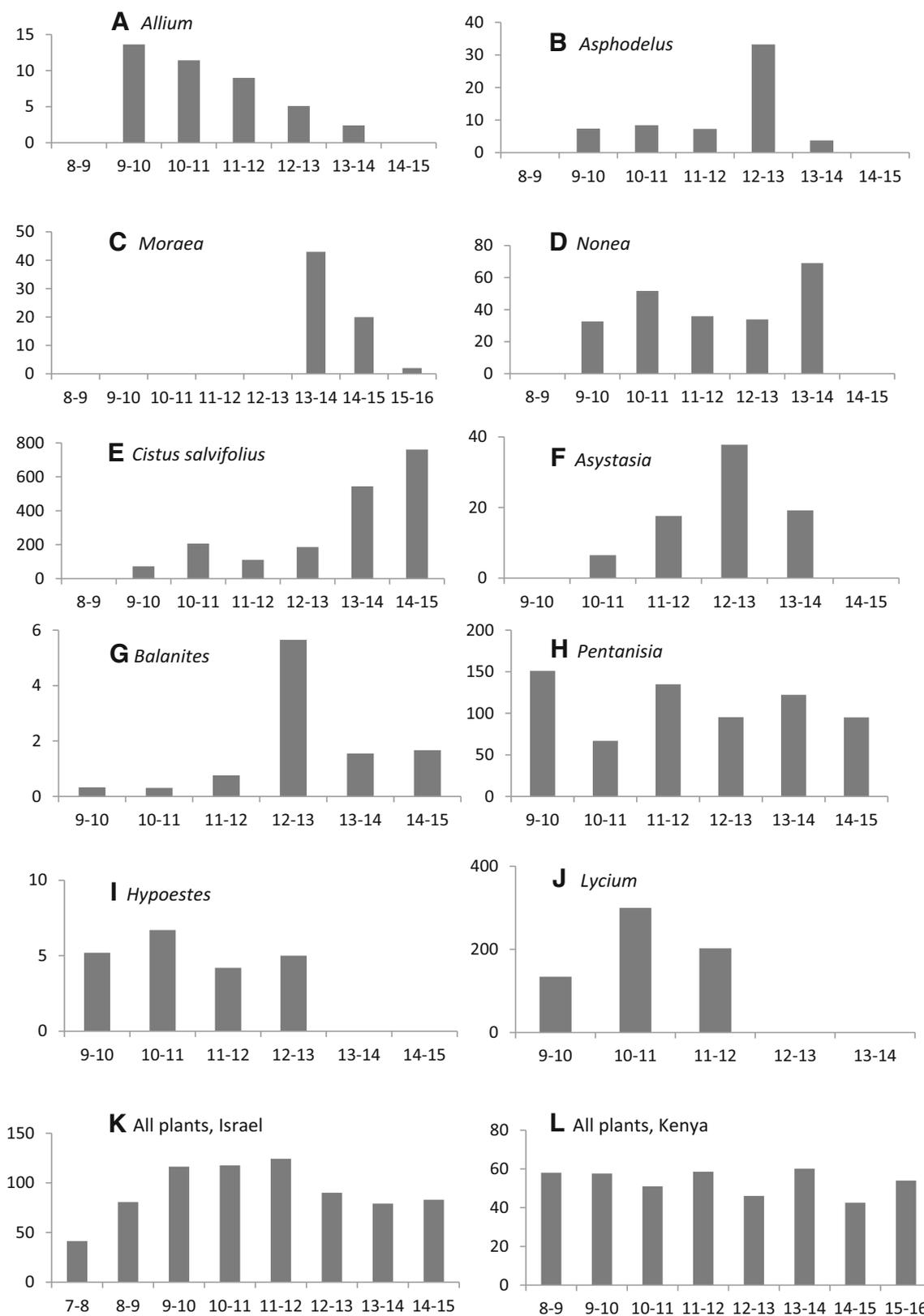


Fig. 1 Examples of differing patterns of SVD (number of pollen grains deposited, y axis throughout) through time of day (hourly bands local time, x axis) grouped for all visitors to a particular plant, giving a proxy

of pollen presentation/availability for that plant species. **a–e** from Israeli Mediterranean garigue, and **f–j** from Kenyan savanna. **k** and **l** show the mean SVDs for all plants combined for Israel and Kenya, respectively

(B) How do mean pollen deposition levels per visit compare for bees and for other visitors?

Table 1 also shows the mean SVD values recorded for bees and for other flower visitors, for each of our five communities. Overall, the mean SVD value for all bees was significantly greater than for non-bees at all four main sites (Table 2: $p < 0.01$ for all), with very different median values (and with means differing by a factor of 1.4–2.3) at these sites where most of the concurrently flowering plants were included in the study.

The range of values of SVD inevitably varies greatly between plants depending on how much pollen they produce and deliver to stigmas per flower, in turn partly also related to pollen grain size (reviewed by Cruden 2000). Hence, our mean values also varied across the communities. It could be that the higher mean SVD for bees arose from more bee visits occurring to particular plants with high pollen availability, but Table 1 additionally gives the numbers of plant species visited by each visitor type, and since this was a high proportion of the total for most visitor groups at most sites (especially for small solitary bees), the SVD means per group have not been weighted. Likewise, it could be that bees produced higher SVD scores because they preferred plants with smaller pollen and so inevitably visited flowers that had more pollen to pick up and then deposit; but in practice, there was no relation between proportions of bee visits to a plant and that plant's pollen size (categories shown in Supplementary Material Table 1) (e.g. Pearson correlations: for Israel, -0.24 $p = 0.26$, NS; and for Kenya, -0.14 $p = 0.56$ NS), and plants receiving >90% bee visits had pollen grain sizes covering the whole range, so this alternative explanation for higher SVD scores in bees is unlikely.

Note that the ratio of mean SVD for bees to non-bees was artificially much higher at 12.9 in the Fife garden, because just a few examples of specifically bee-specialist flowers were studied.

Within the bees, *Bombus* species were effective pollen depositors at all the UK sites, and somewhat better than *Apis*, but solitary bees were often the best. Statistical details are again given in Table 2. In the heathland site, *Bombus* were significantly more effective than *Apis*, whilst the small solitary bees (see Sect. “[What proportions of all visits made, in the community and for individual plants, were from bees?](#)”) had a higher SVD (35.7 ± 6.1) than any other bees (significantly higher than for *Apis* but NS for *Bombus*). In the Kent garden site, the highest SVD/pollinator effectiveness (244.7 ± 23.8) for the whole community was delivered by the medium-sized solitary bees, dominated by megachilids; SVDs for small and large solitary groups were significantly lower than this, but not significantly different from each other, whereas both small

and large solitaires and *Apis* were significantly less effective than *Bombus*. *Bombus* had a lower absolute mean SVD than the medium solitaires, though not quite significantly so, and in this case, the megachilid data were uniquely influenced by high visitation to *Campanula* flowers which have high pollen grain number, so that in reality bumblebees were the most effective visitors when the data were weighted. In Israel (with *Bombus* extremely rare), both *Apis* and solitary bees had high mean SVD values, with the small solitary taxa (here including *Andrena*, *Hylaeus*, *Lasioglossum*, *Chelostoma* and *Panurgus*, though the small and shiny *Hylaeus* bees were very poor depositors) together giving the highest mean (156.0 ± 2.5), significantly higher than both medium and large groups and *Apis*. In Kenya (with no *Bombus*), all the solitary bee size groupings outperformed *Apis* very significantly (around 2–3 fold higher mean SVD) and also visited in higher numbers. In summary, solitary bees (and bumblebees in temperate sites) were routinely better pollen depositors than honeybees (Westerkamp 1991).

For the non-bee categories, flies were the best-performing group when averaged across all non-bee visitors in a given community. Particularly high SVD values were often recorded for bombyliids and syrphids; these two families are widely reported as the best pollinators amongst dipteran flower visitors (cf. Willmer 2011) on certain plants. As an example, in Kenya, the mean SVD for bombyliids was 107 ± 15 , but 49 ± 16 for syrphids (although higher at 91 ± 26 if just the larger and more effective eristaline hoverflies were included; cf. Kwak and Bekker 2006). Values were lower at 18 ± 5 for caliphorids and muscids, and 26 ± 16 for small non-muscid flies. Specialist bombyliid-type floral morphologies in Israel (*Convolvulus*, *Linum*, *Ornithogalum*) and in Kenya (*Heliotropium*, *Pentanisia*) did yield high proportions of visits (seen as low % bee visits in Supplementary Material Table 2) and we found at or well above average SVD values (73 ± 16 , 72 ± 9 , 33 ± 11 ; and 217 ± 52 , 148 ± 22 , respectively) for these taxa. Likewise, where flower types were clearly identifiable as having specialist butterfly/moth morphologies (notably *Buddleja* in UK, *Barleria* in Kenya), high proportions of lepidopteran visits were recorded (see low % bees again), still with strong SVD values for that plant (516 ± 46 , 16 ± 2 , respectively) (cf. Roque et al. 2016).

(C) How well is peak visitation time matched to peak pollen availability through the day for different visitors?

Taking the time of day at which peak SVD values were recorded as proxy for the time of peak pollen availability in a given species (see Methods and Discussion), pollen

availability peaks for some plant species (e.g. *Hypoestes*, *Phlomis*, *Nonea*) could be rather broad, across 3 or more hourly time periods, reflecting staggered opening time of individual flowers through a day and/or across days, or could give a clear peak and then a tail-off, often following early morning or midday anthesis (e.g. *Allium*, *Ornithogalum*). Alternatively, there could be a tight midday peak of anthesis giving an even narrower window of high pollen availability (e.g. *Moraea*, less pronounced in *Asphodelus*, *Balanites*). A few plants with many successively dehiscing anthers in a single flower showed rising SVD scores through a day (e.g. *Cistus salvifolius*). Examples of these different patterns are shown in Fig. 1a–j.

Table 3 summarises the matching of peak SVD times and peak visit times, for bees and for non-bees, in the Kenyan and Israeli sites. (The UK Kent garden site was excluded as timings were recorded less precisely, and UK heath data are not shown as there were almost no non-bee visits.) Although quantitative statistics could not readily be applied to the data as gathered retrospectively, there was a positive match using the more conservative scoring (see “Methods” section) of peak bee visits to peak pollen availability in 11 out of 23 plants in Israel, compared with just 5 out of 23 matched timings for non-bees (these mainly attributable to bombyliid or syrphid dipterans). For Kenya, the equivalent values are similar, at 9 out of 19 plants and 4 out of 19, respectively (three of this latter group attributable to many well-timed butterfly visits), and matches were still substantially better for bees than for non-bees. (The more relaxed scoring described in Sect. “Methods” gave higher numbers of positive matches (15/19 cf. 12/19, and 14/23 cf. 9/23), but always preserved the greater number of matches in bees compared to non-bees.) It is noteworthy that bee visits matched well to pollen peaks for some plants where non-bees were much the more common visitors (e.g. *Acacia*, *Achyranthes*—see Supplementary Material Table 2), but where the non-bees did not achieve a temporal match.

For the simple UK heath community, bees’ visit timings matched with the relatively broad pollen availability times for the two gorse species, but were a poor match for the three heathers. This was largely because in this low-diversity flowering site, bumblebees (making 66% of all visits) used all the available plants all day as the weather permitted.

(D) How does visit length vary for different visitors?

Table 4 shows (a) the visit length means for each plant in the Israeli and Kenyan datasets, for bees and for non-bees, and (b) the mean visit lengths per visitor group, also including the Fife UK garden site. Bee visits were

Table 3 Matching of peak visit times to peak pollen availability times (based on peak SVD values, for Kenyan and for Israeli plants), as a yes/no outcome

	Peak of bee visits?	Peak of non-bee visits?
<i>At peak SVD time</i>		
Kenya		
<i>Abutilon</i>	No	No
<i>Acacia</i>	Yes	No
<i>Achyranthes</i>	Yes	No
<i>Asystasia</i>	Yes	Yes
<i>Balanites</i>	No	No
<i>Barleria</i>	Yes	Yes
<i>Chlorophytum</i>	No	No
<i>Commelina</i>	Yes	No
<i>Gutenbergia</i>	No	No
<i>Heliotropium</i>	No	No
<i>Hibiscus</i>	No	No
<i>Hypoestes</i>	Yes	No
<i>Ipomoea</i>	No	No
<i>Lycium</i>	Yes	No
<i>Monechma</i>	No	No
<i>Pentanisia</i>	No	Yes
<i>Plectranthus</i>	Yes	Yes
<i>Solanum</i>	Yes	No
<i>Tribulus</i>	No	No
Match?	9/19	4/19
Israel		
<i>Allium</i>	No	No
<i>Asphodel</i>	No	No
<i>Bellevalia</i>	Yes	Yes
<i>Centaurea</i>	Yes	No
<i>Cistus incanus</i>	No	No
<i>Cistus salvifolius</i>	No	No
<i>Convolvulus</i>	Yes	Yes
<i>Cynoglossum</i>	Yes	No
<i>Echium</i>	Yes	–
<i>Hirschfeldia</i>	Yes	No
<i>Linum</i>	–	Yes
<i>Lomelosia</i>	No	No
<i>Moraea</i>	Yes	–
<i>Nonea</i>	No	–
<i>Ochthodium</i>	Yes	Yes
<i>Ornithogalum</i>	No	No
<i>Phlomis</i>	Yes	–
<i>Prasium</i>	No	–
<i>Ruta</i>	Yes	Yes
<i>Salvia</i>	No	No
<i>Scandix</i>	Yes	No
<i>Stachys</i>	No	No
<i>Tordylium</i>	No	No

Table 3 continued

	Peak of bee visits?	Peak of non-bee visits?
Match?	11/23	5/23

The more conservative pragmatic method for determining a temporal match (see Sect. [Methods](#)) is shown. For both sites, and also for the less conservative method described in the text, bee visits always achieved a greater proportion of temporal matches with plant pollen availability

significantly shorter than non-bee visits for both Israel and Kenya (Table 2: $p < 0.0001$); this was also true for the Kent UK garden where the mean visit length for bees was 6.8 s, and for non-bees was 20.9 s ($p < 0.001$). Within the non-bees, where visits were particularly long (often individually in excess of 5 min), coleopterans were usually responsible, typically resting in flowers and/or eating floral tissues. Fly visits were highly variable in duration (but with bombyliids and syrphids usually shorter than generalist muscids), and visits by lepidopterans and wasps generally shorter than flies (Table 4b).

For every species of plant receiving both bee and non-bee visitors in Israel, the non-bee visits were longer, the ratio of greater durations varying between 1.1 and 32.0. For Kenyan plants, all of which received both kinds of visitors to some degree, the same effect was evident, the duration ratio varying between 1.1 and 15.0 for 18 of the 19 plants. For just one plant, *Heliotropium*, the ratio was below unity (0.6), with the rare bee visits (all by a very small species of *Ceratina*, able to handle these particularly small and narrow corolla flowers) being longer than the much more frequent non-bee visits (dominated by the sphecid wasp *Ammophila*).

Interestingly, for all visitor categories, the flowers received shorter visits in Kenya than in Israel, with the data from the UK garden sites giving values for *Apis* and for flies much closer to the Kenyan mean (and shorter still for *Bombus*); hence, the Israeli site appears to be the unusual outlier here, which may also link to the greater heterospecific pollen deposition note in section (E) below.

From a plant pollination perspective, flower visits by bees, though almost always shorter, nevertheless gave better pollen deposition (cf. Table 1) than non-bees, and since shorter visits additionally offer potentially much higher visit frequency to flowers, there is also a much greater chance of effective pollen flow.

(E) How does heterospecific pollen deposition vary between visitor groups?

Table 5 shows the percentage of heterospecific pollen (HP) grains recorded for bees collectively, bees of different

taxonomic status, and non-bees collectively, across our five sites (statistical details in Table 2). Bees contributed lower HP deposition than the small numbers of non-bees in UK heathland (3.3% compared to 9.2%, $p = 0.1$, NS) but the low rates, especially for *Apis*, resulted largely from non-overlapping flowering phenologies in this low-diversity flora (only five species). Heterospecific deposition was substantially higher in Israel, where there was much greater floral diversity and phenological overlap; here foreign pollen deposition by bees was significantly lower than for the much less numerous non-bees (24.2% cf. 32.1%, $p < 0.03$). In the more dispersed flora of the Kenyan savanna, rates of HP deposition were similar to UK heath, but here non-bees had lower rates overall than bees (7.5% cf. 4.3%, $p < 0.0005$). Supplementary Material Table 3 gives data for individual plant species, showing that 10 of the 19 plants in Kenya received more heterospecific pollen when visited by bees: in some bee-specialist flowers (e.g. *Hypoestes*, *Plectranthus*), foreign pollen on flies and wasps was particularly rare as these visitors could not fully enter the corolla and/or touch the stigma in these flowers, and likewise for large flowers with broad open corollas (e.g. *Abutilon*), any crawling visitors would not contact the central stigma and anthers. For Israel, just 4 of 23 species received more HP when visited by bees, but for three of these the sample size of the non-bee category was too low for further analysis; for *Ruta*, however, the non-bees were all syrphid and small muscid flies and these produced a slightly lower (non-significant) HP deposition (18.4%, $n = 28$) than the bees (25.2%, $n = 63$). The contrasting findings for the two non-UK sites reflect both the presence of some specialist non-bee flowers and the much more dispersed and patchy floral community in Kenyan savanna, where bees would rarely be able to remain flower-constant whilst gathering sufficient daily pollen and nectar supplies for their offspring.

In the Kent garden site, the HP deposition values were lower for non-bee visitors (4.8%) than for bees (6.9%), but particularly varied, between 1 and 72% for the different plant species. This again is not surprising, as in most garden communities bees are less likely to, and less able to, remain flower-constant given that there are rather few plants of any one species, and a very large range of plants are on offer in a small area, whereas non-bees (mostly not pollen-feeders, and needing far lower nectar inputs individually and not collecting directly for their offspring) have less need to move between plants and so deposit less heterospecific pollen. In the Fife garden, there was prolific flowering of the three bee-specialist plants deliberately selected for study, and bees in general (especially bumblebees) rarely moved to other plants on any one trip so producing very low HP deposition (less than 3% for each of the three common *Bombus* species).

Table 4 a Mean visit lengths for bees and for non-bees to each of the plants at the Israeli and Kenyan sites (with number of records in parentheses), and the overall mean for that site

	Bee	Non-Bee	Ratio
<i>(a) Visit durations per plant (s)</i>			
Israel			
<i>Allium</i>	29.6 (66)	187.0 (8)	6.3
<i>Asphodel</i>	14.1 (96)	6.0 (2)	2.4
<i>Bellevalia</i>	7.9 (74)	253.2 (5)	32.0
<i>Centaurea</i>	17.9 (94)	86.1 (8)	4.8
<i>Cistus incanus</i>	28.0 (91)	140.3 (21)	5.0
<i>Cistus salvifolius</i>	21.8 (74)	135.0 (26)	6.2
<i>Convolvulus</i>	8.4 (38)	51.9 (59)	6.2
<i>Cynoglossum</i>	8.9 (55)	35.7 (31)	4.0
<i>Echium</i>	7.2 (138)	42.0 (2)	5.8
<i>Hirschfeldia</i>	7.8 (81)	8.2 (15)	1.1
<i>Linum</i>	–	123.5 (68)	–
<i>Lomelosia</i>	20.8 (86)	76.7 (33)	3.7
<i>Moraea</i>	11.8 (97)	76.3 (4)	6.5
<i>Nonea</i>	5.1 (70)	–	–
<i>Ochthodium</i>	7.4 (72)	15.1 (7)	2.0
<i>Ornithogalum</i>	9.6 (33)	25.7 (46)	2.7
<i>Phlomis</i>	11.8 (105)	–	–
<i>Prasium</i>	17.1 (102)	–	–
<i>Ruta</i>	11.0 (63)	30.0 (28)	2.7
<i>Salvia</i>	13.6 (152)	19.1 (9)	1.4
<i>Scandix</i>	4.4 (62)	12.7 (39)	2.9
<i>Stachys</i>	3.2 (81)	9.3 (10)	2.9
<i>Tordylium</i>	5.7 (45)	11.9 (64)	2.1
Mean	12.4	67.3	5.4
Kenya			
<i>Abutilon</i>	9.1 (94)	15.5 (36)	1.7
<i>Acacia</i>	21.2 (22)	43.7 (77)	2.1
<i>Achyranthes</i>	3.1 (16)	4.5 (97)	1.5
<i>Asystasia</i>	3.3 (45)	11.3 (45)	3.4
<i>Balanites</i>	4.7 (10)	19.6 (63)	4.2
<i>Barleria</i>	2.0 (25)	4.9 (82)	2.5
<i>Chlorophytum</i>	10.9 (69)	18.0 (5)	1.7
<i>Commelina</i>	3.5 (83)	24.9 (9)	7.1
<i>Gutenbergia</i>	2.8 (76)	16.1 (34)	5.8
<i>Heliotropium</i>	5.0 (5)	2.8 (100)	0.6
<i>Hibiscus</i>	16.8 (56)	38.3 (49)	2.3
<i>Hypoestes</i>	1.6 (122)	7.4 (7)	4.6
<i>Ipomoea</i>	25.9 (78)	121.0 (9)	4.7
<i>Lycium</i>	12.7 (74)	37.8 (12)	3.0
<i>Monechma</i>	2.7 (63)	24.0 (31)	8.9
<i>Pentanisia</i>	2.1 (50)	2.4 (124)	1.1
<i>Plectranthus</i>	1.7 (111)	5.0 (23)	2.9
<i>Solanum</i>	4.7 (72)	70.5 (21)	15.0
<i>Tribulus</i>	5.4 (19)	21.3 (73)	3.9

Table 4 continued

	Bee			Non-Bee				Ratio
Mean	7.3			25.7				3.5
	<i>Apis</i>	<i>Bombus</i>	Solitary bee	Fly	Beetle	Butterfly	Wasp	Ant
<i>(b) Mean visit lengths per visitor group (s)</i>								
Kenya	3.9	–	7.6	20.9	123.4	8.5	6.6	25.4
Israel	13.7	–	12.3	41.3	179.0	14.9	17.3	11.7
UK Fife Garden	4.1	2.5	–	12.6				

(Ratios of the visit lengths are shown for convenient comparison; bee visits are shorter in all but one case, *Heliotropium* in Kenya, see Text.)
 (b) Mean visit lengths per visitor group, for the same two sites and with available data for the UK Fife garden site

Discussion

In these studies, across five temperate and warm arid sites habitats, we have explicitly demonstrated and quantified just how much better bees are as pollen depositors (and therefore as likely pollinators) for most of the 76 plants we tested. This is the case despite site differences: for example, there were longer visit durations with higher HP deposition in Israel, and shorter floral longevity in Kenyan flowers which were more likely to be open for one day only (as may be true of tropical sites more generally, Willmer 2011), and pollen grains were also on average smaller for the UK garden plants. These differences occurred even though the flowers we used (representing many families) had similar mean stigma accessibility and stigma size at all our main sites (Supplementary Material Table 1).

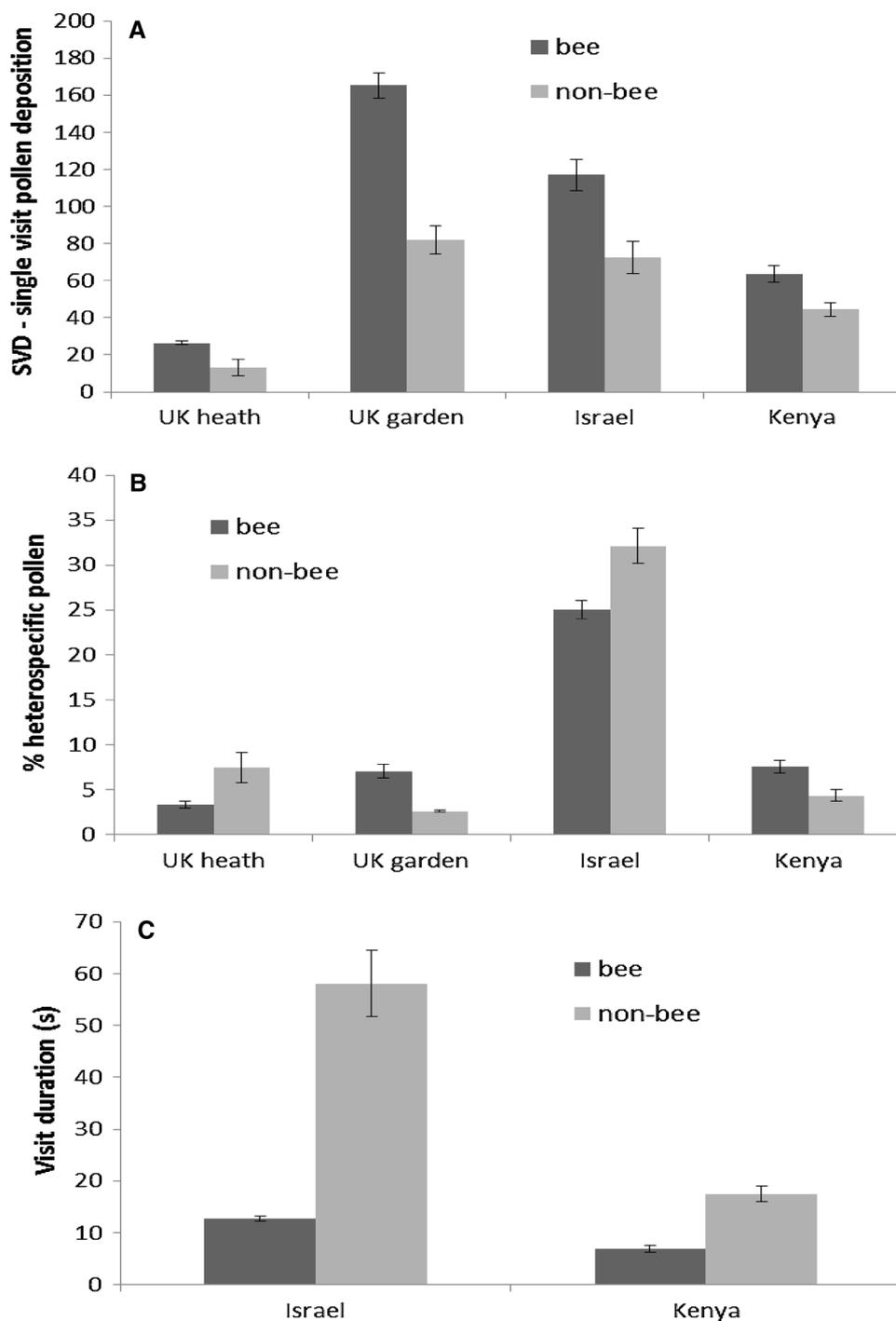
Figure 2 offers a pictorial summary of the key differences in bee performance and characteristics. Bees were the commonest visitors to nearly all our study plants, and better SVD performers than non-bees for most plants at all sites (Table 1). Solitary bee genera were highly effective in all sites, though social bumblebees also performed well in temperate locations. Honeybees (*Apis mellifera*) were often the least effective type, though often the most abundant. This ties in with accumulating recent literature on the relative benefits of wild bees and of commercial honey bees, as pollinators of natural habitats and urban spaces (Lowenstein et al. 2015; Hausmann et al. 2016). Wild bees are also vital, and often better than *Apis*, as crop pollinators, with the importance of honeybees often over-emphasised in the past (see Breeze et al. 2011; Garibaldi et al. 2013). For example, halictid bees are important for melon (Rodrigo-Gomez et al. 2016) and watermelon (Garantonakis et al. 2016), bumblebees are important for blueberries (Button and Elle 2014) and several wild bees are better than managed honeybees at pollinating apples (Mallinger and Gratton 2015), although it is only a few relatively common solitary bee species that are crucial across crops in general (Kleijn et al. 2015).

Table 5 Heterospecific deposition by different groups of bees and non-bees for all plant species pooled, at each study site. (Table 2 gives statistical comparisons for bee and non-bee groups; Supplementary Material Table 3 gives values for individual plant species.)

	% heterospecific	n
Dorset heath		
<i>Apis</i>	0.89	321
<i>Bombus</i>	4.01	894
Solitary bees	6.42	49
All bees	3.35	1264
All non-bees	9.21	61
Israel garigue		
<i>Apis</i>	21.75	483
<i>Bombus</i>	0	1
Solitary bees	25.02	1314
All bees	24.16	1795
All non-bees	32.11	481
Kenya savanna		
<i>Apis</i>	9.81	181
Solitary bees	7.06	910
All bees	7.52	1091
All non-bees	4.33	898
UK Kent garden		
<i>Apis</i>	4.67	250
<i>Bombus</i>	6.40	1129
Solitary bees	9.25	604
All bees	6.83	1983
All non-bees	2.62	526
UK Fife garden		
<i>Apis</i>	6.95	55
<i>Bombus</i>	2.22	475
Solitary bees	5.83	14
All bees	2.64	564
All non-bees	8.33	121

Numbers in red highlight the occasions where non-bee visitors produced lower heterospecific deposition, commoner in Kenya than in Israel; text gives more details of these cases

Fig. 2 A summary of the key aspects of better pollinator performance identified for bees compared with non-bees across sites. **a** Compares the mean SVD values, and **b** compares percentages of heterospecific pollen deposition, both of these across the four main sites, whilst **c** shows mean visit durations for Israel and Kenya



Daily timing effects, though difficult to quantify, indicated a better ability by bees to visit particular flowers when their pollen was most abundant and thus available to pick up on the body. However, limitations of SVD as a ‘pollination availability’ proxy must also be addressed here. Firstly, the number of immediately preceding visits to the same species that a particular visitor has made will potentially affect the amount of pollen it then deposits on the virgin flower we sampled; but there is no intrinsic

reason (other than sheer floral density) why this influence will vary markedly amongst the various plants studied here, other than that some hybrid garden plants may have modified pollen amounts or accessibility compared to the native species (e.g. Garbuzov and Ratnieks 2014). Secondly, SVD records may be directly correlated with floral density, especially for bees, since multiple quick visits may move a greater percentage of the pollen from the pollinator’s body onto the next flower, whereas in sparsely

flowering areas more pollen may fall off between visits, and (for bees) may be groomed off into scopal sites from which it normally cannot be deposited onto stigmas, making SVD a less reliable proxy for pollen availability. However, in practice, we found similar proportions of matches of visit timing to ‘pollen availability’ in the sparser flowering community in Kenya (Table 2) compared with the denser flowering in Israel, and despite their tendency to groom between visits, timing matches were better for bees than for non-bees at both these sites. We therefore propose that the use of SVD as a proxy for pollen availability is reasonable.

Most strikingly, visit lengths for bees were substantially lower for bees in all sites, giving a community level assurance to somewhat scattered data for particular plant species (e.g. raspberries, Willmer et al. 1994). Shorter visits should certainly allow for a higher visit frequency. Interestingly, for all categories of visitor (Table 4a), flowers received longer visits in Israel than elsewhere, perhaps reflecting the higher proportion there of the more bee-specialist morphologies that require more complex handling (eight species from Lamiaceae, Boraginaceae and Iridaceae, compared with just two in Kenya). Within the bees, *Apis* visits were shorter than solitary bee visits in Kenya, but not in Israel (Table 4b), and *Bombus* visits were shorter than *Apis* visits in the UK, a phenomenon also documented for other garden plants and for some crops (e.g. Willmer et al. 1994).

Turning to heterospecific pollen (HP) deposition, bees were better performers than non-bees (i.e. lower levels of foreign pollen imported to flowers) for natural heathland and scrubland communities in the UK and Israel. In gardens, they not surprisingly tended to move more heterospecific pollen onto stigmas than non-bees, since they had rather smaller amounts of a greater number of plants to work with. The values of HP deposition we recorded were comparable to general levels reported elsewhere (e.g. Ashman and Arceo-Gomez 2013; Fang and Huang 2013; Arceo-Gomez et al. 2016a), though these studies highlight the great variation in HP deposition within individuals (range 0–95%) and species (range 0–80%), often linked to corolla and stigma morphology/size (e.g. Montgomery and Rathcke 2012). Effects of HP deposition on stigma interactions and the resultant success rates of conspecific pollen germination are highly varied between plants with obvious potential fitness costs for the plant (see Morales and Traveset 2008), and there may be particularly detrimental donors and particularly vulnerable recipients (Ashman and Arceo-Gomez 2013). However, there is also evidence that plants may develop tolerance to HP when they are more exposed to it (Arceo-Gomez et al. 2016b), which may be particularly likely in garden sites over time (though

perhaps not important as many garden plants will never be allowed to breed on site anyway).

That bees deposit lower HP levels is likely to be in part an indication of their better floral constancy (as defined by Waser 1986), which is usually taken to be higher in bees and particularly high in some bumblebees (e.g. Raine and Chittka 2005) but poor in many other flower visitors (see Ellis and Johnson 2012; Pohl et al. 2011). Low HP deposition and constancy may also reflect differential pollen placement on the body as bees move and behave differently on different plants (Huang et al. 2015).

So when are bees not the best? From our studies, just a few plant species substantially benefitted from bee flies, and less often from hoverflies (these two families being the top-performing fly groups overall, and widely reported as the most effective of dipteran flower visitors). Even fewer plants were well-served by butterflies and moths, with much more occasional deposition efficiency from wasps or muscid flies, whilst beetles and ants were largely ineffective. And although ‘bees are usually best’, and wild bees often better than honeybees, it is also crucially important to recognise that non-bee insects can be vital to particular cases of global crop pollination, as most recently highlighted by Rader et al. (2016), and for some more specialised angiosperms (e.g. those that are vertebrate-pollinated) in other ecosystems.

Some further points emerging from our multiple datasets are worth mentioning here. Firstly, our extensive records of SVD values through daily time (examples in Fig. 1), and across a flowering season, show just how varied the pattern of pollen availability from a plant can be, and thus how diurnal pollen movement in a community may be more complex than network analyses can show. Simple predictions of dehiscence patterns and pollen provision from flowers will often be erroneous. Many plants did present their pollen from early morning onwards with a morning peak and afternoon decline, as often assumed for specialist bee plants given bees’ activity patterns (Willmer and Stone 2005), but equally many did not, showing upright or inverted bell-shaped curves, roughly constant means through several hours of the day, or one or two clear peaks. Even the SVD patterns for all plants combined in Israel and Kenya differed (Fig. 1k, l), with daily mean SVD values being somewhat bell-shaped in Israel (0700–1500 h) but fairly constant (0800–1600 h) in Kenya.

Secondly, the mean SVD levels for all plants at the four main sites differed considerably, as shown in SM Table 2: for Dorset heath 25.6 ± 1.0 , for Israeli garigue 107.4 ± 6.9 , for Kenyan savanna 54.8 ± 4.2 and for the Kent garden site 155.7 ± 5.9 . For the natural communities, the strikingly higher overall SVD in Israel may again reflect the higher proportion of traditionally bee-specialist plants (possibly selected to provide more pollen to their

main visitors); for the Kent garden, the high value is perhaps more likely to be related to the selection of especially attractive and/or multi-anther-bearing floral types (often non-native and/or hybrids) by human gardeners (cf. Salisbury et al. 2015).

Thirdly, our inclusion of more limited data from the Fife garden study, gathered for other purposes but with the same methodology for assessing SVD, highlights an important issue for experimental approaches to community pollination, since there a concentration on a few highly visited plants that were easier to study and particularly preferred by bees distorted the perspective on overall pollinator performances. It is obviously crucial to include, as far as possible, a substantial proportion of the total flora and an unbiased sample of all the available flowers at a given time, whether in natural habitats or gardens.

Finally, and as also demonstrated by King et al. (2013), SVD measures of pollinator effectiveness as reported here accord well with traditional pollination syndrome predictions; the match of visit frequencies and pollinator effectiveness to syndrome traits is evident for most of the 76 plants we studied, as highlighted in Supplementary Material Table 1, using trait predictions (with the important exception of nectar rewards) comprehensively covered in Willmer (2011); this matching with syndrome predictions occurs despite the site differences outlined earlier.

Conclusions

Across a range of flowering communities and of floral types, bees—both social and solitary—are the most frequent flower visitors, and are better pollen depositors and potentially effective pollinators than non-bees. They are also better at timing their visits to flowers for maximally efficient pollen pick-up, and have much shorter visit durations so giving potentially higher rates of flower visits. Furthermore, they are more flower-constant than other floral visitors, as indicated by lower heterospecific pollen deposition, so reducing the chances of pollen clogging and interference competition between germinating pollen grains. In all these aspects, solitary bees and (for temperate habitats) bumblebees usually perform better than honeybees. Our accumulated data have allowed us to explicitly quantify the benefits of bees, collectively and more specifically, as pollinators.

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