Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects

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Summary

1. Pollinating insects are globally declining, with one of the main causes being the loss of flowers. With the value of countryside reducing, urban areas, particularly gardens, are increasingly recognized as of benefit to wildlife, including flower-visiting insects.

2. Many gardeners specifically select plant varieties attractive to wildlife. Given the wide public interest, many lists of recommended varieties have been produced by both amateurs and professional organizations, but appear not to be well grounded in empirical data. These lists, however, are not without merit and are an obvious starting point. There is clearly a need to put the process onto a firmer footing based more on data and less on opinion and general experience.

3. We collected data over two summers by counting flower-visiting insects as they foraged on 32 popular summer-flowering garden plant varieties in a specially planted experimental garden, with two smaller additional gardens set up in year two to check the generality of the results. With many thousands of plant varieties available to gardeners in the United Kingdom, and other countries or regions, it would have been an impossible task to make a comprehensive survey resulting in a complete and authoritative list.

4. Our results are valuable and encouraging. Garden flowers attractive to the human eye vary enormously, approximately 100-fold, in their attractiveness to insects. Insects, especially bees and hover flies, can be attracted in large numbers with clear differences in the distribution of types attracted by different varieties.

5. Our results clearly show that there is a great scope for making gardens and parks more bee- and insect-friendly by plant selection. Horticulturally modified plant varieties created by plant breeding, including hybrids, are not necessarily less attractive to insects and in some cases are more attractive than their wild-type counterparts. Importantly, all the plants we compared were considered highly attractive to humans, given that they are widely sold as ornamental garden plants.

6. Helping insect pollinators in gardens does not involve extra cost or gardening effort, or loss of aesthetic attractiveness. Furthermore, the methods of quantifying insect-friendliness of plant varieties trialled in this study are relatively simple and can form the basis of further research, including 'citizen science'.

Key-words: bumblebees, butterflies, conservation, honeybees, hover flies, ornamental plants, pollinators, urban ecology, wildlife friendly gardening

Introduction

Global biodiversity is in decline (Barnosky *et al.* 2011). Pollinating insects are no exception, with the main factor being loss of flowers, driven primarily by human activities, such as development and agricultural intensification, which lead to habitat loss and degradation (Goulson *et al.* 2005; Biesmeijer *et al.* 2006; Potts *et al.* 2010). With the wildlife value of the countryside reducing, the value of urban areas is increasingly being recognized (Frankie & Ehler 1978; Cane 2005; Dearborn & Kark 2010; Sanderson & Huron 2011). High species diversity has been recorded in urban

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green spaces, such as parks and gardens (Helden & Leather 2004; Matteson, Ascher & Langellotto 2008; Owen 2010), with private gardens often being the largest and probably the most important component (Goddard, Dougill & Benton 2010). In the United Kingdom, 87% of households are associated with a garden (Davies *et al.* 2009) and gardening is a popular hobby (Taylor 2002). In addition, many gardeners are supportive of wildlife, with most UK gardeners (74–78%) engaging in some form of 'wildlife gardening'. That is, doing something to attract or encourage wildlife (Good 2000), including the 31% who select plants attractive to wildlife or the 66% who feed birds in their garden (Mew *et al.* 2003; DEFRA 2007).

Garden plants are often non-native, and this may reduce their usefulness to some wildlife. For example, many herbivorous insects have a narrow range of suitable food plants (Novotny & Basset 2005; Dyer *et al.* 2007). However, this does not prevent them from being useful to flower-visiting insects seeking nectar and pollen, as these are general resources. Nectar, for example, is mainly sugar and water (Nicolson & Thornburg 2007), and so it is edible whether from a native or a non-native plant. Many garden plants have also been bred to alter their appearance, such as by the 'doubling' of petals, which may reduce floral rewards or their accessibility (Comba *et al.* 1999; Corbet *et al.* 2001).

Given the public interest in helping wildlife, a large number of recommended plant lists have been produced, by both amateurs (e.g. Baines (2000); Lavelle & Lavelle (2007)) and professional organizations (e.g. Royal Horticultural Society (2011); Xerces Society (2011)). However, these appear not to be well grounded in empirical data. For example, Thompson (2006) referred to one list of wildlife friendly plants produced by Natural England, a government-funded agency responsible for protection and improvement of the natural environment, as 'looks very much as if it was put together late one Friday afternoon'. In addition, lists of bee- and butterfly-friendly plants vary greatly even when they are for the same country, suggesting that the underlying information is based mainly on personal observations, experience, opinion and, perhaps, uncritical recycling of earlier lists (M. Garbuzov & F.L.W. Ratnieks, unpublished data).

Lists of bee- and butterfly-friendly plants are not without merit and are an obvious starting point for determining which plants are good for flower-visiting insects. However, there is a need to put the process onto a firmer footing based more on data and less on opinion and general experience. This study is an attempt to do this. We collected data over two summers in which flower-visiting insects were counted as they foraged on 32 popular garden plant varieties in a specially planted experimental garden. In addition, two smaller gardens were set up in year two to check the generality of the results. With many thousands of plant varieties available to gardeners in the United Kingdom, it would have been an impossible task to make a comprehensive survey resulting in a complete and authoritative list. What our data do show, however, is valuable and encouraging. Garden flowers attractive to the human eye vary enormously, approximately 100-fold, in their attractiveness to insects. This shows that plant selection can make a great difference in the value of gardens and parks to flower-visiting insects, and at no additional cost. Insects, and especially bees, can be attracted in large numbers with clear differences in the distribution of types attracted by different garden plant varieties.

Materials and methods

EXPERIMENTAL PLANT VARIETIES AND FLOWER BEDS

We studied 32 garden plant varieties that include 19 species and hybrids, both native and exotic to Britain, with particular focus on varieties of lavender (*Lavandula* spp.), as it is known to be attractive to bees (Pawelek *et al.* 2009; for full list see Table S1, Supporting information). Varieties were selected based on the following three criteria: they were (i) popular as garden plants in their own right due to their attractive flowers or foliage (e.g. Lamb's ear, *Stachys byzantina*), (ii) widely and easily available for purchase and (iii) flowered mainly or exclusively in late summer, July and August, as these are the months when honeybee foraging distances in the same area are greatest (M.J. Couvillon, R. Schürch & F.L.W. Ratnieks, unpublished data), indicating challenging foraging conditions and, therefore, the period when garden flowers can be particularly beneficial to flower-visiting insects.

The main experimental flower bed was on the University of Sussex campus (lat: 50·865646, long: −0·090771943) on chalky soil of the South Downs. All 32 varieties were planted in 1×1 m patches, two patches per variety, in two concentric circles (inner diameter 12·2 m, outer 19·2 m), with one variety per circle in a random position (Fig. 1). There were gaps of c. 0·5 m (inner) and 1·0 m (outer) between adjacent patches within the same circle and 1·5 m between the circles. This arrangement was chosen to eliminate any edge effects, which might have affected insect visitation. Data were collected in both 2011 and 2012.

Additionally, to ensure our results were not location specific, for example, due to local soil conditions or insect abundance, 13 of the 32 varieties (Table S1) were planted at two additional locations in 2012. This subset was chosen to confirm certain notable trends seen in the data at the end of the first season (2011). For example, *Borago* was mostly visited by honeybees, while *Lavandula* mostly by bumblebees. *L. × intermedia* received more insect visits than *L. angustifolia*, while sharp colour contrast (traditional blue/purple vs. white) had no effect on the number of visits. Open-flowered *Dahlia* varieties were more attractive than those with more modified flower forms. *Origanum* and *Stachys* seemed to have disproportionately large numbers of visits by 'other' wild bees, while *Erysimum* was most attractive for butterflies and moths. One location was 4·5 km away at Plumpton College (lat: 50·905665, long: −0·074753791) where the soil is also chalky, and the other 26·3 km away in FR's private garden in Magham Down (lat: 50·880426, long: 0·28488247), where the soil is sandy. Only one 1×1 m patch per variety was planted, and the patches were arranged in a line with 30 cm gaps.

Perennials were bought in pots from nurseries and garden centres and planted in June 2011 (University of Sussex) and May-June 2012 (Plumpton College & Magham Down). Borage (*Borago officinalis*), which is an annual, was sown in May each year to give peak flowering in July–August. Viper's bugloss (*Echium vulgare*) is a biennial, flowering in the second year of its life cycle. However, we were able to induce flowering in the first year by keeping young seedlings in a greenhouse at 24:0 light/dark
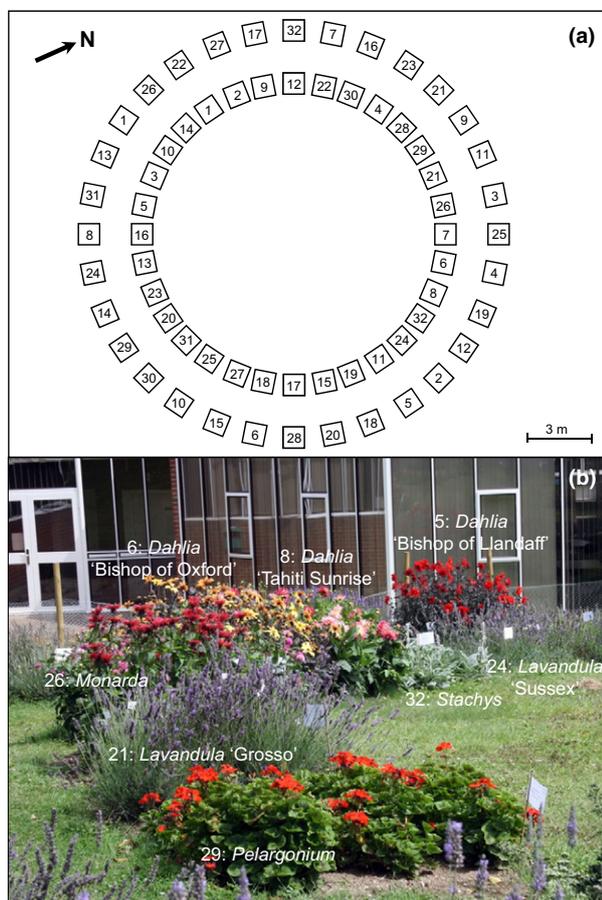
Fig. 1. (a) Schematic layout of the experimental flower garden on the University of Sussex campus, showing the two concentric circles, each consisting of 32 1 × 1 m flower patches. Numbers correspond to the varieties, as listed in Table S1. (b) Photograph showing a section of the inner circle, taken in August 2011 when most varieties were in full bloom.

photoperiod for 8 weeks before transplanting them to patches in the flower bed. The non-hardy anise hyssop (*Agastache foeniculum*) and geranium (*Pelargonium × hortorum*) were dug out at the end of 2011 season, overwintered in a heated greenhouse and replanted in May 2012. The four *Dahlia* varieties, which are also non-hardy, were grown from tubers in a greenhouse starting in March each year and planted out 8 weeks later. Prior to planting, all patches were fertilized with multipurpose organic fertilizer (Fish, Blood & Bone, Sinclair) and controlled release fertilizer (Sincrocell 9, Sinclair). Table S1 gives the suppliers of each plant variety.

PLANT AND PATCH CHARACTERISTICS

In each patch, an appropriate number of plants were planted according to their size (Table S1) such that the patch was nearly fully covered, but allowing for some further growth. Plants were trimmed as necessary to ensure that they did not overgrow the patch perimeter. In some cases, slow growth or plant death (only in *E. vulgare* at the University of Sussex) resulted in patches that were not covered completely. To allow for <100% plant cover, on each day of data collection, patches were photographed from above to determine plant cover using ImageJ 1.45s software (National Institute of Health, USA).

On each day of data collection, the bloom intensity of patches was quantified by assigning a score 0 (absence of bloom), 1 (<⅓ of maximum), 2 (⅓–⅔ of maximum) or 3 (full bloom, >⅔ of maximum; after Anderson & Hubricht 1940) and included as a covariate in the analyses. In addition, as corolla length is known to influence the type of flower-visitors and their ability to gather nectar (e.g. Balfour, Garbuzov & Ratnieks 2013), it was estimated in each variety by measuring 20 non-systematically selected flowers (10 from each patch at bloom intensity 2 or 3) to the nearest 0·1 mm using digital callipers.

RECORDING INSECT FLOWER-VISITORS

In the main flower bed at the University of Sussex, insects visiting the flowers were counted on 13 days from 14 July to 7 October 2011 and 12 days from 29 June to 18 September 2012. Counts were made only on days with favourable weather. That is, based on our experience, the combination of sunlight, temperature and wind was such as to allow all insect categories to be active. Counts were made at approximately weekly intervals throughout the main flowering period of most plant varieties (Fig. S1). In addition, insects were recorded on 6 days from 18 August to 18 September 2012 at Plumpton College and on 8 days from 9 August to 10 September 2012 at Magham Down.

The number of insect flower-visitors on each patch was quantified using 'snapshot' counts, in which the number of foraging insects was determined near instantaneously (<10 s) by eye. This 'snapshot' method was chosen over other possible methods, such as counting the number of insects arriving at a patch in a defined time interval, as it is quick to implement and therefore practical for assessing many patches. In the main flower bed at the University of Sussex, one snapshot was taken from each patch at hourly intervals between 9:30 and 16:30 BST, yielding eight snapshots per patch per day. In the two additional flower beds, 10 snapshots per patch were taken per day, typically during a c. 2-h period. As insects generally remained on the same patch for only a few minutes during a foraging trip, the 60-min intervals between snapshots meant that the same insect was unlikely to have been counted twice on the same patch visit. Thus, the data represent independent foraging choice decisions even though individual insects may make multiple visits to the same patch. Even when multiple visits by the same insect to the same patch do occur, this shows a real preference rather than the mere persistence of the same insect at the same patch during a single patch visit.

The insects counted in the snapshots were identified and grouped to taxa as follows: (1) honeybees (*A. mellifera* L.), (2) two-banded white-tailed bumblebees (*Bombus terrestris/lucorum* group, after Fussell & Corbet (1992)), (3) three-banded white-tailed bumblebees (*Bombus hortorum* group), (4) brown bumblebees (*Bombus pascuorum* group), (5) other bumblebees, (6) other bees (non-*Apis* and non-*Bombus*), (7) hover flies (Diptera: Syrphidae), (8) butterflies and moths (Lepidoptera) and (9) all other insects. Additionally, Lepidoptera (group 8) were identified to species, other bees (groups 5, 6) and other insects (group 9) to species or other taxonomic ranks, as appropriate. However, they were grouped in analyses due to the low numbers of individual species or subgroups in the data sets (Table 1, Fig. 2). The levels of identification used were appropriate given the counting method, in which insects were identified as they foraged and were not collected. In practice, this meant that most insects (87–92% per data set) other than flies, Diptera, were identified to species or to groups of species that could easily be separated in the field (e.g. the different bumblebee subgroups). These taxonomic groups also reflect functional insect groups in relation to flower morphology. For example, short- (honeybees) and long-tongued (bumblebees) eusocial bees, solitary bees, very long-tongued Lepidoptera and short-tongued hover flies.

Table 1. Breakdown of main insect groups that were grouped together in the analyses

	Common name	University of Sussex 2011 (%)	University of Sussex 2012 (%)	Plumpton College 2012 (%)	Magham Down 2012 (%)
Other *Bombus* groups					
Black-bodied red tails		12	20	–	45
Banded red tails		84	78	100	7
Unidentified		4	2	–	48
Other bees					
Anthidium manicatum	Wool-carder bee	Not identified	95	100	100
Unidentified		Not identified	5	–	–
Lepidoptera					
Butterflies					
Aglais urticae	Small tortoiseshell	3	10	–	38
Aphantopus hyperantus	Ringlet	–	1	–	–
Gonepteryx rhamni	Brimstone	–	1	–	–
Inachis io	Peacock	–	1	–	–
Lycaena phlaeas	Small copper	–	1	–	–
Maniola jurtina	Meadow brown	22	62	71	52
Ochlodes sylvanus	Large skipper	2		–	–
Pieris brassicae	Large white	3	1	–	5
Pieris rapae	Small white	34	4	29	–
Polygonia c-album	Comma	3	–	–	–
Polyommatus coridon	Chalkhill blue	2	–	–	–
Polyommatus icarus	Common blue	–	9	–	–
Pyronia tithonus	Gatekeeper	–	1	–	–
Thymelicus sylvestris	Small skipper	2	4	–	–
Vanessa atalanta	Red admiral	3	1	–	–
Vanessa cardui	Painted lady	2	–	–	–
Moths					
Autographa gamma	Silver Y	–	1	–	5
Macroglossum stellatarum	Hummingbird hawk-moth	22	–	–	–
Pyrausta aurata	Mint moth	–	2	–	–
Zygaena spp.	Burnet moths	–	1	–	–
Other insects					
Coleoptera	Beetles	20	9·5	11	4
Diptera	True flies	63	90	89	92
Vespula spp.	Yellowjacket wasps	17	0·5	–	4

Bombus subgroups follow Fussell & Corbet (1992). For the relative abundance of groups see Figs 2 and S2.

STATISTICAL ANALYSES

The number of insects per snapshot was divided by plant area cover to form the response variable in the analyses. This is justifiable, because the number of insects per snapshot is linearly related to the area (M. Garbuzov, A. Madsen & F.L.W. Ratnieks, unpublished data). All statistical analyses were performed in R v.3.0.0 (R Development Core Team 2013). Prior to analyses, the data were explored as advised by Zuur, Ieno & Elphick (2010). General linear models [GLMs; function *gls*, package *nlme* (Pinheiro *et al.* 2012)] were used to examine the relationships between the response variable, plant variety, bloom intensity and mean corolla length as main fixed effects. No interactions were modelled, as they were not part of the *a priori* hypotheses to be investigated. The data set was 'collapsed' by averaging out across the two patches of each plant variety, and also within each day, by taking daily means. Further, to account for temporal autocorrelation within the data recorded at approximately weekly intervals across the season, the AR-1 correlation structure was added to the models (Zuur *et al.* 2009). One model was fitted for each insect group in both the 2011 and 2012 University of Sussex data sets. The significance of *P*-values was judged against the Bonferroni-corrected α-level (0·05 divided by the number of models per data set). As plant variety and mean corolla tube length were highly correlated (i.e. each variety had a different mean length), only one of these variables was included in a model at a time.

The significance of terms was determined using *F*-tests on a full model, which is appropriate, because the main aim was to analyse the significance of terms, rather than to use the models predictively (Whittingham *et al.* 2006). *Post hoc* pairwise comparisons of plant varieties were performed using Tukey's HSD test [function *glht*, package *multcomp* (Hothorn, Bretz & Westfall 2008)].

Consistency among data sets was tested using Spearman's rank correlation test. This is more appropriate than a parametric correlation test, because consistency in rank is both more conservative and more relevant to the underlying aim of the study than consistency in the absolute numbers of insects attracted, which may vary among years and locations. All other relationships (in the attractiveness of plant varieties among different insect flower-visitor groups) were tested using Pearson's correlation test (function *cor.test* for all correlation tests).

Results

ATTRACTIVENESS OF PLANT VARIETIES TO INSECT FLOWER-VISITORS

The relative abundance of insect groups at the University of Sussex is shown in Fig. 2. Across the 2 years, over
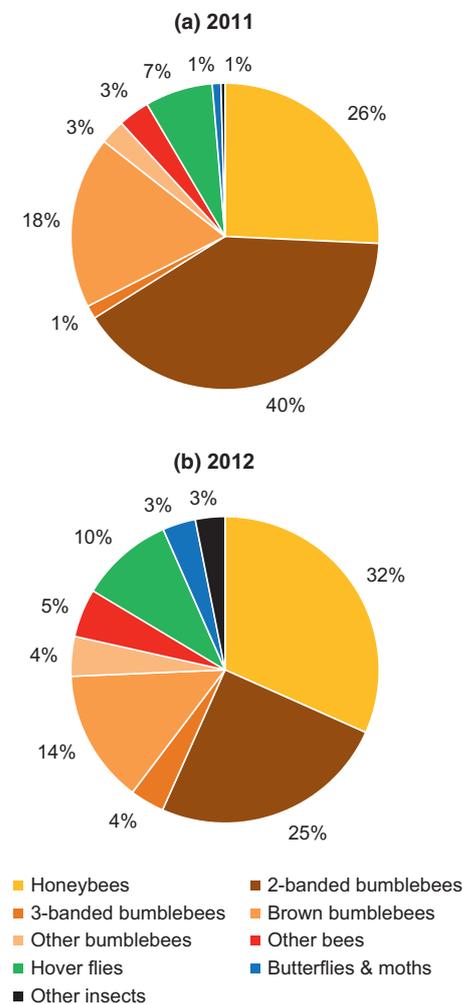
(a) 2011

(b) 2012

■ Honeybees   ■ 2-banded bumblebees
■ 3-banded bumblebees   ■ Brown bumblebees
■ Other bumblebees   ■ Other bees
■ Hover flies   ■ Butterflies & moths
■ Other insects

Fig. 2. Relative abundance of insects in nine main groups recorded in the 2 years at the University of Sussex in 2011 (a) and 2012 (b). More detailed taxonomic breakdowns of other bumblebees, other bees, butterflies & moths, and other insects are given in Table 1.

84% of insects recorded were bees, comprising 47–62% *Bombus* spp., 26–32% *A. mellifera* and 3–5% other bee species. Hover flies were 7–10%, butterflies and moths 1–3% and other insects 1–3%. Further taxonomic breakdowns of these groups are given in Table 1. The mean number of insects per snapshot per m^2 was significantly affected by plant variety in most main insect groups (Table S2). Bloom intensity (covariate) was also significant in most models (Table S2). The length of flower corolla tube was a significant predictor in only a few models (Table S2). However, the slope estimates of relationships were close to zero (0·01–0·04), making these relationships of little importance. The results of *post hoc* Tukey's HSD tests comparing plant varieties are shown in Fig. 3. Due to the very large numbers of pairwise comparisons, the test had low power to differentiate between varieties. Nevertheless, it was sufficient to reveal the broad picture.

CONSISTENCY AMONG YEARS AND LOCATIONS

The relative abundance of insect groups and plant variety attractiveness at Plumpton College and Magham Down in 2012 (Fig. S2) were similar to those recorded at the University of Sussex in both years. In addition, the mean number of insects per snapshot per m^2 recorded on different varieties at the University of Sussex correlated highly between 2011 and 2012 (Spearman's correlation: $r_s = 0.754$, $S = 1343.62$, $P < 0.001$, Fig. 4a). The numbers of insects per variety recorded at the University of Sussex in 2012 were also significantly related to those recorded at both Plumpton College ($r_s = 0.650$, $S = 127.35$, $P = 0.016$, Fig. 4b) and Magham Down ($r_s = 0.791$, $S = 76.00$, $P = 0.002$; Fig. 4b) flower beds. This suggests that the results are general, rather than being year or location specific.

COMPARISON OF LAVENDER VARIETIES

Closer examination of lavender varieties showed that (i) not all varieties were equally attractive (GLM: $F_{12,13} = 9.75$, $P < 0.001$) and (ii) *L. × intermedia* as a group (mean ± SE = 2·91 ± 0·31 insects snapshot^{-1} m^{-2}) were more attractive than both the *L. angustifolia* group (mean ± SE = 0·88 ± 0·09 insects snapshot^{-1} m^{-2}) and *L. stoechas* (mean ± SE = 0·66 ± 0·54 insects snapshot^{-1} m^{-2}; $F_{1,20} = 34.86$, $P < 0.001$; Fig. 5a). However, the number of insects attracted was not affected by either total bloom duration ($F_{1,20} = 3.52$, $P = 0.075$; Fig. 5b) or corolla tube length ($F_{1,20} = 0.0004$, $P = 0.985$).

Honeybees and bumblebees together comprised the majority (mean 90%, range 73–97%) of flower-visitors on *Lavandula* varieties. The number of honeybees, as a proportion of honeybees and bumblebees together, varied considerably among varieties (range 11–55%). However, this was not consistent between 2011 and 2012 ($r = 0.290$, $P = 0.337$) and did not correlate with corolla tube length in 2011 ($r = -0.199$, $P = 0.515$), 2012 ($r = 0.202$, $P = 0.508$) or the mean of 2011 and 2012 ($r = 0.094$, $P = 0.759$).

CORRELATIONS OF PLANT VARIETY PREFERENCE AMONG INSECT GROUPS

There was no significant correlation between the number of honeybees and bumblebees per snapshot per m^2 among the 32 varieties ($r = 0.257$, $P = 0.155$; Fig. 6a), suggesting that their preferences do not, generally, coincide. However, visitation by short-tongued bumblebees (*B. terrestris/ lucorum* group) correlated significantly with visitation by long-tongued bumblebees (*B. hortorum* and *B. pascuorum* groups; $r = 0.565$, $P < 0.001$; Fig. 6b). We then looked at correlations in preference between both honeybees and bumblebees vs. other bee species, hover flies and butterflies and moths and found only one of these correlations to be significant (bumblebees vs. butterflies & moths ($r = 0.665s$, $P < 0.001$; Fig. 7c). All other correlations were
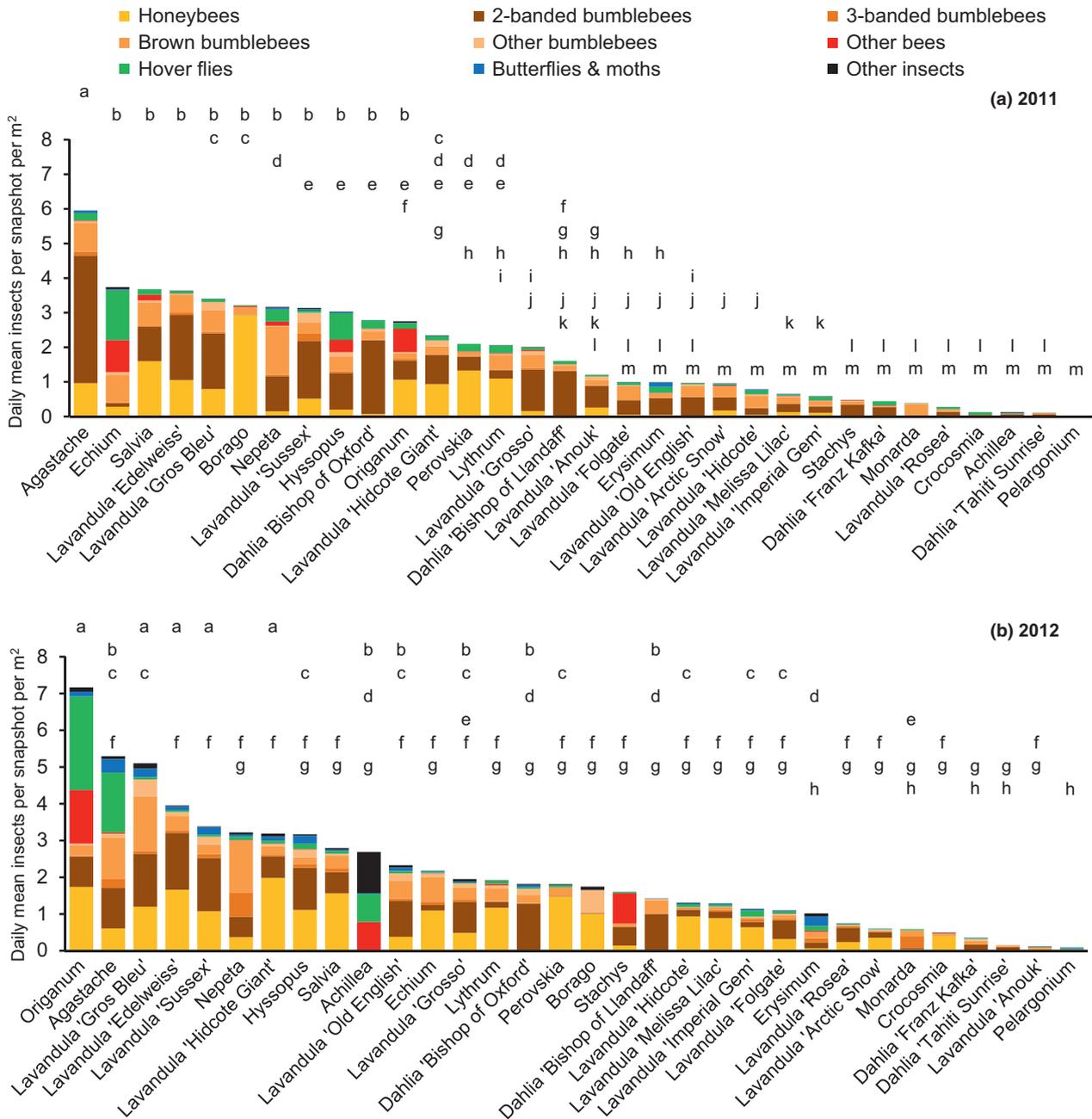
Fig. 3. Daily mean numbers of insects per snapshot per 1 × 1 m patch recorded on 32 garden plant varieties at the University of Sussex in 2011 (a) and 2012 (b), Letters above bars represent significant differences based on Tukey's HSD test, where varieties sharing a common letter are not significantly different from each other at α = 0·05. Full plant names are given in Table S1.

non-significant [honeybees vs. other bees ($r = 0.169$, $P = 0.354$), honeybees vs. hover flies ($r = 0.251$, $P = 0.165$), honeybees vs. butterflies & moths ($r = 0.157$, $P = 0.390$), bumblebees vs. other bees ($r = -0.077$, $P = 0.675$), bumblebees vs. hover flies ($r = 0.266$, $P = 0.141$)] (Fig. 7a–c). The significant correlations (Figs 6b and 7c) remained significant after Bonferroni correction (α = 0·05/8).

Discussion

The results showed very large, approximately 100-fold (c. 300-fold in 2011, c. 80-fold in 2012), variation among

the 32 plant varieties at the University of Sussex in the total number of insects attracted. This clearly shows that there is great scope for making gardens and parks more bee- and insect-friendly by judicious plant selection. Importantly, this need not involve extra cost or gardening effort, or, indeed, a loss of aesthetic attractiveness, given that all the plants we compared were considered to be highly attractive, and were easily available at comparable and low prices. Our results can be considered as a contribution to the lists of recommended garden plants. However, this should be done with caution, as we only compared 32 varieties, which is a very small proportion of
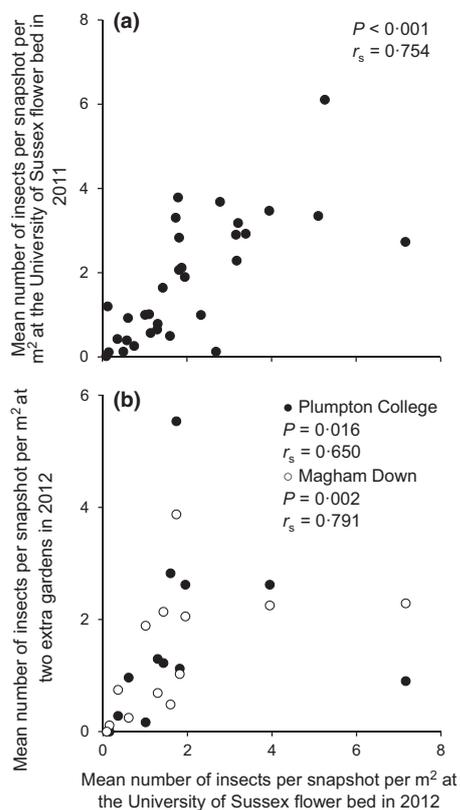
Fig. 4. Correlations between the number of insects per snapshot recorded on different plant varieties at the University of Sussex flower bed in 2012 with that in (a) 2011, and (b) the additional flower beds at Plumpton College (●) and Magham Down (○) in 2012.

the thousands of varieties available (Cubey & Merrick 2011) with similar habit (small shrubs and herbaceous plants suitable for a mixed border).

Attractiveness of plant varieties correlated strongly between 2011 and 2012 at the University of Sussex (Fig. 4a). It also correlated between the University of Sussex and the two additional flower beds at Plumpton College and Magham Down (Fig. 4b). This shows that our results apply generally to a wider area and are not unduly year- or location-specific. Some variation among locations may be due to local conditions (e.g. microclimate or soil type) or differences in the flower-visiting insect communities present. However, most insect species or groups we recorded are common, so would be present in almost any area, but not necessarily in the same proportions. Similarly, some variation between the 2 years could be driven by annual fluctuations in insect populations. Additionally, in our study, the variation observed between years could be due to the different stages of establishment of perennial plant varieties. In 2011, the plants had been put into the patches soon after being delivered from suppliers, who grew them in pots, while in 2012, most varieties had had an extra year in the ground to establish.

Although variation in relative abundance of insects may explain a small proportion of variation in plant

attractiveness, it cannot be a major factor, because the relative abundances of different taxa were broadly very similar among years and locations (Fig. 2). The majority of insects, at least 84% in each data set, were bees, of which approximately one-third were honeybees, two-thirds were bumblebees plus a small percentage of other bee genera. Hover flies were always the next most abundant taxon (7–10%). Butterflies and moths (1–3%) and all other insects (1–3%) were always a small percentage. Overall, our results suggest that garden plants can easily help bees, which showed up in large numbers, by providing forage. This agrees with Goulson *et al.* (2010), who found evidence of positive influence of urban gardens on bumblebee nest density and survival on a landscape scale. Bumblebees [maximum foraging range c. 1·5 km, (Osborne *et al.* 2008)] and especially honeybees [maximum foraging range c. 10 km, (Beekman & Ratnieks 2000)] can forage at long distances from their nest and thus are able to exploit garden resources. By contrast, butterflies and moths, being relatively scarce garden flower-visitors, can perhaps not be as easily helped by garden flowers, despite not being central place foragers. There is also little evidence that the abundance of adult resources, apart from shelter, has any impact on population size or trends in European butterflies (Thomas, Simcox & Hovestadt 2011).

The absence of a positive correlation between the attractiveness of plant varieties to honeybees and bumblebees (Fig. 6a) suggests that their foraging preferences do not, generally, coincide. Furthermore, the absence of a negative correlation seems to suggest that these bees do not appear to be in competition with each other. However, N.J. Balfour, S. Gandy & F.L.W. Ratnieks (unpublished data) showed competition on *L.* × *intermedia* 'Grosso' experimentally. In particular, honeybee numbers increased c. 30 fold on patches from which bumblebees were excluded (Fig. 6a). It is likely, therefore, that the lack of correlation between honeybees and bumblebees reflects both the effects of preferences and competition. As these two types of bees were the most abundant flower-visitors, each probably has the capacity to affect the other via consumptive competition (N.J. Balfour, S. Gandy & F.L.W. Ratnieks unpublished data). In the case of *L.* × *intermedia* 'Grosso', the mean corolla tube length of 7·2 mm was experimentally shown to disadvantage honeybees (mean tongue length 6·6 mm) vs. bumblebees (mean tongue length 7·8 mm) by causing longer flower-handling times (Balfour, Garbuzov & Ratnieks 2013).

Plant variety attractiveness was similar between the short-tongued (*B. terrestris/lucorum* group) and the long-tongued (*B. hortorum* and *B. pascuorum* groups) bumblebees, perhaps, reflecting preferences common to *Bombus* in general (Fig. 6b) or the fact that tongue length variation among bumblebees had little effect in our gardens, despite reported effects being noted in the literature (Goulson *et al.* 2005; Goulson, Lye & Darvill 2008). *Nepeta* × *faassenii* 'Six Hills Giant' stood out from this correlation, being very attractive to long-tongued bumble bees [length
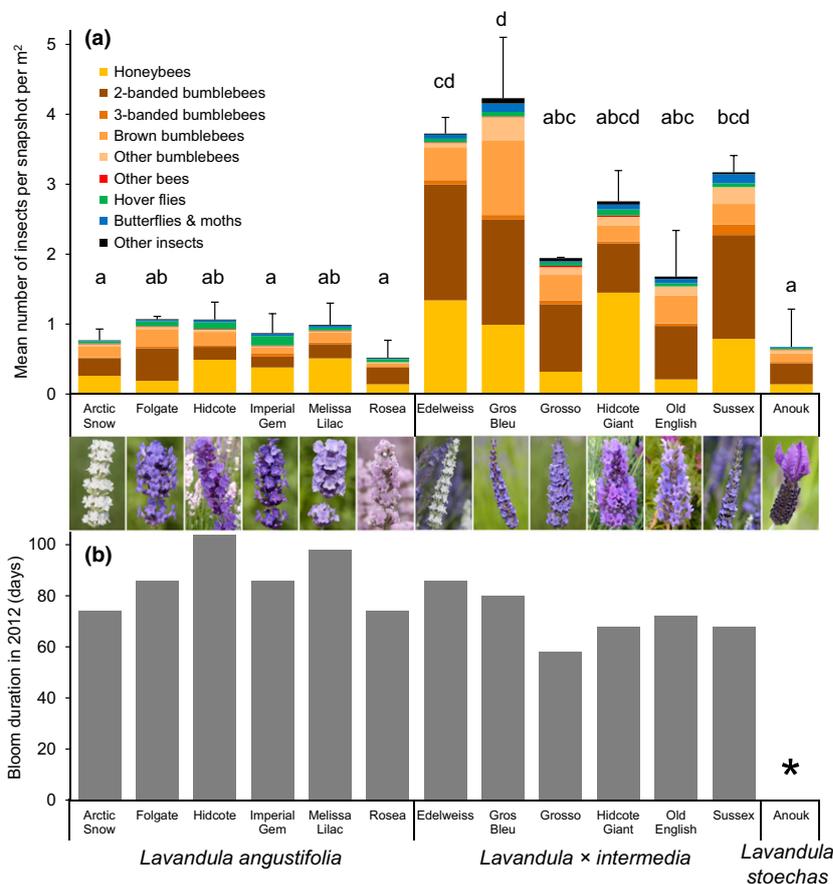
Fig. 5. (a) Numbers of insects per snapshot per m^2 on 13 *Lavandula* varieties. Bar heights are grand means of two data sets (University of Sussex 2011 & 2012) ± SE. Letters above bars denote results of *post hoc* Tukey's HSD pairwise comparison tests. (b) Total bloom duration of each variety in 2012, c. 15 months after planting out when plants were well established, thus showing natural phenology. * *L. stoechas* 'Anouk' was in poor condition and did not reach full bloom in 2012. Photographs courtesy Dr. Simon Charlesworth.

8·5–12·5 mm (Goulson *et al.* 2005)], but relatively unattractive to short-tongued species (length 7·5–7·6 mm), possibly due to its relatively long corolla tube (11·9 ± 0·2 mm). However, other plant species with similarly long corolla tubes were attractive to short-tongued species due to large corolla width (e.g. *E. vulgare*), which allowed short-tongued insects to place their whole head or body far into the flower, reducing or eliminating the need for a long tongue. In general, attractiveness did not correlate between honeybees and bumblebees on the one hand, and other bees, hover flies and butterflies + moths on the other, with the exception of the positive correlation between bumblebees vs. butterflies + moths (Fig. 7). However, certain plants stood out as particularly good for other, non-*Apis* and non-*Bombus*, bees (*Origanum vulgare*, *E. vulgare*, *S. byzantina*, *Achillea millefolium*), hover flies (*O. vulgare*, *A. foeniculum*, *E. vulgare*) and butterflies & moths (*A. foeniculum*, *Erysimum linifolium*). Interestingly, three of the four species particularly attractive to other bees are also native to Britain, suggesting that native plants may be more important for non-*Apis* and non-*Bombus* bees.

The factors potentially responsible for variation in attractiveness among plant varieties are diverse (e.g. size, shape, colour or scent, reviewed by Pellmyr (2002)). However, as the insects counted were flower-visiting foragers, this variation is presumably largely a result of foraging

choices based on nectar and pollen rewards in bees (Seeley 1995; Goulson & Osborne 2010) and hover flies (Haslett 1989) and nectar rewards in other insects (Kim, Gilet & Bush 2011). Our data showed no effect of corolla tube length (Table S2). However, in specific cases, corolla tube length may be important. In the case of lamb's ear (*Stachys byzantina*), its attractiveness to wool-carder bees (*Anthidium manicatum*) is probably due to the abundant leaf trichomes (pubescence) and possibly trichome secretions, which are collected by females as nest lining material (Müller, Topfl & Amiet 1996; Payne, Schildroth & Starks 2011). In addition, lamb's ear flowers are also visited by wool carders. Some plants may be more attractive than others by virtue of their longer flowering period. For example, *N.* × *faassenii* 'Six Hills Giant' and *Erysimum linifolium* 'Bowles Mauve', which are sterile hybrids unable to set seed, had flowering periods extending far beyond our c. 3-month observation periods. Indeed, *E. linifolium* flowers for approximately 9 months per year in Sussex. The attractiveness of such varieties is, therefore, underestimated in our data.

Closer examination of lavenders showed that hybrid *L.* × *intermedia* varieties were more attractive than both *L. angustifolia* varieties and *L. stoechas* (Fig. 5). This difference was not explained by either bloom duration or corolla tube length. In addition, flower colour, which ranged from light (e.g. white 'Arctic Snow', 'Edelweiss', rose
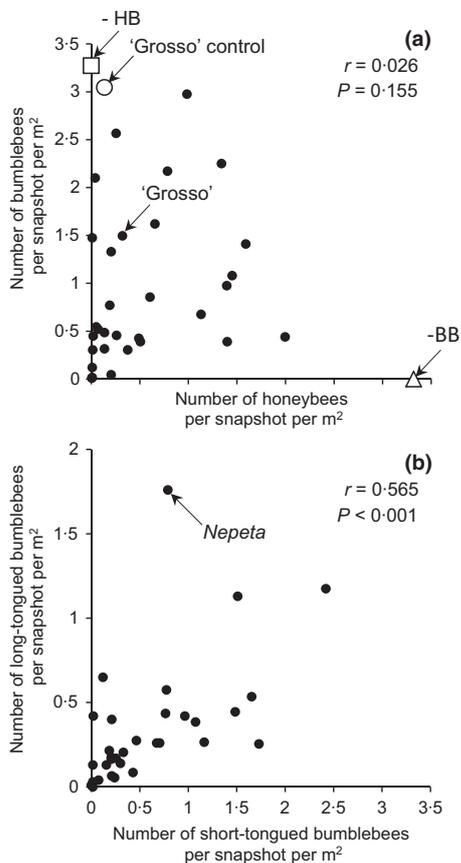
Fig. 6. (a) The absence of correlation between the attractiveness of plant varieties to honeybees and bumblebees. Coloured dots refer to three experimental treatments: honeybee exclusion (-HB, open square), bumblebee exclusion (-BB, open triangle) and control (open circle) on *Lavandula × intermedia* 'Grosso' (N.J. Balfour, S. Gandy & F.L.W. Ratnieks, unpublished data). 'Grosso' control (open circle) attracted a higher number of bumblebees than 'Grosso' in our data (closed circle) due to the data being gathered on 4 days during the flowering peak in the former case, and over c. 3 months in the latter case. (b) Significant correlation between the attractiveness of plant varieties to short-tongued bumblebees (*Bombus terrestris/lucorum* group) and long-tongued bumblebees (*B. hortorum* and *B. pascuorum* groups). Black dots are means of two data sets (University of Sussex 2011 & 2012).

'Rosea') to more typical shades of blue, did not appear to be an important factor (Fig. 5). We note that *L. × intermedia* varieties tended to be larger plants with taller inflorescences than *L. angustifolia* or *L. stoechas*. However, the definitive explanation causing the difference in attractiveness remains unknown and would be a valuable subject for further research.

Within the *Dahlia* genus, the two open-flowered varieties (Bishop of Llandaff and Bishop of Oxford) were consistently more attractive compared with the two varieties with highly modified flower forms (pompon 'Franz Kafka', semi-cactus 'Tahiti Sunrise'). This was likely due to the limited accessibility of disc florets, which provide nectar and pollen, due to the unusual shapes of the ray florets resulting from plant breeding. Additionally, the increased size and number of ray florets may be accompanied by a reduction in the number of disc florets, as compared to the open-flowered varieties. These results are supported by data from a survey of garden plants in a public garden in the nearby town of Lewes, where 'open' flowered varieties attracted significantly more insects than 'closed' flowered varieties (M. Garbuzov, E.E.W. Samuelson & F.L.W. Ratnieks, unpublished data).

Among other notable results is the pattern seen on *B. officinalis*, where the vast majority of its visitors were honeybees (mean 81·3% per data set). The highest proportions of butterflies and moths were recorded on *E. linifolium* (mean 11·1% per data set). *Pelargonium × hortorum* 'Cramden Red' was consistently the least attractive variety in each data set, with only 0·027 mean insects per snapshot per m[2] recorded. The four native species and the four wild-type varieties (Table S1) were not consistently more or less attractive than exotic or horticulturally modified varieties, showing that nativeness *per se* is not an important factor, and that horticultural modification need not reduce flower attractiveness to insect flower-visitors. Indeed, the case of lavender shows that the breeding of hybrid varieties can make plants more attractive to insects. In addition, varieties with very long bloom durations, such as *E. linifolium*
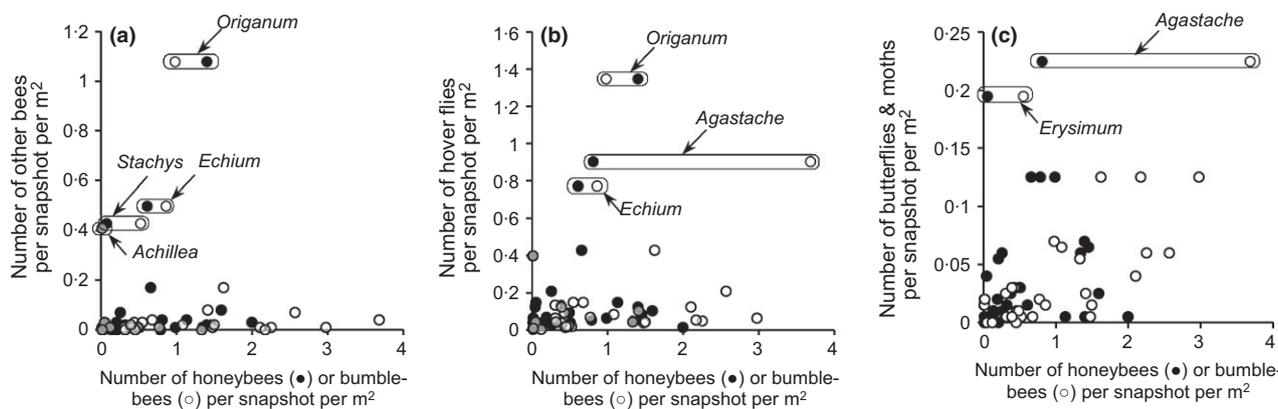

Fig. 7. Correlations between the attractiveness of plant varieties to honeybees (●) & bumblebees (○) vs. other bees (a), hover flies (b), and butterflies & moths (c). The only significant correlation found was between bumblebees and butterflies & moths (*r* = 0·665, *P* < 0·001).

'Bowles Mauve' and *N. × faassenii* 'Six Hills Giant', were sterile hybrids. As the plant hormones associated with seed and fruit development may inhibit flowering [e.g. gibberellins in woody angiosperms (Pharis & King 1985; Anthony 2006; Davies 2010)], sterility is an obvious way in which a garden plant can be simultaneously made more attractive to humans and flower-visiting insects. Sterility may also reduce the risk of invasiveness.

Our study used deliberately planted patches of 1 × 1 m. However, patch size does not affect the number of insects per unit area that visit garden plants in a range of patch areas from 0·1 to 3·6 m^2 (M. Garbuzov, A. Madsen & F.L.W. Ratnieks, unpublished data). Thus, studies to quantify flower attractiveness to insects can use existing patches in less standardized settings, such as gardens and parks, where patch size is measured and rates are calculated per unit area. The insect groups, including the bumblebee subgroups (Fussell & Corbet 1992), used in this study are simple enough to be differentiated by the public with little training, as was demonstrated by us in a series of workshops in 2011, 2012 and 2013 using the experimental flower bed at the University of Sussex. These methods could form the basis of large-scale 'citizen science' projects involving the help of many volunteers in gathering the data (Dickinson *et al.* 2012; Tweddle *et al.* 2012), or smaller projects run by interest groups, such as gardening or beekeeping clubs, or even schools or colleges.

Acknowledgements

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. List of plant varieties used in the study, arranged in alphabetic order.

Table S2. *P*-values of factors affecting the daily average number of insects per m^2 of each insect group in a series of GLMs.

Fig. S1. Bloom intensity scores of the 32 plant varieties.

Fig. S2. Relative abundance and insect visitation to a subset of 13 varieties in two extra locations (Plumpton College and Magham Down).