Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should we plant native or exotic species?

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Summary

1. Domestic gardens typically consist of a mixture of native and non-native plants which support biodiversity and provide valuable ecosystem services, particularly in urban environments. Many gardeners wish to encourage biodiversity by choosing appropriate plant taxa. The value of native and non-native plants in supporting animal biodiversity is, however, largely unknown.

2. The relative value of native and non-native garden plants to invertebrates was investigated in a replicated field experiment. Plots (deliberately akin to garden borders) were planted with one of three treatments, representing assemblages of plants based on origin (native, near-native and exotic). Invertebrates and resource measurements were recorded over four years. This paper reports the abundance of flower-visiting aerial insects ('pollinators') associated with the three plant assemblages.

3. For all pollinator groups on all treatments, greater floral resource resulted in an increase in visits. There was, however, a greater abundance of total pollinators recorded on native and near-native treatments compared with the exotic plots. Short-tongued bumblebees followed the same pattern whilst more hoverflies were recorded on the native treatment than the other treatments, and more honeybees on the near-native treatment. There was no difference between treatments in abundance of long-tongued bumblebees or solitary bees. The lack of difference in solitary bee abundance between treatments was probably due to a third of individuals from this group being recorded on one exotic plant species.

4. The number of flower visitors corresponded to the peak flowering period of the treatments, that is there were fewer flower visitors to the exotic treatment compared with the other treatments in early summer but relatively more later in the season.

5. *Synthesis and applications.* This experiment has demonstrated that utilizing plants from only a single region of origin (i.e. nativeness) may not be an optimal strategy for resource provision for pollinating insects in gardens. Gardens can be enhanced as a habitat by planting a variety of flowering plants, biased towards native and near-native species but with a selection of exotics to extend the flowering season and potentially provide resources for specialist groups.

Key-words: biodiversity, *Bombus*, bumblebees, floral resources, garden flowers, honeybee, hoverflies, plant choice, pollinators, solitary bees

Introduction

Domestic gardens are 'private spaces adjacent to or surrounding dwellings, which may variously comprise lawns, ornamental and vegetable plots, ponds, paths, patios, and temporary buildings such as sheds and greenhouses' (Gaston *et al.* 2005). They vary from a few square metres to several hectares and can contain a diversity and density of plants that exceeds those of natural or semi-natural habitats (Smith *et al.* 2006c; Loram *et al.* 2008). In this

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respect, gardens contain unique ecological features and unlike most other habitats are not defined by geography, geology and biota (Loram *et al.* 2007).

Gardens are recognized as important habitats in rural and especially in urban environments, and the pioneering studies of Owen (2010) and Smith *et al.* (2006a,b) show that they can support a wealth of animal diversity. The majority of the human population is now urban (United Nations 2011). Domestic gardens comprise a substantial proportion of the mosaic of land use in urban areas and are often the largest component of green space. For example, 16% of the area of Stockholm, Sweden (Colding, Lundberg & Folke 2012), 36% of Dunedin, New Zealand (Mathieu, Freeman & Aryal 2007), and 19–27% of cities in the UK is garden (Loram *et al.* 2007). Gardens provide positive ecosystem services including air cooling, flood mitigation, habitat resources and improvements to human health and well-being, although these effects are largely unquantified (Cameron *et al.* 2012).

The animal biodiversity supported by resources provided by garden plants has not been well documented, particularly the relative value of native and non-native species. This is an important information both for assessing the ecological health of urban areas and for the motivation of gardeners, half of whom in the UK actively encourage wildlife (biodiversity) into their gardens (Davies *et al.* 2009). Domestic gardens contain a high proportion of non-native plant species: approximately, 70% in the UK (Loram *et al.* 2008). This reflects the range of plants available to gardeners; more than 70 000 plant taxa (ca. 14 000 distinct species) are available to purchase in the UK (Cubey 2014), whilst the list of plant taxa considered native or naturalized is approximately 4800 (Stace 2010). It is often assumed that native plants provide the best resources for biodiversity, but this is not universally accepted (Kendle & Rose 2000; Schlaepfer, Sax & Olden 2011). Indeed, Smith *et al.* (2006a,b) found that plant structural heterogeneity and plant taxon richness rather than native or non-native status had the strongest influence on invertebrate abundance and species richness.

The aesthetic appeal of flowers is one of the primary drivers for selection of plants by gardeners (Garbuzov & Ratnieks 2013). Flowers can provide food resources (nectar and pollen) for invertebrates, and invertebrates may pollinate the plant. Flower visitation should not be considered a 'synonym for pollination' (Waser *et al.* 1996), but most of the flying insects that visit flowers have the potential to, and often do, carry out this function (Memmott & Waser 2002). Consequently, flying insects that visit flowers are referred to as 'pollinators' in this paper. Regarding these pollinators, urban gardens in Europe and North America support higher densities of bumblebees and solitary bees than farmed areas, due to higher floral density and diversity together with greater nest site availability (Fetridge, Ascher & Langellotto 2008; Osborne *et al.* 2008; Samnegård, Persson & Smith 2011). The variables having the principal effect on bee and butterfly species richness in New York were sunlight and total floral area, whilst the origin (nativeness) of plants was not significant (Matteson, Ascher & Langellotto 2008). There is also evidence that some non-native plants provide a resource that native plants do not; the bumblebee *Bombus terrestris* (L.) relies on winter-flowering 'exotic' plants as a nectar source in the absence of winter-flowering native plants in London gardens (Stelzer *et al.* 2010). However, rigorously designed manipulative experiments required to investigate and quantify the relative value of native and non-native plant assemblages for biodiversity are rare (Zuefle, Brown & Tallamy 2008).

These studies are particularly necessary since there is strong evidence that pollinators are in decline (Potts *et al.* 2010), which has led to initiatives such as the National Pollinator strategy for England (Defra 2014). Whilst the importance of gardens in supporting pollinator populations has been recognized, the comparative value of native and non-native garden plants remains largely unassessed. Management of the resources in domestic gardens should be a priority if biodiversity in gardens is to be retained and enhanced (Davies *et al.* 2009).

This paper describes an experiment testing the null hypothesis that 'there is no difference in invertebrate abundance associated with assemblages (artificial communities) of UK native and non-native garden plants'. Responses are likely to vary between invertebrate functional groups (Noss 1990), so the experiment sampled an extensive array of invertebrate fauna: subterranean organisms, pollinators, soil surface and epigeal arthropods. This paper reports the abundance of pollinators associated with the assemblages, taking account of the floral resources of the treatments.

Materials and methods

The design and methodology of the experiment followed the concepts adopted by the farm-scale evaluations of genetically modified herbicide-tolerant crops (Firbank *et al.* 2003). Following Perry *et al.* (2003), the design was chosen to relate directly to the conditions and practices of domestic horticulture, so that the findings could be applied unequivocally to gardens.

PLOT AND TREATMENT LAYOUT

The experiment was replicated on two 25 × 13 m sites at Wisley, Surrey, UK; one within the Royal Horticultural Society (RHS) Garden at Howard's Field and the other at the adjacent Deers Farm. The study areas were protected from rabbits by fencing. At each site, eighteen 3 × 3 m plots were surrounded with wood (treated softwood, 150 × 25 mm at Deers Farm; 150 × 50 mm at Howard's Field), with a 1-m guard row separating the plots. The wooden surrounds were drilled with 25-mm-diameter holes at 25-mm intervals, throughout their length, allowing the free movement of ground fauna. The plot size was chosen to represent a typical size for UK garden borders (Smith *et al.* 2006c). Each plot was planted with an assemblage of 14 plant species originating from one of three geographical regions, referred to as native,

near-native or exotic (defined below). At each site, these three treatments were randomly assigned to plots within each of six blocks oriented in an east–west direction. Within each treatment, there were three sets of 14-plant assemblages, termed plant groups 'A', 'B' and 'C', each formed from an overall list of 24 plant species (see Appendix S1 in Supporting information and subsection Plant Choice, below), the purpose being to maximize the representativeness of the plant species within plant origin treatments. Most individual plant species consequently occurred in two plant groups. The three plant groups were assigned to the six blocks using restricted randomization, to ensure an even distribution along the north–south direction.

The guard rows were lined with woven polypropylene (Mypex) landscaping fabric and filled with bark mulch (fine softwood bark, Petersfield Growing Mediums, Cosby and hardwood chips, AHS Ltd, Northiam). All plots were given a surface dressing with the fine softwood bark mulch in July 2009. The mulch in the guard rows was topped up as necessary; mulch in the plots was applied only once. An application of fertilizer (magnesium sulphate at 60 g m^{-3} and sulphate of ammonia at 16 g m^{-3}) was applied to Deers Farm plots in July 2009 to aid plant establishment after soil analysis indicated a lack of some nutrients at this site. No further fertilizer was applied.

PLANT CHOICE AND PLANTING PLAN

Plant species within each category of geographical origin were chosen on the basis of horticultural merit rather than ecological functionality. All the plants were herbaceous perennials or shrubs, enabling the experiment to continue for several years. Within plots, species were planted according to a standardized pattern (see Appendix S1). The plant assemblages were chosen to appear as similar as possible in terms of plant height, density and structure, with equivalent plants for each of the treatments in the same position. Planting took place between May 2009 and June 2010.

The three plant origin treatments were defined geographically:
1. Native. A species that arrived in the British Isles without anthropogenic intervention, whether intentional or unintentional (Pyšek *et al.* 2004), and of sufficient aesthetic merit to be considered suitable for use as an ornamental garden plant.
2. Near-native. A species occurring naturally only in the Northern Hemisphere but not native or naturalized in the British Isles, matched in terms of general growth habit and garden usage with one of the species chosen as a native plant and taxonomically related to it at familial, and usually generic, level.
3. Exotic. A species occurring naturally only in the Southern Hemisphere, matched in terms of general habit and garden usage with one of the species chosen as a native plant but not necessarily related to it at any particular taxonomic rank and not naturalized in the British Isles.

PLOT AND PLANT MANAGEMENT

Plot and plant management followed recommended UK horticultural practice to reproduce, as far as possible, typical garden conditions aiming to achieve visually appealing, weed-free plots (see Appendix S1).

DATA COLLECTION

The methods for recording pollinators were adapted from established protocols (Haughton *et al.* 2003), modified as indicated below to reflect the design of the experiment and the heterogeneous nature of the plant treatments. Field recording of pollinators began in March 2010 and continued for 4 years.

Aerial insect flower visitors (Pollinators)

Pollinators were recorded by a single expert recorder (A. Salisbury) on all plots on four or five occasions each year (2010 to 2013), from March to September inclusive, with a minimum 4-week interval between recording events. This covered the main period of flying insect activity. Between May and September recording took place when temperatures were above 17 °C, it was neither raining nor likely to rain, and wind speeds were less than five on the Beaufort scale (10·7 m s^{-1}). In March and April, recording took place when temperatures were above 8 °C, cloud cover was <25%, it was not raining and wind speed was less than two on the Beaufort scale (3·3 m s^{-1}).

Observations were made by counting all flying insects that landed on or were already on flowers in the plots whilst the observer stood at the centre of each side of the plot for 1 min. Each insect was counted only once. It took between 1·5 and 2 h to complete recording from all plots at a site per visit. To minimize potential effects of fluctuations in insect visits (due to possible changes in attractiveness of plots during the day as a consequence of different nectar flow or time of floral opening), two visits to each plot were made on each recording occasion; a morning recording event started between 09:00 and 10:00 h and an afternoon recording event starting between 13:00 and 14:00 h. Thus, each plot was recorded for 8 min in total on each recording occasion. The two sites were visited on different days with recording at the second site completed within 7 days of the first. The order in which blocks and plots within blocks were recorded was randomly assigned prior to each recording event.

Insects were categorized as they landed on flowers. Counts were made of honeybees (*Apis mellifera* L.); bumblebees (*Bombus* spp.), identified to colour group (Prys-Jones & Corbet 2011); other Hymenoptera, categorized as sawflies, solitary bees, social, solitary or parasitic wasps; butterflies and moths (Lepidoptera), identified to species; flies (Diptera), categorized as hoverflies (Syrphidae); or other flies and beetles (Coleoptera), identified to family.

Flowering units covariate

Availability of floral resources was estimated based on methodology used by Heard *et al.* (2007). For each plant species (excluding grasses, ferns and analogous plants) at each recording event, an estimate of the number of flowering units (a single flower or umbel, spike or capitulum for species with reduced or compound flowers) was made within the following range: 0, 1–5, 6–20, 21–100, 101–500, 501–1000. For analysis, flowering units were expressed as the median value within the range for each plant and summed to give a total for each plot.

ANALYSIS

Analysis was carried out on distinct taxonomic or functional groups from which a minimum number of 400 individuals were recorded over the 4 years. Six groups were chosen for analysis: total pollinators; short-tongued bumblebees (*Bombus terrestris/lucorum* and *B. lapidarius/ruderarius* colour groups); long-tongued bumblebees (*B. pascuorum* (Scopoli)*, and B. hortorum* (L.) colour

groups); honeybees (*A. mellifera*); solitary bees; and hoverflies (Syrphidae). Dates when zero individuals of the particular group concerned were recorded were omitted from the analysis.

The number of flower visitors per plot per occasion, c, was transformed logarithmically to $y = \log_{10}(c + 1)$. The covariate total flowering units per plot per occasion, f, was transformed similarly to $x = \log_{10}(f + 1)$. For each occasion, three linear regression models of flower visitors on flowering units were compared: a single line through all three plant origin treatments; three parallel lines allowing the intercept to vary with treatment; and three separate lines allowing both slope and intercept to vary with treatment. This analysis was performed using GENSTAT 16th Edition (VSN International 2013). Discrimination between models was by standard partial F-tests on two degrees of freedom (Perry 1982; Hawes *et al.* 2003). Preliminary analysis confirmed that regressions for the two sites were similar for all treatments, so data from the two sites were merged for analysis. However, results differed between years, which were therefore analysed separately, as well as combined. Linear regression was chosen following preliminary analysis involving quadratic and other nonlinear terms, which showed no significant curvature; therefore, there was no need to fit a more complex model.

The modal range of values for flowering units, f, was 100–1000, so a representative value of x was 2·5. Estimated values of y, denoted $\hat{y}_{2·5}$, were computed for each treatment, native, near-native and exotic, under the regression model that usually gave the best fit (treatments with different intercepts and different slopes) at this value of $x = 2·5$, to give a summary statistic facilitating the comparison of treatment differences on logarithmic scales, between the number of flower visitors at typical levels of flowering. For ease of interpretation, computed values of $\hat{y}_{2·5}$ were backtransformed to the natural scale using $d_{2·5} = 10^{\hat{y}_{2·5}}$.

In addition, a summary statistic, r, was derived to measure to what extent, if at all, any differences between the treatments exceeded those between the plant groups within the treatments. In a first stage, the standard deviation between the above estimates of $\hat{y}_{2·5}$(native), $\hat{y}_{2·5}$(near-native) and $\hat{y}_{2·5}$(exotic) was calculated and is denoted here as s_t. In the second stage, similar estimates were calculated for the plant groups for each treatment: $\hat{y}_{2·5}$(native,A), $\hat{y}_{2·5}$(native,B) and $\hat{y}_{2·5}$(native,C) for the native treatment, and similarly for the other treatments. Then, an analogous value was computed to represent the average, over the three treatments, of the standard deviations of similar estimates of variability between the plant groups within the treatments; this is denoted here as s_{pg}. The ratio, r, of these two estimates of variability, $r = s_t/s_{pg}$, was adopted as the summary statistic to aid interpretation. Values of $r > 1$ imply that differences between the treatments exceeded those between the plant groups within the treatments.

Results

The regressions showed a good linear dependence of transformed flower visitors on transformed flowering units. Regression lines with different slopes and intercepts for the three treatments provided the best fit, and so results are given for this form of model.

The observed data and fitted relationships for the three treatments for the total 7979 pollinators recorded are shown in Fig. 1; estimates of regression coefficients and significance tests are given in Table 1. There was little difference between the abundance of pollinators for the native and near-native treatments, but considerably fewer flower visitors for the exotic treatment, which had about 40% fewer visitors at typical values of flowering units. The value of r was 2·0 for all years combined, demonstrating that the treatment differences considerably exceeded those between plant groups within treatments.

Changes in the covariate, the geometric mean number of flowering units per plot between sampling occasions, within each of the 4 years, are shown in Table 2 for each of the three treatments. In each year, between May and September when flowering units were greatest, the number of flower units reached a maximum notably later in the exotic plots than in the native and near-native plots, which were similar to each other. Fig. 2 demonstrates that the number of flower visitors for total pollinators responded to differences in the timing of peak flowering, being relatively smaller for the exotic treatment compared with the other treatments earlier in the season but relatively greater later in the season. The other pollinator subgroups showed similar seasonal patterns in response to flowering.

The five pollinator subgroups contained 83·0% of the insects recorded. The observed data and fitted relationships for the three treatments for the 1100 (13·7% of total pollinators) short-tongued bumblebees, 615 (7·7% pollinators) long-tongued bumblebees, 2420 (30·3% pollinators) honeybees, 691 (8·6% pollinators) solitary bees and 1796 (22·5% pollinators) hoverflies recorded during the experiment are shown separately in Appendix S2; estimates of regression coefficients and significance tests are in Table 3.
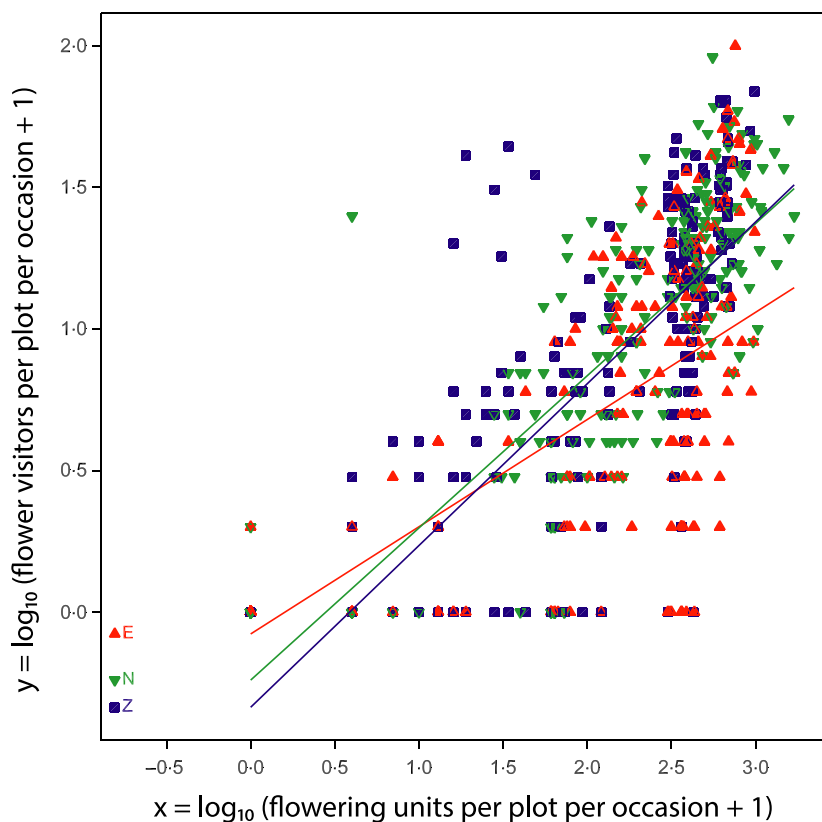
As with the total pollinator group, there was little difference between the abundance of short-tongued bumblebees for the native and near-native treatments, but considerably fewer visits to the exotic treatment, which had about 40–50% less visitors at typical values of flowering units. The value of r was 2·85 for all years combined, demonstrating that the treatment differences considerably exceeded those between plant groups within treatments.

There was no significant difference between the abundance of long-tongued bumblebees recorded on the treatments. The value of r was 1·26 for all years combined.

There was only a small difference between honeybee abundance on native and exotic treatments. There were considerably more honeybee visitors on the near-native treatment, which had greater than 50% more visitors at typical values of flowering units compared with the other treatments. The value of r was 1·69 for all years combined, demonstrating that the treatment differences exceeded those between plant groups within treatments.

There was no significant difference between the abundance of solitary bees for the three treatments. The value of r was 0·24 for all years combined.

There was little difference between the abundance of hoverflies for the near-native and exotic treatments, but

Fig. 1. Dependence of total pollinators on plant flowering units. Observed data and fitted regressions for total pollinators ($n = 7\,979$), over all years 2010–2013 combined. Native (N) green, downward triangles; near-native (Z) blue, squares; exotic (E) red, upward triangles. Estimated intercepts and slope are shown in Table 1. The fitted regressions differ ($F_{2,678} = 14.66$, $P < 0.001$).

Table 1. Fitted regressions for total pollinators for native (N), near-native (Z) and exotic (E) treatments. *F*-statistics for slopes have 2,*m* degrees of freedom where $m > 100$. The value $d_{2.5}$ is a backtransformed estimate of the total number of flower visitors per occasion, when the number of flowering units is approximately 316. The value *r* is a ratio of two standard deviations, representing, respectively, the variability between the treatments and the variability between plant groups within the treatments (see text). The estimated intercept and slope are fitted values. *F* slopes is the *F*-statistic for the test of differences between the slopes of the linear relationships for the three treatments, with probability level given by *P* slopes

Treatment	Estimated intercept	SE	Estimated slope	SE	*F* slopes	*P* slopes	$d_{2.5}$	*r*
2010								
N	0·143	0·010	0·143	0·053	12·55	<0·001	11·8	1·73
Z	1·100		1·100				12·3	
E	−0·041		−0·041				8·7	
2011								
N	−0·447	0·080	−0·447	0·038	13·21	<0·001	13·1	4·17
Z	−0·668		−0·668				16·6	
E	−0·585		−0·585				8·9	
2012								
N	−0·327	0·105	−0·327	0·049	5·02	0·008	16·2	7·05
Z	−0·250		−0·250				10·2	
E	−0·123		−0·123				6·4	
2013								
N	0·003	0·139	0·003	0·062	2·65	0·074	11·9	1·61
Z	−0·073		−0·073				13·8	
E	0·102		0·102				6·2	
All years combined								
N	−0·240	0·048	−0·240	0·023	14·66	<0·001	12·7	2·00
Z	−0·336		−0·336				12·4	
E	−0·077		−0·077				7·4	

considerably more hoverfly visitors for the native treatment, which had about 45% more visits at typical values of flowering units. The value of *r* was 1·64 for all years combined, demonstrating that the treatment differences exceeded those between plant groups within treatments.

Discussion

The positive responses of pollinator abundance to increased floral resource in the three treatments are to be expected as floral abundance is a primary driver for insect visits regardless of plant origin (Memmott & Waser 2002; Williams *et al.* 2011). It could therefore be supposed that, in gardens, the more flowers there are, regardless of 'nativeness', the greater the abundance of pollinating insects. This, however, is an oversimplification since there were
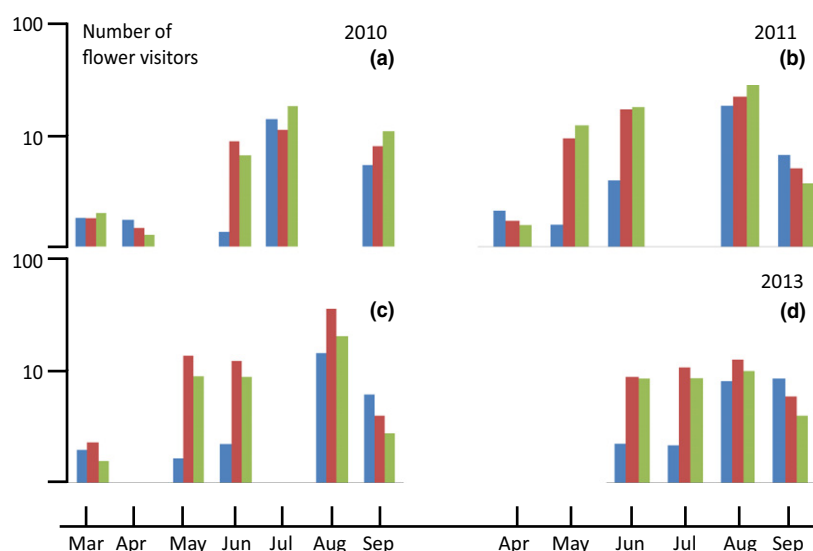
marked differences in the responses of different pollinator groups to plant origin treatments.

Whilst foraging activity was not directly recorded the responses observed are likely to be genuine as pollinating insects are highly mobile and have the ability to respond rapidly to changes in floral resource and so counts were likely to quantify preferences for a location (i.e. plot or treatment) (Pollard & Yates 1993). It can be assumed that the majority of visiting insects were gaining nutrition and providing a pollination service (Waser *et al.* 1996) rather than merely resting. We infer from the strong response of flower visitors to relative flower (resource) abundance that the observed differences are likely to be due to floral resource. Ideally, the measurement of floral abundance would have been coupled with a measure of nectar and pollen quality and quantity, providing a more detailed assessment of resource availability (Haslett 1989). This would, however, have involved sampling individual flowers on several occasions which was beyond the scope of this experiment. Recording foraging behaviour in addition to flower visits will also provide further insights and should be considered for future research.

The close correspondence of the number of flower visitors to the respective timing of peak flowering of the three treatments indicates that the exotic plots were in effect extending the flowering period. Similar observations have been made in North America (Memmott & Waser 2002), and these results support the proposition that non-native plants can act as mutualists aiding in the maintenance of pollinator populations. This emphasizes the necessity of recording the pollinator community at different temporal scales, also stressed by Waser *et al.* (1996). Recording on several occasions within a year and over

Table 2. Mean number of flowering units per plot for treatments and occasions

Year	Sampling occasion	Native (N)	Near-native (Z)	Exotic (E)
2010	March	1·5	47·0	0·0
	April	42·0	81·3	1·3
	June	715·5	519·8	190·0
	July	219·0	108·0	51·2
	September	387·0	299·5	536·2
2011	April	42·7	31·7	0·2
	May	378·2	461	70·0
	June	1262·7	450·2	462·2
	August	841·2	760·5	796·8
	September	106·0	71·8	702·2
2012	March	35·7	87·7	0·2
	May	383·2	487·5	97·0
	June	532·5	348·5	391·8
	August	789·0	608·2	795·0
	September	87·7	108·8	462·5
2013	June	306·0	256·5	66·8
	July	719·8	339·5	418·5
	August	397·2	317·2	464·2
	September	162·5	107·5	562·0

Fig. 2. Number of pollinators per plot per sampling occasion for total pollinators combined (*n* = 7 979). On each occasion, order of treatments shown is left-hand, blue column: exotic; middle, red column: native; right-hand, green column: near-native. (a) 2010: sample occasions were March, April, June, July and September; (b) 2011: April, May, June, August, September; (c) 2012: March, May, June, August, September; (d) 2013: June, July, August, September.

Table 3. Fitted regressions for five different groups of pollinators for native (N), near-native (Z) and exotic (E) treatments. *F*-statistics for slopes have 2,*m* degrees of freedom where $m > 100$. The value $d_{2.5}$ is a backtransformed estimate of the total number of flower visitors per occasion, when the number of flowering units is approximately 316. The value *r* is a ratio of two standard deviations, representing, respectively, the variability between the treatments and the variability between plant groups within the treatments (see text). The estimated intercept and slope are fitted values. *F* slopes is the *F*-statistic for the test of differences between the slopes of the linear relationships for the three treatments, with probability level given by *P* slopes

Treatment	Estimated intercept	SE	Estimated slope	SE	*F* slopes	*P* slopes	$d_{2.5}$	*r*
Short-tongued bumblebees								
N	−0·412	0·064	0·317	0·028	14·68	<0·001	2·4	2·85
Z	−0·154		0·240				2·8	
E	−0·037		0·072				1·4	
Long-tongued bumblebees								
N	−0·080	0·0437	0·128	0·0198	2·72	0·067	1·7	1·26
Z	0·051		0·098				2·0	
E	−0·011		0·053				1·3	
Honeybees								
N	−0·276	0·0868	0·275	0·0382	6·61	0·001	2·6	1·69
Z	−0·473		0·433				4·1	
E	−0·159		0·211				2·3	
Solitary bees								
N	−0·098	0·0584	0·134	0·0257	0·74	0·476	1·7	0·24
Z	−0·190		0·169				1·7	
E	−0·104		0·121				1·6	
Hoverflies								
N	−0·084	0·0546	0·290	0·0247	5·24	0·006	4·4	1·64
Z	−0·035		0·173				2·5	
E	−0·037		0·170				2·4	

several years reduced the likelihood that these results were a consequence of annual fluctuations in insect populations.

RESPONSES OF THE POLLINATOR GROUPS

The results with total pollinators and the subgroup short-tongued bumblebees suggest that gardens rich in native and near-native plants will have greater numbers of pollinators than those dominated by exotic flowering plants. This is similar to observations in the USA where flowers of non-native plants with 'taxonomic affinity' to native plants (broadly analogous to the near-native treatment) were visited by more pollinator species than non-natives that were distantly related (analogous to the exotic treatment) (Memmott & Waser 2002). The short-tongued bumblebees are considered generalist pollinators that have little preference for native plant species over non-natives (Hanley, Awbi & Miguel 2014). This pattern of response was not borne out by other pollinator subgroups.

The preference of honeybees for the near-native treatment is unexpected as *A. mellifera* is considered a 'super-generalist' that visits flowers of a wide range of plants regardless of origin (Memmott & Waser 2002). The honeybee is unlikely to be native to the UK although it has been present for more than 4000 years (Carreck 2008). It is therefore possible that its preference for near-native plants is a consequence of its origins. However, the responses of *A. mellifera* can be affected by interaction with bumblebees, and this species' true preferences may

only be observed when *Bombus* species are excluded (Garbuzov & Ratnieks 2013).

There is a dearth of literature of the floral preferences of adult hoverflies. Whilst in gardens, native plant richness has previously shown a strong positive relationship with hoverfly abundance (Smith *et al.* 2006b), these authors suggested that human population density, number of houses and the presence of a pond also had strong positive relationships, although some of the apparent associations may have been due to chance. The results of this experiment corroborate the observation that hoverfly abundance is related to native floral resource. The floral preferences of hoverflies require further investigation as the hoverflies are a large family with more than 250 species in the UK (Stubbs & Falk 2002) and, whilst some are selective in their flower foraging, many are generalists (Haslett 1989).

It is possible that the experiment was not sufficiently sensitive to detect the more subtle effects of plant origin on floral response for long-tongued bumblebees and solitary bees.

The lack of significance with solitary bees appears to contest Smith *et al.* (2006b) where native plant richness was positively correlated to abundance. The variation in response between the plant groups within the treatments was greater than that between treatments, the likely cause is that the exotic plant (*Eryngium agavifolium* Griseb.) recorded 230 visits by solitary bees over the 4 years; 33% of visits. Whilst there is a high degree of floral specialism in some solitary bees, many species show some degree of generalism and opportunism (Waser *et al.* 1996). It is

therefore possible that the disproportionate response to *E. agavifolium* was a case of opportunistic foraging by one or more species of solitary bee. This supports the view that in some cases, individual exotic plant species can have a strong positive effect on some pollinators (Stouffer, Cirtwill & Bascompte 2014). Whether this effect was limited to just one or a small number of relatively specialist species or to generalist solitary bees would require identification to species of individual bees.

Long-tongued bumblebees are considered to be more selective in the flowers they visit than short-tongued bumblebees, being more likely to take nectar from long, tubular flowers and usually specializing in foraging from leguminous plants (Hanley, Awbi & Miguel 2014). Garbuzov & Ratnieks (2013) also reported that short- and long-tongued bumblebees visited garden plant varieties; however, they concluded that this reflected the effects of preferences in conjunction with a potential inter-action with honeybees. Therefore, whilst our experiment demonstrates that the foraging preferences of long- and short-tongued bumblebees may differ and that these groups should continue to be considered separately, further investigation is required.

APPLICABILITY OF THE RESULTS AT THE SPATIAL AND TEMPORAL SCALE

The relative abundances of insect orders in the pollinator community can differ with location. For example in Poland, Diptera dominated on the outskirts of Warsaw and Hymenoptera towards the centre whilst pollinator network size and structure were similar for both communities (Jędrzejewska-Szmek & Zych 2013). The responses of bees to flower resources in communities of plants in different areas of the USA were also alike, although species composition differed (Memmott & Waser 2002; Williams *et al.* 2011). Observations on garden plants in different sites across southern England indicate that pollinator responses are not location dependent (Garbuzov & Ratnieks 2013). Our experiment gave comparable results with other locations; for example to overall pollinator abundance in the USA (Memmott & Waser 2002) and hoverflies in northern England (Smith *et al.* 2006b). Thus, whilst pollinator composition will differ in proportions on the spatial scale, it appears that the relative responses of each group remain similar.

The responses of crepuscular and nocturnal pollinator groups were not investigated in this experiment and require further study.

CONCLUSIONS AND IMPLICATIONS FOR GARDEN MANAGEMENT

This experiment has shown that flowering garden plant assemblages can provide a resource for pollinators regardless of the plants' origin and that the greater the resource available the more pollinators will visit. This accords with the concept that there is generalization and opportunism in pollinator systems (Waser *et al.* 1996; Stouffer, Cirtwill & Bascompte 2014) and demonstrates the value that communities of garden plants can provide for pollinators.

In this experiment, assemblages of native and near-native garden plants saw the greatest abundance of pollinators compared with exotic plants. Exotic plants extended the flowering season and provided additional resources to pollinators when the abundance of flowers on native and near-native plants was low. In addition, we saw interactions between an exotic plant and some pollinators suggesting that exotic plant species can provide resources of particular value. Therefore, utilizing plants from one region of origin may not be the optimal strategy for providing resources for pollinating insects in gardens. It seems that the best advice is to plant a variety of flowering plants in gardens biased towards native and near-native species with a careful selection of exotics to extend flowering season and perhaps provide resources for some groups, for example solitary bees. This advice needs further refinement and verification before it can be widely promulgated.

Acknowledgements

Data accessibility

Pollinator abundance and flower count data are available from the Dryad Digital Repository doi:10.5061/dryad.8hq3s (Salisbury *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Further details of Materials and Methods.

Appendix S2. Further details of Results.