

1 **Title**

2 Two Bee-pollinated Plant Species Show Higher Seed Production When Grown in Gardens
3 Compared to Arable Farmland.

4

5 **Authors and Affiliations**

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11

12 **Abstract**

13 **Background**

14 Insect pollinator abundance, in particular that of bees, has been shown to be high where there is a
15 super-abundance of floral resources; for example in association with mass-flowering crops and also
16 in gardens where flowering plants are often densely planted. Since land management affects
17 pollinator numbers, it is also likely to affect the resultant pollination of plants growing in these
18 habitats. We hypothesised that the seed or fruit set of two plant species, typically pollinated by
19 bumblebees and/or honeybees might respond in one of two ways: 1) pollination success could be
20 reduced when growing in a floriferous environment, via competition for pollinators, or 2) pollination
21 success could be enhanced because of increased pollinator abundance in the vicinity.

22 **Methodology / Principal Findings**

23 We compared the pollination success of experimental plants of *Glechoma hederacea* L. and *Lotus*
24 *corniculatus* L. growing in gardens and arable farmland. On the farms, the plants were placed either
25 next to a mass-flowering crop (oilseed rape, *Brassica napus* L. or field beans, *Vicia faba* L.) or next to
26 a cereal crop (wheat, *Triticum spp.*). Seed set of *G. hederacea* and fruit set of *L. corniculatus* were
27 significantly higher in gardens compared to arable farmland. There was no significant difference in
28 pollination success of *G. hederacea* when grown next to different crops, but for *L. corniculatus*, fruit
29 set was higher in the plants growing next to oilseed rape when the crop was in flower.

30 **Conclusions / Significance**

31 The results show that pollination services can limit fruit set of wild plants in arable farmland, but
32 there is some evidence that the presence of a flowering crop can facilitate their pollination
33 (depending on species and season). We have also demonstrated that gardens are not only beneficial
34 to pollinators, but also to the process of pollination.

35

36 Introduction

37 The anthropogenic introduction of large quantities of flowering plants has occurred both in arable
38 and urban habitats. In urban gardens high densities of flowering plants are cultivated for their
39 amenity value, while in agriculture the cultivation of mass-flowering crops such as oilseed rape
40 (*Brassica napus* L.) and field beans (*Vicia faba* L.) in the UK has been arguably the most dramatic
41 change to the floral landscape for centuries. Oilseed rape crops began to be cultivated on a large
42 commercial scale in the mid-1970's in the UK and are now grown on an unprecedented scale. In
43 2009 oilseed rape was cultivated on approximately 15% of UK arable land (~600 000ha [1]), and it
44 has become a familiar part of our spring landscape, yet the potential ecological impacts of this
45 change in agricultural practice are only just starting to be recognised [2,3,4,5]. It is possible that,
46 during the flowering period, the nectar and pollen provided by these crops greatly exceeds that
47 provided by all other flowers combined in arable landscapes. A similar situation exists in urban
48 gardens where floral resources provided by cultivated plants are plentiful over large areas. In the
49 case of garden plants though, there tends to be nectar and pollen available from different species
50 through most of the year [6] whereas the mass-flowering crops only provide resources from one
51 species over a relatively short period of a few weeks.

52 For mass-flowering crops, there is sparse evidence of the impact that this brief glut of floral
53 resources has on the seed or fruit set of flowers that share pollinators with the crops. Do they
54 impact negatively on levels of seed set in wild flowers in neighbouring hedgerows through
55 competition for pollinators, or do they have a positive impact (facilitation) through attracting more
56 pollinators to the area and thus boosting pollination and subsequent seed production? Diekötter et
57 al [2] found no effect of the proportion of landscape covered with oilseed rape on seed set in red
58 clover (*Trifolium pratense* L.); although they did detect a positive effect of the amount of semi-
59 natural vegetation in the area. In contrast, our study examines the local effect of a neighbouring
60 crop, and utilises plant species that share pollinators with the crops. There has been growing
61 interest in the possible effects of co-flowering plant species on pollen limitation [7,8,9], particularly
62 in relation to invasive alien species of flowering plant affecting native plant species. Evidence of
63 effects is variable, with some species positively affected, others negatively [10,11,12,13]. The
64 direction of a response in seed or fruit production is likely to vary depending on the species of
65 pollinators and the species of wild flowers.

66 In agricultural settings there is some evidence that the species of the crop sown in the field, or the
67 management thereof, can influence the abundance of bumblebees and other pollinators in the field
68 margin in the short term as a result of re-distribution of bees [3,5,14] and possibly in the longer term
69 as a result of increase colony density and growth [4,15].

70 If there are effects on plant pollination (positive or negative) then they may be temporally localised
71 if they are a result of changed pollinator behaviour, for example if their choice of forage is changed
72 and they are attracted into the area in large numbers. Alternatively the effects may be spread out
73 over the season if the copious floral resources (in gardens or farmland) are driving changes in the
74 insect pollinators' population dynamics. The variety, abundance and continuity of floral resources
75 provided in gardens is thought to positively affect bumblebee populations [6,16,17,18]. Against a
76 backdrop of evidence that urbanization generally leads to species loss and reduction in biodiversity
77 [19,20] there is increasing evidence pointing to the potential for urban areas to act as a refuge for

78 certain bumblebee species. Several studies have found bee abundance and diversity to be high in
79 urban and suburban areas [21,22] although it depends on the degree of urbanisation [23,24] and
80 Osborne et al [25] found there was a higher density of bumblebee nests in gardens compared to
81 largely agricultural countryside. In addition Fetridge, Ascher & Langellotto [26] found the bee
82 (Apoidea) fauna of suburban gardens closely resembled that found in nearby natural forest.
83 Goulson et al [27] found that the survival of bumblebee nests from May to August was positively
84 associated with the area of gardens in the vicinity of the colony. This relatively positive picture for
85 social bees may be at odds with the global picture of urbanization but, for these species at least,
86 urban areas can provide an important resource for population survival. This positive impact of
87 gardening on bumblebee populations may have a knock-on effect on pollination levels of plants
88 growing in the surrounding environment.

89 Although studies comparing urban and agricultural settings have assessed bee abundance, as have
90 studies comparing the field margins of mass flowering crops with other crops, to our knowledge no
91 studies have reported on the relative seed production of insect-pollinated wild plants growing in
92 these different settings. We carried out a replicated experiment to determine whether mass-
93 flowering crops and the floral resources in gardens have a competitive or facilitatory effect on
94 pollination and seed-set of *Glechoma hederacea* L. (ground ivy) and *Lotus corniculatus* L. (birdsfoot
95 trefoil). These species were selected because they are entirely or largely self-incompatible, relying
96 on insect pollination, primarily by social bees [28,29,30]. They vary in morphology and phenology
97 and occur naturally in field margins and hedgerows in the study area.

98 We tested the null hypothesis that pollination, and resultant seed and fruit set of *G.hederacea* and
99 *L.corniculatus* were not different when the plants were growing in contrasting locations. If the null
100 hypothesis is rejected, we predict one of the two following outcomes for the wild flowers: 1) the
101 presence of a mass flowering crop in the near vicinity or placement in a suburban garden has a
102 facilitatory effect on pollination, resulting in increased fruit or seed-set; or 2) the presence of a
103 flowering crop or placement in a suburban garden reduces pollination and consequent fruit or seed-
104 set, because of competition and increased pollen limitation [9].

105 We tested these predictions using oilseed rape and field beans. Seed yield in both crops is increased
106 by insect pollination (although self pollination also occurs, and wind pollination in oilseed rape), and
107 when pollinated by insects the two crops have contrasting pollinator guilds. Oilseed rape is
108 pollinated by short-tongued pollinating insects (including honeybees) whilst field beans are
109 pollinated by long-tongued bumblebees (although the flowers are frequently robbed by short-
110 tongued bees). The control treatment was winter wheat which is not visited by bees. In addition a
111 comparison was made with suburban domestic gardens. We also quantified relative abundance of
112 flowers and bees in the vicinity, because our hypotheses assume that changes in the relative
113 abundance of pollinators would be the likely mechanism for increased or decreased seed and fruit
114 set in the experimental plants. The results will increase our ability to predict the impact of
115 agricultural practices and urbanisation on populations of wild plants in the landscape.

116 **Materials and Methods**

117 *G.hederacea* and *L.corniculatus* plants were bought as small plugs and reared in a glasshouse to
118 ensure they were of similar age, provenance and growth stage. The plants were transferred into

119 large, 25cm pots which were placed in 80 litre tubs of sand (60cm in diameter). Plants in natural
 120 populations are highly variable, depending on the conditions in which they grow, so we used pot-
 121 grown experimental plants to ensure that, as far as possible, resources were controlled to prevent
 122 differences in plant growth and development between treatments and sites.

123 The experimental sites were on 15 field margins on commercial farms within 10 km of Rothamsted
 124 Research station, Harpenden, Hertfordshire, UK (Ordnance Survey coordinates TL 13415 13598) and
 125 five domestic garden sites in the urban area of Harpenden (Fig 1). In April four tubs, each containing
 126 one *G. hederacea* plant and one *L. corniculatus* plant, were placed in a group (subsequently referred
 127 to as a patch) at each of the 20 sites. For each species, the number of flowers in these patches gave
 128 densities similar to the sparse and small natural patches found in the field margins (see results).

129 The field margins were on five farms (considered as blocks in the analysis) which were at least 1750
 130 m apart and there were three crop treatments on each farm (Fig 1). So within each block there was
 131 a patch of tubs on a margin adjacent to winter oilseed rape, one adjacent to winter field beans and
 132 one adjacent to wheat (the control). These margins were located within a circle of 1000 m on each
 133 farm. We consider the blocks to have insect pollinators from different colonies or populations as
 134 most individuals are likely to fly less than the separation distance of 1750 m [31,32]; but within each
 135 farm, the same individuals are likely to be choosing between treatments. It was not feasible to
 136 spread the sites more widely. The field margins were each 4-6 m wide, sown with grass or naturally
 137 regenerated with a mixture of grass/herbaceous species and adjacent to a hedgerow. The tubs were
 138 placed adjacent to the hedge to prevent shading from the different crop treatments.

139 At each of the five domestic garden sites (Fig 1), a patch of four tubs was placed adjacent to a border
 140 or boundary. It is difficult to ensure comparability between the farmland and garden sites because
 141 of the different structures of these habitats. However, we aimed to make them as comparable as
 142 possible by using the most “linear” features in each garden, for example a herbaceous or perennial
 143 border next to a lawn, or a boundary hedge. At all 20 sites (in both farmland and gardens), the tubs
 144 were positioned adjacent to south-facing boundaries to reduce the effects of differential shading or
 145 shelter between sites.

146 When the plants were placed at the sites, they were all of similar size and growth stage; and the soil
 147 and space available to the plants were matched. During the course of the experiment a watering
 148 system was set up so that all the tubs were maintained at the same soil moisture. These steps were
 149 taken to ensure that the plants’ access to nutrients, water and light were controlled and comparable
 150 among treatments and sites. Records of flower abundance, bee visitor abundance and seed set
 151 were taken during each of four observation periods from April to August. Each period was about
 152 four weeks long to fit in all the observations required (start dates: 18 April, 25 May, 25 June, 27 July)

153 **Test for self-incompatibility**

154 In a separate experiment seed set in plants grown in insect-proof cages versus open-pollinated
 155 plants was compared to confirm that the plant species used were at least partially self-infertile (this
 156 can vary between races and populations) and require insects to mediate pollen transfer. Twelve
 157 plants each of *L. corniculatus* and *G. hederacea* were grown. At the point at which the plants began
 158 to flower, six plants of each were transferred into an insect-proof cage. On each plant, 15 flowers

159 were individually marked with coloured tape (Scotch® 35 Colour Coding PVC Electrical Insulation)
 160 and the seed or fruit set for each flower was assessed as described below.

161 **Local flower abundance**

162 During each of the four observation periods an assessment was made of the flower density of a) the
 163 sown wild plants in tubs, b) the crop and c) other flowering plants in the margins or garden border
 164 next to the tubs. The number of flowers of each plant species present in a 200 m length of each field
 165 margin were counted (Table S1). In each garden, a transect counting flowers of each plant species
 166 was also walked during each period. The transect incorporated the garden boundary or border next
 167 to the tubs and utilised other linear features in the garden (e.g. around the perimeter). In some
 168 cases it was not possible to walk a 200 m length (we only had access to individual gardens) so the
 169 resulting data are expressed per 200 m to make comparisons with the field margins. Every plant
 170 species encountered during the margin transects was assigned a score for the likely usage by
 171 bumblebees and honeybees: 0 = not used as forage; 1 = used as forage (Table S1). These scores
 172 were assigned using the methods of Osborne et al [32] who examined records in comparative forage
 173 studies and reviews and using the combined observational experience of the authors. Visitation
 174 records were verified using Knuth [30,33,34]. A score of zero represented an absence of positive
 175 records of visitation by bees in any of the above references. Species given a score of 1 were included
 176 in the list of “bee forage plant species” and used in the analysis. It was not possible to record
 177 attractiveness or reward levels in further detail in this experiment.

178 **Local flower visitor abundance**

179 To assess the local abundance of potential pollinators, flower visitors were surveyed by observing
 180 the number and species of all flower visits taking place along the same length of field margin or
 181 garden boundary that was used to assess local flower abundance using a standard walk, between
 182 10.00 h and 17.30 h in standard weather conditions (temperature above 13 °C with at least 60%
 183 clear sky or above 17 °C in any sky conditions apart from heavy rain; Beaufort wind speed of less
 184 than 5) [3]. One transect was performed during each observation period. Counts of the number of
 185 insects visiting the experimental patches of plants were taken during 4 x 10 minute sessions spent
 186 watching each patch during each observation period during standard weather conditions (above),
 187 but the numbers were too low for analysis.

188 **Seed and fruit production**

189 The number of flowers produced on the plants in tubs during each of the four observation periods
 190 was determined by marking the stems with coloured tape (Scotch® 35 Colour Coding PVC Electrical
 191 Insulation) at the beginning and end of the period, and counting the number of flowers in between
 192 the coloured tape marks. Seed heads were gathered from these marked stems before seed shed in
 193 order to assess seed production. When they were gathered, seed heads that showed signs of
 194 herbivory or contained larvae were not included in the analyses. For *G. hederacea* an average of
 195 352.5 (\pm 17.3) flowers per patch were collected in each of the first two sampling periods (n=40). A
 196 count was made of the number of seeds formed in each flower (with four ovules), including flowers
 197 which produce no seeds (from here on described as ‘seed-set’). The seeds mature at different rates
 198 both within and between the plant species. *G.hederacea* stems were sampled 1 -2 weeks after the
 199 flowers were counted, when the “youngest” seeds near the tops of the stems were swollen and
 200 green. The “older” seeds further down the stem were mature and some had already been shed, but
 201 it was possible to score them from the scars left at the flower base. There were not enough *G.*

202 *hederacea* flowers present during the third and fourth observation period to collate seed-set data.
 203 *L.corniculatus* ripe fruits were collected approximately four weeks after the flowers were marked
 204 and counted. A mean of 96.9 (\pm 3.9) flowers were sampled from the four plants in each patch during
 205 each time period (n=80). The proportion of these flowers producing fruits was counted (from here
 206 on described as 'fruit-set'). A repeated measure ANOVA showed that the number of flowers sampled
 207 per patch was not significantly different between treatments or observation periods for either plant
 208 species.

209 **Statistical analysis**

210 Repeated measures ANOVAs were used to examine the effect of treatment and observation period
 211 on the abundance of bee forage flowers (Table S1) in the margins, social bee abundance along the
 212 margins and experimental plant seed or fruit production. The bee abundance data were
 213 transformed to \log_{10} (bees + 1) because the data were highly skewed and the transformation
 214 ensured the data fitted assumptions of normality more closely. An additional variable was derived
 215 weighting bee abundance by forage availability ($= \log_{10}$ (bees + 1) / no. bee forage flowers) and a
 216 repeated measures ANOVA was also performed on this. With the experimental design described,
 217 two statistical comparisons were possible: 1) the comparison between urban gardens and arable
 218 field margins, and 2) the comparison between the three different arable crops. It should be noted
 219 that because of the spatial design of the experiment (farms as blocks, and gardens in a different
 220 area) it was not possible to make statistical comparisons between individual arable crop margins and
 221 urban gardens. The repeated measures analyses were also used to test if there were interactions
 222 between these treatments effects and the observation periods. For *G. hederacea*, an average value
 223 of seed set per flower was used for each patch (1 patch x 4 treatments x 5 sites x 2 time observation
 224 periods). For *L.corniculatus*, an average proportion of flowers setting fruit per plant was used, and
 225 there were 4 plants per patch (4 plants per patch x 4 treatments x 5 sites x 4 observation periods).
 226 Since the number of sampled flowers was so high, the data (although proportional) were
 227 approximately normally distributed and did not require transformation.

228 The experiment was structured for the above analyses, and it was not statistically appropriate to
 229 include flowers as a co-variate in the bee analysis; or to include bees as a covariate in the seed or
 230 fruit analyses. Instead, and in order to explore the observed patterns more fully, three simple
 231 regressions were performed (post-hoc). For the margin/border data, the relationship (at the site
 232 level) between bee numbers (\log_{10} (bees+1)) and margin bee forage flowers was examined using
 233 linear regression. For the pollination data, linear regressions (at the site level) were performed for a)
 234 *G.hederecea* seed set and margin bee abundance; b) *L.corniculatus* fruit set and margin bee
 235 abundance.

236 **Results**

237 **Test for self-incompatibility**

238 For *G. hederacea* the number of seeds produced per flower was significantly higher (Mann-Whitney
 239 U test: P=0.02, n=12) in the open-pollinated plants (mean = 3.53 \pm 0.25) compared to the caged
 240 plants (mean = 0.05 \pm 0.05). The proportion of *L. corniculatus* flowers producing fruits was
 241 significantly higher (Mann-Whitney U test: P=0.02, n=12) for open-pollinated plants (mean = 0.88 \pm
 242 0.05) than for caged plants (0.13 \pm 0.04). This effectively demonstrates that both of the populations
 243 of plants used in this experiment benefited significantly from insect visits to set fruit and seed.

244 **Local flower abundance**

245 The oilseed rape crop flowering coincided with the first observation period (April-May), and the first
 246 part of the second period (May-June). The field bean crop flowering coincided with the second
 247 observation period (May-June). From the field margin and garden border transects, *G.hederacea*
 248 was observed growing naturally at eight of the 20 sites (1 garden and 7 field margins). The average
 249 density of the species (where it occurred) was 51 flowers per 200 m of garden border and 48 flowers
 250 per 200 m of arable field margin. For *L.corniculatus* the number of sites where plants were observed
 251 in the vicinity of the experimental tubs was four (1 garden site and 3 field margins). The average
 252 density of the species (where it occurred) was 388 flowers per 200 m of garden border and 278 per
 253 200m of field margin transect.

254 For bee forage plant species in the 200 m margin and border transects (Table S1), there were
 255 significantly more flowers in garden borders than in field margins (of oilseed rape, wheat and bean
 256 crops) over all observation periods (Fig 2A; $F_{1,8}= 5.39$; $P=0.049$;). There were no significant
 257 differences between the average number of bee forage flowers per 200 m observed in the margins
 258 of the different arable crops (Fig 2B) and no significant interaction between the observation period
 259 and the treatment effects.

260 **Local flower visitor abundance**

261 The frequency of insect visits to the experimental plants was low such that the data were too few to
 262 analyse statistically. Qualitatively, *G. hederacea* received most visits (total for observations given in
 263 brackets) from *Bombus hortorum* (17) and *Bombus pascuorum* (14), with some visits from *Bombus*
 264 *terrestris/lucorum* (7; not separated taxonomically) and *Bombus lapidarius* (2). *L. corniculatus*
 265 received most visits from *B. pascuorum* (25) with a few visits from unidentified solitary bees (5), *B.*
 266 *lapidarius* (3) and *B. hortorum* (1).

267 Table 1 shows the number of flower visitors belonging to different insect groups observed in the
 268 field margin and garden border transects. The number of individuals of each species was low, so
 269 they have been combined into bumblebees, honeybees, solitary bees and other visitors (a group
 270 dominated by small flies). Most visitors were social bees (bumblebees and honeybees) and since
 271 these are considered the most likely pollinators, and were observed on the experimental plants, we
 272 focussed our analysis on this group. Significantly more social bees were observed visiting flowers in
 273 the garden borders than in the arable field margins (Fig 3A; $F_{1,8} = 8.33$; $P = 0.02$). There were no
 274 significant differences between the average number of social bees foraging per 200 m of margins of
 275 the different arable crops (Fig 3B) and no significant interaction between the observation period and
 276 the treatment effects.

277 The number of social bees ($\log_{10}(x+1)$) per margin or border transect was positively and significantly
 278 correlated with number of bee forage flowers per transect ($n = 20$; $R^2 = 0.64$, $P < 0.001$). When a
 279 repeated measures ANOVA was performed on the ratio of bees to flowers ($\log_{10}(\text{bees} + 1) / \text{no. bee}$
 280 forage flowers), then there were no significant differences between gardens and arable field margins
 281 ($F_{1,8}=2.83$; $P = 0.131$), suggesting that the higher relative abundance of bees at the garden sites was
 282 partly due to the increased number of bee forage flowers available.

283 **Seed and fruit production**

284 During the first two observation periods (which coincided with oilseed rape and field bean flowering
285 times respectively) there was significantly higher *G. hederacea* seed set in gardens than in the arable
286 field margin settings (Fig 4A; $F_{1,8} = 7.07$; $P = 0.029$). Neither the observation period nor the
287 placement next to different arable crops had a significant effect on *G. hederacea* seed set (Fig 4B).

288 For *L. corniculatus*, fruit-set was also significantly different between the gardens and the arable field
289 margin setting (Fig 5A; $F_{1,8} = 7.69$; $P = 0.02$). For this species there was also a significant interaction
290 between the treatment (garden versus arable) and the observation period ($F_{3,197} = 12.50$; $P < 0.001$).
291 Fruit-set was consistently high over the season for plants placed in gardens, but was lower in later
292 observation periods for plants placed in the arable margins. The contrast between garden and arable
293 locations was highest at the 4th sample date (Fig 5A). For the plants placed next to field margins,
294 there was no significant difference in fruit set between crop treatments, but there was a significant
295 interaction between observation period and crop treatment (Fig 5B; $F_{6,197} = 2.94$; $P = 0.014$). The
296 strongest pattern was seen for the *L. corniculatus* plants situated next to oilseed rape fields where
297 fruit set was highest in April-May when the oilseed rape was in flower, and then lower in the
298 following observation periods (Fig 5B).

299 Linear regressions showed that *G. hederacea* seed set was significantly positively correlated with the
300 number of bees observed visiting flowers in the margins and borders ($n = 20$; $R^2 = 0.24$, $P = 0.017$)
301 and *L. corniculatus* fruit set was also significantly positively correlated with bees in the margins ($n =$
302 20 ; $R^2 = 0.15$, $P = 0.048$).

303 **Discussion**

304 For two plant species, *G. hederacea* and *L. corniculatus* for which seed set is significantly enhanced
305 by insect pollination, measurements of seed and fruit set (respectively) showed there were
306 significantly higher levels of pollination in plants growing in tubs in gardens, compared to those
307 growing in tubs in arable field margins in Hertfordshire (Fig 4; Fig 5). The pollination in gardens was
308 consistently higher throughout the season, as was the density of other flowers in the locale (Fig 2)
309 and the number of pollinating insects visiting these other flowers (Fig 3).

310 This effect on seed and fruit set could be a result of differing patterns of insect pollination: including
311 visit quantity or quality. Unfortunately the sampling effort on the tubs did not give enough data on
312 insect visitation rate to experimental plants to allow correlations to be made. Interpretation of the
313 patterns is therefore made with caution using the surrogate measure of the abundance of social
314 bees foraging in the adjacent margin or border, and the abundance of co-flowering bee forage plants
315 in the margin (and the presence or absence of a flowering crop). There were more co-flowering
316 forage plants in the gardens than in the arable margins (Fig 2), and there were relatively more bees
317 foraging in the garden borders than in the margins (Fig 3). These figures, combined with the seed
318 and fruit set data suggest that there is a facilitatory effect of other co-flowering plants within the
319 gardens, providing a good “pollination environment” for the experimental plant species. The co-
320 flowering species attracted foraging bees into the vicinity in proportion to the floral abundance
321 (there was a high correlation between flower abundance and bee abundance). When the data for
322 social bee abundance in margins were expressed as the number of bees per flower, there was no
323 significant difference between treatments. Thus in this experiment, the number of bees per 200 m

324 (Fig 3A) which did vary significantly between treatments, was the more suitable variable to be
325 correlated with seed and fruit set in both species. The significant positive correlations suggest that
326 some of the differences in seed and fruit set can be explained by local pollinator abundance per unit
327 area (rather than the number of bees per flower).

328 It is possible that other differences in abiotic and biotic conditions between field margins and garden
329 borders also contribute to differences in seed and fruit set, but the experiment was designed to keep
330 abiotic conditions (e.g. microclimate, shading and resources) as constant as possible. Herbivory and
331 seed predation could also be important factors in overall reproduction of the plants but were not
332 responsible for the observed effects because flowers that showed herbivory damage, or contained
333 larvae, were removed from the samples before the seed and fruit counts were done.

334 It is also likely that the characteristics of urban areas that lead to the higher abundances of bees
335 reported here and by others [6,22] go beyond the availability of forage. One factor (highlighted in
336 [6]) is that gardens and parks in urban areas provide a robust and diverse supply of forage for
337 pollinators throughout the year (Fig 2A). The availability of safe sites for nests is also a key feature of
338 urban areas [25] so that the overall population levels are higher than in an arable setting (although
339 see [23]). It is not possible from our results to say what the causal mechanism is; and it could be a
340 combination of these factors.

341 In arable farmland, we found seed and fruit set levels in both species were lower than in the
342 gardens, suggesting some degree of pollen limitation at our study sites. There was also some
343 evidence that flowering oilseed rape had a facilitatory effect on *L. corniculatus* fruit set in the first
344 observation period (since there was a significant interaction between crop and observation period),
345 an effect that was not sustained after the flowering of the crop. This is suggestive of the hypothesis
346 that a mass-flowering crop attracts pollinators into the area to the benefit of other plants, and the
347 lower seed set later in the season suggests that this local boost is not maintained through the
348 season although more highly resolved data on bee densities and visitation patterns on the crops
349 would be required to confirm or disprove these suggestions. Bumblebees fly long distances to find
350 forage [36,37] and, even if they have a successful nest in the margin next to a crop, they may not
351 stay in the vicinity to search for small patches of forage (such as our experimental plants) if there are
352 larger, more profitable patches at a further distance [38].

353 Our results are specific to two species of experimental plant, both chosen as plants favoured by
354 bumblebees but with differing phenology and floral attributes. It is interesting to note that the only
355 significant interaction with crop type was a positive one between oilseed rape and *L. corniculatus*.
356 Both have yellow flowers and, although they differ considerably in morphology and olfactory cues,
357 they are both frequently visited by short-tongued bumblebees and thus “share” a pollinator guild.
358 *G. hederacea* may be more dependent on bumblebees with longer tongues (it was most visited by
359 *B. hortorum* and *B. pascuorum* in this experiment) and so shares a pollinator guild with field beans,
360 although the flowers are markedly different in colour and no effect on seed set was seen in
361 combination with this crop. This is similar to the results of Diekötter et al [2] who studied *T.*
362 *pratense*, another species pollinated by long-tongued bumblebees (although this flowers much later
363 than the crops).

364 We found no evidence of competition either between mass-flowering crops and experimental plants
365 in the field margins for pollinators; or between garden plants and experimental plants for

366 pollinators. If the interactions were competitive we would, in theory, have expected the number of
 367 bees per flower in the margins to be lower in the treatments where there were most bee forage
 368 flowers available (e.g. in gardens and when the oilseed rape was flowering) and consequently the
 369 more abundant flowers would have to compete for pollinator visits, but this was not observed.
 370 Although we have studied different habitats, our results support those of Hegland et al [39] who
 371 showed, for bumblebee visitation rates of grassland plant species, positive plant intra-specific and
 372 inter-specific interactions were far more frequent than negative ones. In summary, there is
 373 evidence that plants growing in small patches, in the vicinity of large quantities of anthropogenically
 374 introduced flowers, may have increased seed or fruit set but this will depend on the floral
 375 phenology and attributes. In particular, gardens in Hertfordshire seem to be a beneficial
 376 environment for pollination by bees, compared to the arable farmland surrounding the town,
 377 irrespective of crops growing in the fields.

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472 interactions for pollinator attraction in a plant community. *Ecological Research* 24: 929-936.
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476

477 **Figure legends**478 **Figure 1. Map of experimental sites.**

479 The extent of each farm hosting the field margin sites is shown in contrasting shading. Field bean
 480 sites are indicated with circle symbols, oilseed rape sites with triangles and wheat sites with squares.
 481 The garden sites are shown with crosses. The area of the map is entirely located within Ordnance
 482 Survey square containing Rothamsted Research (TL 13415 13598). Sites on different farms are a
 483 minimum of 1750 m apart. Sites next to contrasting crops on the same farm fit within a circle of
 484 radius 1000 m. The garden treatment sites are all within the Harpenden town conurbation. ©
 485 Crown Copyright/database right 2010. An Ordnance Survey/EDINA supplied service.

486

487 **Figure 2. Bee forage flower density in field margins and garden borders.**

488 Average number of flowers (\pm s.e.m.) of bee forage flower species in field margins and garden
 489 borders (expressed per 200 m of transect length) for each observation period. **A** Comparison
 490 between garden borders and arable field margins; **B** Comparison of the abundance of flowers in the
 491 margins of three different arable crops.

492

493 **Figure 3. Density of social bees visiting flowers in field margins and garden borders.**

494 Mean number of social bees (\pm s.e.m.) observed visiting flowers in arable field margins or garden
 495 border (expressed per 200 m of transect length) for each observation period. **A** Comparison
 496 between garden borders and arable field margins; **B** Comparison of the number of bees visiting
 497 flowers in arable field margins of three different crop species.

498

499 **Figure 4. Seed set in *G.hederacea* (ground ivy) plants growing in different habitats.**

500 Average number of seeds set per flower (\pm s.e.m.) in ground ivy (*G. hederacea*) which only flowered
 501 during the first two observation periods. **A** Comparison between plants in gardens and those in
 502 arable habitats; **B** Comparison of seed-set for plants grown next to three different arable crops.

503

504 **Figure 5. Fruit set in *L.corniculatus* (birdsfoot trefoil) plants growing in different habitats.**

505 Average proportion of pods setting fruit (\pm s.e.m.) in bird's foot trefoil (*L. corniculatus*) in different
 506 observation periods. **A** Comparison between plants in gardens and those in arable habitats; **B**
 507 Comparison of fruit-set for plants grown next to three different arable crops.

508

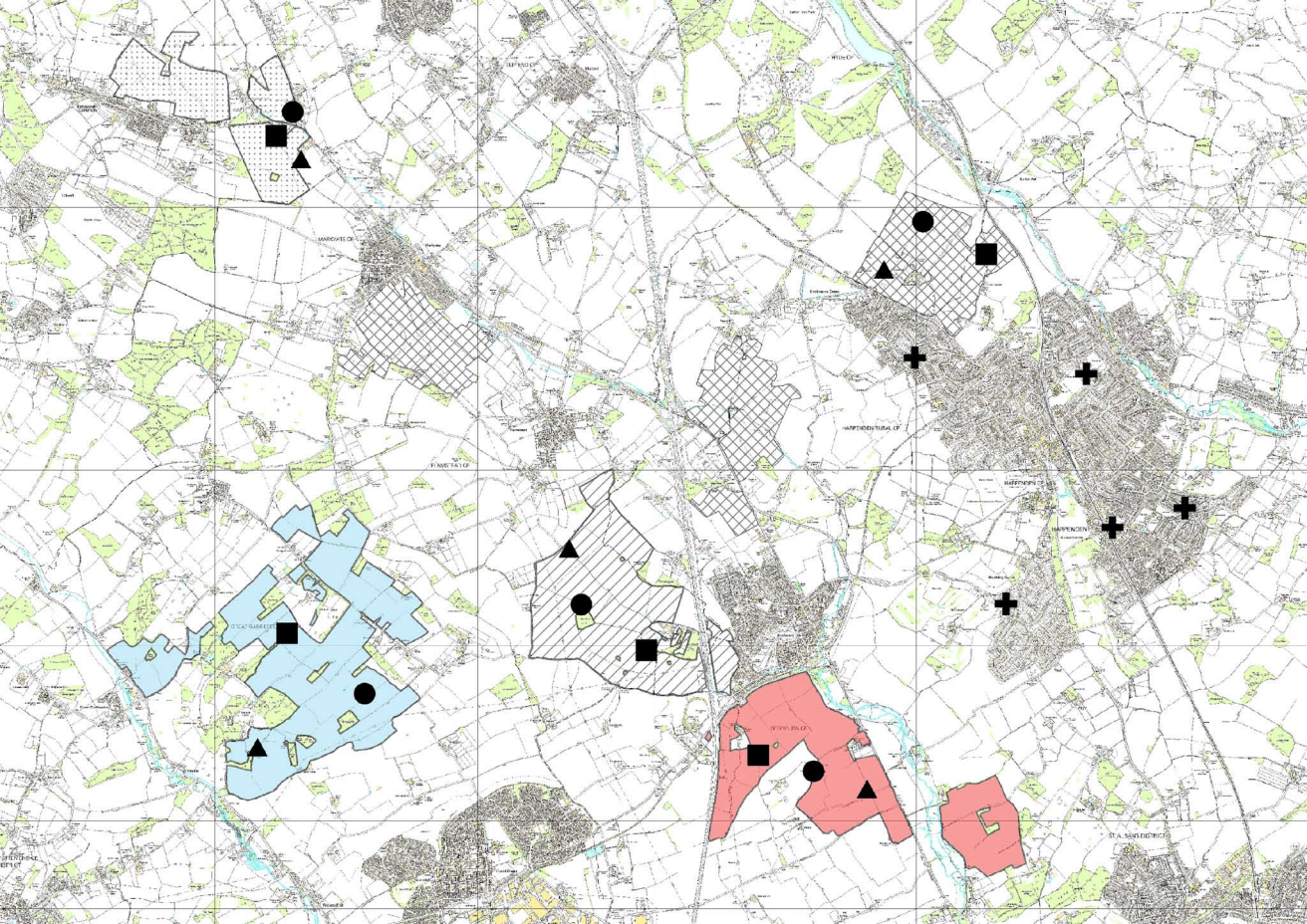
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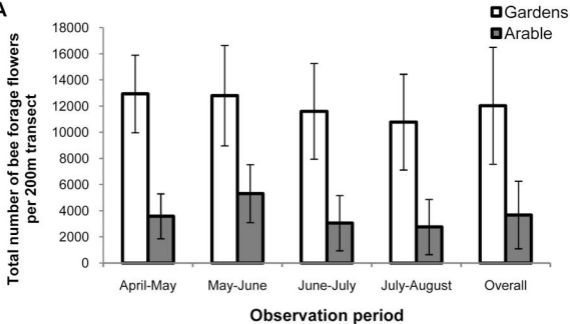
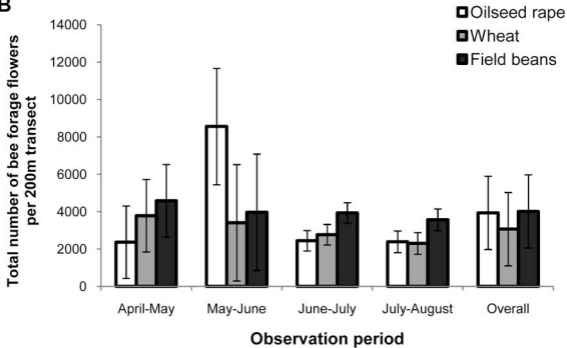
510 **Tables**511 **Table 1. Types of insect flower visitors observed on field margins and garden borders.**

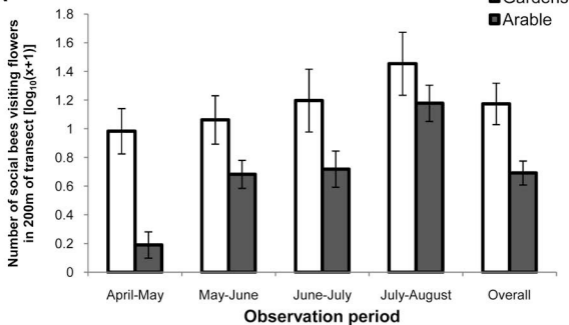
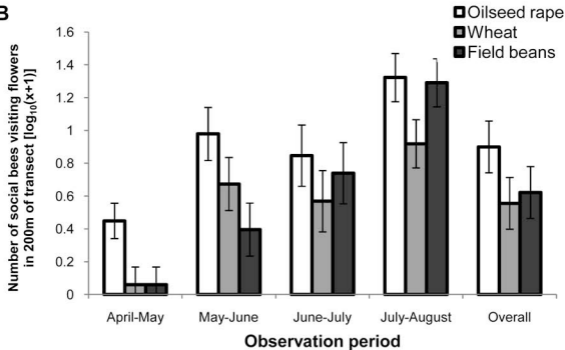
	Garden border	Arable field margin
Bumblebees	13.20 ± 2.58	7.98 ± 1.57
Honey bees	5.63 ± 1.18	1.13 ± 0.34
Solitary bees	0.95 ± 0.70	1.53 ± 0.41
Other flower visitors	7.6 ± 5.21	18.3 ± 3.01

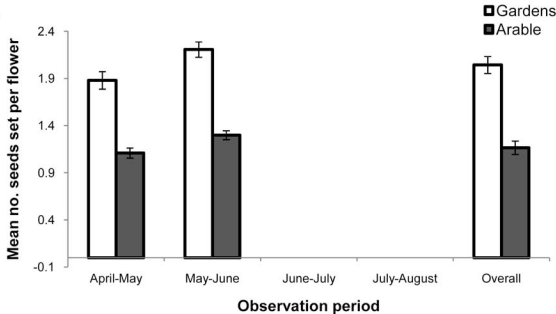
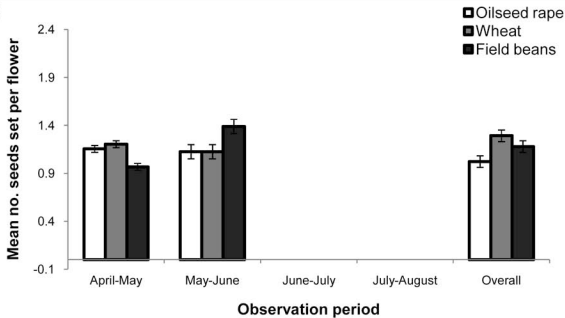
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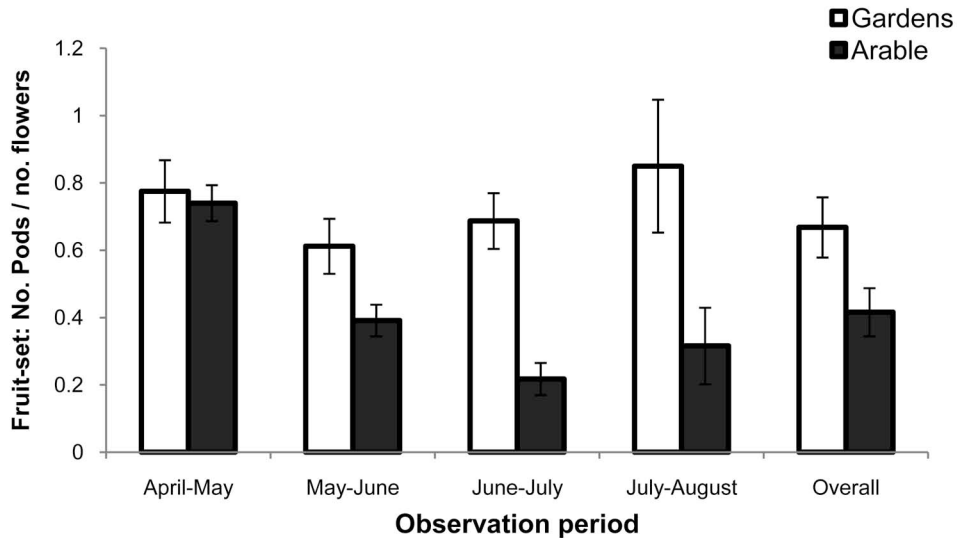
513 The average number of insects observed visiting flowers in transects along garden borders and
 514 arable field margins (expressed as per 200 m transect length). Values given are means of all four
 515 observation periods (± s.e.m.). In all cases n=20 for garden border, and n=60 for arable field
 516 margins.



A**B**

A**B**

A**B**

A**B**