

# *Apple pollination: demand depends on variety and supply depends on pollinator identity*

Article

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# 1 Apple pollination: Demand depends on variety and supply

## 2 depends on pollinator identity

3 Authors: M. P. D. Garratt<sup>1\*</sup>, T. D. Breeze<sup>1</sup>, V. Boreux<sup>2</sup>, M. T. Fountain<sup>3¶</sup>, M. McKerchar<sup>4¶</sup>,  
4 S. M. Webber<sup>1¶</sup>, D. J. Coston<sup>1</sup>, N. Jenner<sup>5</sup>, R. Dean<sup>1</sup>, D. B. Westbury<sup>4</sup>, J. C. Biesmeijer<sup>6&</sup> and  
5 S. G. Potts<sup>1&</sup>

6 <sup>1</sup>Centre for Agri-Environmental Research, School of Agriculture, Policy and Development,  
7 University of Reading, Reading, UK.

8 <sup>2</sup>Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany.

9 <sup>3</sup>East Malling Research, East Malling, UK.

10 <sup>4</sup>Institute of Science & the Environment, University of Worcester, Worcester, UK<sup>5</sup>

11 <sup>5</sup>Avalon Produce, Kent, UK.

12 <sup>6</sup>Naturalis Biodiversity Centre, Leiden, The Netherlands.

13

14 \*Corresponding author: Dr Michael P. D. Garratt

15 Email: [M.P.Garratt@reading.ac.uk](mailto:M.P.Garratt@reading.ac.uk)

16 ¶These authors contributed equally to the work

17 &These authors are senior authors

## 18 **Abstract**

19 Insect pollination underpins apple production but the extent to which different pollinator  
20 guilds supply this service, particularly across different apple varieties, is unknown. Such

21 information is essential if appropriate orchard management practices are to be targeted and  
22 proportional to the potential benefits pollinator species may provide. Here we use a novel  
23 combination of pollinator effectiveness assays (floral visit effectiveness), orchard field  
24 surveys (flower visitation rate) and pollinator dependence manipulations (pollinator exclusion  
25 experiments) to quantify the supply of pollination services provided by four different  
26 pollinator guilds to the production of four commercial varieties of apple. We show that not  
27 all pollinators are equally effective at pollinating apples, with hoverflies being less effective  
28 than solitary bees and bumblebees, and the relative abundance of different pollinator guilds  
29 visiting apple flowers of different varieties varies significantly. Based on this, the taxa  
30 specific economic benefits to UK apple production have been established. The contribution  
31 of insect pollinators to the economic output in all varieties was estimated to be £92.1M across  
32 the UK, with contributions varying widely across taxa: solitary bees (£51.4M), honeybees  
33 (£21.4M), bumblebees (£18.6M) and hoverflies (£0.7M). This research highlights the  
34 differences in the economic benefits of four insect pollinator guilds to four major apple  
35 varieties in the UK. This information is essential to underpin appropriate investment in  
36 pollination services management and provides a model that can be used in other  
37 entomophilous crops to improve our understanding of crop pollination ecology.

## 38 **Key words**

39 Apples, bumblebees, economic benefit, honeybees, hoverflies, pollination, solitary bees

## 40 **Introduction**

41 Insect pollination is a key ecosystem service for agriculture, influencing the productivity of  
42 ~75% of crop species [1] and contributing ~\$361bn to global crop markets in 2009 [2]. The  
43 area of insect pollinated crops has grown substantially in recent decades, resulting in greater

44 demands for pollination services [3]. In the UK, evidence suggests that supplies of  
45 pollination services, both from managed honeybees [4] and wild pollinators [5,6], do not  
46 match these increasing demands. Of the insect pollinated crops grown in the UK, apples  
47 (*Malus domestica*) are among the most valuable per hectare and as a self-incompatible crop  
48 which requires pollen from other compatible varieties (known as pollinisers) to set fruit,  
49 insect pollination services are essential to attaining profitable yields in apples [7] . Garratt *et*  
50 *al.* [8] recently demonstrated that by affecting both the quality and quantity of apples  
51 produced, pollination services underpinned ~65% of market output per hectare in two  
52 important apple varieties (Cox and Gala).

53 Managed European honeybees (*Apis mellifera*) can be used as pollinators in large commercial  
54 orchards to improve productivity [9,10]. A number of wild insects are also thought to be  
55 significant pollinators [11-14]. Notably, mason bees (e.g. *Osmia* spp.), mining bees (e.g.  
56 *Andrena* spp.) and bumblebees (*Bombus* spp.) have all been demonstrated to be effective  
57 pollinators of apples and, in some cases, more effective than honeybees [12,15-17]. Surveys  
58 of pollinator communities visiting UK Cox apple orchards suggest that wild pollinators form  
59 the majority of visitors [18], however, there has not been a systematic assessment of the  
60 relative pollination service contribution made by different pollinator guilds to apple orchards,  
61 or an estimation of the relative economic benefits of different pollinating taxa.

62 There are examples where crop pollination services do not meet the demand of the crop,  
63 resulting in yield and quality deficits [19-21] and sparking interest in the possible economic  
64 benefits of increasing pollinator populations. Previous research has shown that outputs in UK  
65 Gala orchards could be limited by sub-optimal pollination by ~£6,500/ha [8]. Therefore,  
66 improving pollinator management in this crop could provide significant economic returns.  
67 How pollinator dependence and possible yield deficits vary between different crop varieties is  
68 a fundamental question when considering the economic benefits and management of crop

69 pollinators. Impacts of variety on pollination has only been investigated in a few crops  
70 including oilseed [22], blueberry [23] and strawberries [24].

71 In order to sustainably intensify crop production and meet growing global food demands, it is  
72 essential to understand the influence of ecological functions on yield [25]. For insect  
73 pollinated crops such as apples, this includes quantifying the impacts of insect pollination  
74 services and identifying which species are the most important service providers so they can  
75 be appropriately protected and managed. Few studies have considered how crop variety  
76 affects dependence on insect pollination or indeed how crop variety affects visitation by  
77 different pollinators. Furthermore, although the economic benefits of insect pollinators to  
78 crop production have been estimated many times, few studies have estimate the relative  
79 economic benefits of different taxa to a single crop. In order to assess the relative importance  
80 of different pollinators to different varieties of a crop, this study utilises a combination of  
81 pollinator effectiveness measures, visitor observational data and measures of crop  
82 dependency to evaluate the supply of pollination service provided by four major pollinator  
83 guilds (honeybees, bumblebees, solitary bees and hoverflies) to four UK apple varieties (Cox,  
84 Gala, Bramley and Braeburn). In doing so we have: (1) quantified the relative effectiveness  
85 of four pollinators to a major UK crop; (2) provided a unique appraisal of the variation in  
86 pollination service supply provided by different pollinator guilds across four varieties of a  
87 single crop; (3) quantified the demand for insect pollination services of these varieties; and  
88 (4) estimated the economic benefits of each pollinator guild to UK production of each  
89 variety.

## 90 **Materials and methods**

### 91 **Pollinator effectiveness**

92 To compare the ability of different pollinators to pollinate apple flowers, both pollinators and  
93 apple trees were manipulated using insect flight cages. Four potential pollinators were  
94 chosen: the honeybee (*Apis mellifera*), a bumblebee (*Bombus terrestris-audax*), a solitary  
95 mason bee (*Osmia bicornis*) and a hoverfly (*Episyrphus balteatus*) and their ability to  
96 pollinate *Malus domestica* var. Scrumptious was studied. This variety was selected because  
97 a smaller, potted variety was necessary for use in cage studies. As apples are self-  
98 incompatible, a donor variety, Evereste, was also present in all cages. These pollinators  
99 represent four distinct flower visiting insect guilds which may provide important pollination  
100 services in apple orchards [18]. To manipulate trees and pollinators, insect-proof flight cages  
101 were constructed at the University of Reading and University of Leeds experimental farms,  
102 using 2.4 x 2.1m frames covered with a polyethylene mesh with a gauge size of 1.33mm.  
103 During experiments, each pollinator species was housed in separate flight cages. Each  
104 pollinator was provided with appropriate nesting and forage resources within the flight cage  
105 when not directly involved in experiments, thus encouraging natural behaviour for the period  
106 of experimentation. The honeybees, through the use of a double entrance hive, were given  
107 access both to the flight cage and the outside, which could be controlled as needed.

108 Study trees (variety: Scrumptious and variety: Evereste) were kept in 25L pots. During  
109 experiments (spring 2012 and 2013) trees were 2.5 and 3.5 years old respectively and fully  
110 productive. When in flower, but not directly involved in experiments, the trees were stored  
111 inside isolation flight cages to avoid any interaction with potential pollinators.

112 Pollination experiments involved placing two flowering polliniser trees (Evereste) into flight  
113 cages with each of the four pollinator species. The experiment began when a single apple  
114 tree (Scrumptious) was placed in the flight cage. This experimental apple tree was then  
115 observed continuously and any insect visits to flowers were recorded by marking a dot on the  
116 petal of flowers which received individual visits. This was continued until at least three

117 flowers on that apple tree had received five visits. Each flower which had received a visit  
118 was marked with a coloured cable tie; different colours were used to denote flowers which  
119 had received a different number of visits (between one and five). The total number of  
120 flowers which received each visit number was recorded for each tree. The tree was then  
121 stored in an isolation cage until fruit harvest. Pollination experiments were carried out at the  
122 end of April and beginning of May in 2012, and mid-May in 2013. The availability of  
123 flowering apple trees, polliniser trees and active pollinators enabled 18 trees to be pollinated  
124 by bumblebees, 11 by honeybees, three by hoverflies and 13 by solitary bees with a total of  
125 1,831 flowers involved in the study.

126 In September of each experimental year when apples were ripe, a fruit set measurement was  
127 taken. The number of fruit remaining on each tree for each visit number and the original  
128 number of flowers which received that number of visits was used to calculate a percentage  
129 fruit set for each visit number per tree. During apple development, to prevent damage to  
130 trees, non-experimental apples and a small number of experimental fruit were removed from  
131 heavily laden branches. Size (max width cm), weight (g) and seed number per apple was  
132 measured.

### 133 **Pollinator visitation**

134 To compare the flower visitation of different pollinators to different apple varieties, we  
135 combined data from a number of UK apple pollinator surveys. Surveys were carried out in  
136 Cox, Bramley, Braeburn and Gala orchards in the top fruit growing region of Kent, UK  
137 between 2011 and 2014. The owners of the orchards from which data was collected gave  
138 permission to conduct the study on these sites. All surveys were carried out in conventionally  
139 managed orchards, of varying tree age, surrounded by plantations of other varieties of apple  
140 and varying amounts of semi-natural habitat. Orchards of different apple varieties were



141 distributed across data sets and different varieties were often sampled on the same farms,  
142 therefore we anticipate no confounding effects of location on pollinators observed visiting  
143 flowers of different varieties. Honeybees were not typically utilised for pollination in the  
144 orchards although five hives were located close to one of the Gala orchards involved in the  
145 surveys. Surveys involved stationary tree observations or mobile transects within the  
146 orchards depending on the study (Table A in S1 File). Visitors to apple flowers were  
147 recorded to broad taxonomic groups and for transect surveys, where possible, caught and  
148 taken back to the laboratory for identification to species.

## 149 **Pollinator dependence**

150 To measure the dependence of apple production on insect pollination, three Bramley and two  
151 Braeburn orchards were used for experimental trials in 2013. Bramley is the most common  
152 variety of culinary apple grown in the UK, accounting for >90% of planted culinary apple  
153 area [26]. Braeburn is the third most widely grown dessert apple variety after Cox and Gala,  
154 with over 500ha planted as of 2012 [27]. The owners of the orchards from which data was  
155 collected gave permission to conduct the study on these sites. Within each of the orchards,  
156 three centrally located rows were selected, and on those rows, 10 trees at least 25 m from the  
157 orchard edge were involved in the study. Shortly before flowering, two branches on each tree  
158 were selected and randomly assigned to one of two treatments: an open treatment and a  
159 pollinator exclusion treatment. The pollinator excluded branches were covered with a PVC  
160 mesh bag with a mesh size of 1.2 mm<sup>2</sup> which are wind and rain permeable, but exclude  
161 visitation by insects. The number of flowers receiving each treatment was then recorded.  
162 When flowering had finished at all sites, bags were removed and the branches were marked  
163 with coloured cable ties and string so they could be located for harvest.

164 Prior to commercial thinning carried out in the orchards (early July), a visit was made to each  
165 site. For each branch, the number of set apples was recorded. The apples on each branch,  
166 which included any experimental inflorescences, were then thinned according to standard  
167 industry practice whereby apples from experimental inflorescences were removed so no more  
168 than two remained on any one inflorescence. At the end of the season, all apples from  
169 experimental inflorescences were collected one day to a week before commercial harvest  
170 (early September for Bramley and late October for Braeburn). Apples were bagged  
171 individually by treatment, tree, row and orchard and taken back to the laboratory for quality  
172 assessment. Industry standard quality measures for classifying apples for market were taken  
173 for all apples collected.

174 Seed number and maximum width of each apple was recorded. Apples were then scored for  
175 shape, either classified as 'normal' or 'deformed' if there was any shape irregularity. To  
176 calculate the economic benefits of pollination to each variety, apples were classed using  
177 parameters utilised in the industry (Jenner, 2014 pers. comm.). Apples were classified as  
178 class 1 or 2 based on size and shape. Class 1 Braeburn apples are those with no shape  
179 deformities and a width greater than 60 mm. Class 1 Bramley apples are between 80-100  
180 mm wide and all other sizes were class 2.

181 Using the same methodology, the dependence of Cox and Gala apples, and the resultant  
182 economic contribution of pollination to profit, had been established in a previous study [8].  
183 These data are analysed in conjunction with data on Bramley and Braeburn for the  
184 subsequent economic analysis and pollinator contribution estimates. Data for all four  
185 varieties are presented together for the remainder of the manuscript.

## 186 **Economic analysis**

187 The economic benefits of pollination services to producers were calculated for each variety  
188 following the methods in Garratt et al. [8] by comparing fruit set and quality after commercial  
189 thinning, from open pollinated and pollinator excluded treatments. For each treatment, the  
190 estimated monetary output of apples produced (£/ha) was calculated with respect to two  
191 commercial quality classes using average weekly prices for 2012 from DEFRA [28].  
192 Differences in labour costs, the only cost factor expected to vary by yield, were estimated as  
193 the percentage change in the number of apples produced in each treatment multiplied by  
194 industry standard costs (Jenner, 2013 pers. Comm.). The impacts of pollination services on  
195 output are therefore the differences in the output of apples, less the differences in labour costs  
196 from the two treatments (both £/ha). The estimated net change in output was extrapolated to  
197 a national scale using the 2012 area of Braeburn and Gala reported in DEFRA [27] and the  
198 2012/2013 area data from DEFRA [26] for Cox and Bramley. In this manuscript we also  
199 update the estimated economic benefits of pollination services to Cox and Gala apples  
200 reported in Garratt et al. [8] by using 2012 area data alongside 2012 prices. For  
201 completeness, results for Gala, Cox, Braeburn and Bramley are reported together for the  
202 remainder of the manuscript.

## 203 **Pollinator contribution**

204 The contribution of different pollinator guilds to Bramley, Braeburn, Gala and Cox  
205 production in the UK was calculated by incorporating pollinator effectiveness, pollinator  
206 visitation in the field and the economic benefits of insect pollination to each variety of apple.  
207 The effectiveness ( $E$ ) of each pollinator guild ( $i$ ) was estimated based on a product of the fruit  
208 set ( $F$ ) and seed set ( $S$ ) resulting from three visits by the taxa to apple flowers in the cage  
209 study. Three visits were chosen given that, in the field, apple blossoms can expect a varying  
210 number of floral visits and previous research has shown that assuming an apple blossom is

211 receptive for approximately three days and pollinators may be most active for about 6 hours  
 212 on those days, between two and three visits per flower is a realistic number of visits that one  
 213 blossom may receive from these pollinators [18]. Given the significant interactive effect of  
 214 visit number on the pollination effectiveness of our pollinator guilds we also carried out the  
 215 same economic assessment assuming pollination effectiveness following a single visit. This  
 216 may better reflect pollinator contributions in years with low overall visitation rates to flowers  
 217 (Table B in S1 File). The relative pollination service contribution ( $R$ ) of each guild to each  
 218 variety ( $v$ ) was calculated as the effectiveness of each guild, multiplied by the observed  
 219 visitation rate of all members of the guild ( $T$ ) divided by the effectiveness and visitation rate  
 220 of all observed pollinators. The standard deviation of the relative pollination service  
 221 contribution across all sites was taken as a measure of variance.

$$222 \quad R_{ic} = \frac{(E_{iv} \times T_{iv})}{\sum_{i=1}^i (E_v \times T_v)}$$

223 Where  $E_i = (F_i \times S_i)$

224 This percentage was then used to calculate the monetary contribution of each pollinator ( $GP$ )  
 225 to each apple variety based on the economic benefits of insect pollination to each variety  
 226 ( $PB$ ).

$$227 \quad GP_i = R_i \times PB_v$$

228 As *Bombus terrestris*, *Osmia bicornis* and *Ephyserphis balteatus* may not be representative of  
 229 the effectiveness of their pollinator guilds as a whole, the economic analysis was re-  
 230 conducted using only the relative visitation rates of the guild ( $GT$ ) to each variety without  
 231 weighting visits by the pollination service effectiveness (Table C in S1 File).

$$232 \quad GT_{iv} = T_{iv} \times PB_v$$

## 233 **Statistical analysis**

234 Pollinator effectiveness was analysed using generalised linear mixed effects models to  
235 understand effects of pollinator and visit number (1-5) on fruit set and seed set in  
236 Scrumptious apples. Pollinator, visit number and their interaction were included in the model  
237 as fixed effects; year (2012, 2013), location (Reading, Leeds) and tree were random effects.  
238 Fruit set is a proportional response thus a binomial error structure was specified, and seed set  
239 is a count so a Poisson error structure was used. Apple width and weight were normally  
240 distributed and analysed using linear mixed effects models with the same fixed and random  
241 effects as for fruit set and seed number.

242 Orchard pollinator visitation data were analysed using a generalised linear mixed effects  
243 model with pollinator guild (honeybee, bumblebee, hoverfly, solitary bee and other), apple  
244 variety (Cox, Gala, Bramley and Braeburn) and a pollinator:variety interaction as main  
245 effects in the model. The number of pollinators observed visiting flowers on any given  
246 survey day was summed for the analysis so the response variable was a count and thus a  
247 Poisson error distribution was defined. Data set, year, survey round and site were included in  
248 the model as random effects. An observer level random effect was also included to account  
249 for overdispersion. A significant pollinator:variety effect was found so each variety was  
250 analysed separately using the same generalised linear model with appropriate random effects  
251 as necessary for each data set. Again an observer level random effect was used to account for  
252 overdispersion. A Tukey comparison from the 'multcomp' R package was used to  
253 investigate significant differences between pollinator guilds within varieties.

254 The dependence of different varieties on insect pollination was analysed using generalised  
255 linear mixed effects models to investigate pollination treatment effects on fruit set and seed  
256 number. Pollination treatment (open and pollinators excluded) was a fixed effect with tree,

257 nested within row, nested within orchard as random effects. Seed number and fruit set had a  
 258 Poisson and binomial error structure defined, respectively. A linear mixed effects model with  
 259 the same fixed and random effects as for the generalised linear mixed effects model was used  
 260 to analyse apple width. Braeburn width was transformed before analysis. All statistical  
 261 analysis was carried out in R version 3.2.2.

262

## 263 **Results**

### 264 **Pollinator effectiveness**

265 Significant effects of pollinator, visit number and a pollinator:visit number interaction were  
 266 found on fruit set of experimental apple trees. Fruit set was significantly increased with an  
 267 increasing number of visits ( $Z_{1,225} = 2.50$ ,  $P = 0.01$ ) and *E. balteatus* resulted in significantly  
 268 lower fruit set than *B. terrestris* and *O. bicornis* ( $Z_{1,225} > 2.19$ ,  $P < 0.05$ ). A significant  
 269 pollinator:visit number interaction ( $F_{3,225} = 2.65$ ,  $P = 0.047$ ) indicated that fruit set was more  
 270 affected by visitation rate of honeybees than for other pollinators (Fig 1). There was a  
 271 significant effect of pollinator and visit number on seed set per apple. Seed set increased  
 272 with increasing visit numbers ( $Z_{1,568} = 2.24$ ,  $P = 0.025$ ) and *E. balteatus* ( $2.8 \pm 2.2$ ) resulted  
 273 in significantly fewer seeds per apple compared with *B. terrestris* ( $5.1 \pm 0.72$ ), *A. mellifera*  
 274 ( $5.8 \pm 0.45$ ) and *O. bicornis* ( $5.6 \pm 0.37$ ) ( $Z_{1,568} > 4.24$ ,  $P < 0.001$ ). There were no significant  
 275 pollinator:visit number interactions ( $F_{1,568} = 0.44$ ,  $P = 0.72$ ).

276 There were no significant effects of pollinator, visit number or pollinator:visit number  
 277 interaction on apple width (*A. mellifera* [ $68.9 \pm 1.3$ ], *B. terrestris* [ $63.1 \pm 2.9$ ], *O. bicornis*  
 278 [ $66.8 \pm 1.9$ ], *E. balteatus* [ $71.6 \pm 3.1$ ]) (pollinator:  $F_{3,35} = 0.80$ ,  $P = 0.50$ ; visit number:  $F_{1,460}$   
 279  $= 0.20$ ,  $P = 0.66$ ; pollinator:visit number:  $F_{3,457} = 0.23$ ,  $P = 0.87$ ) or apple weight (*A. mellifera*

280 [124.5 ± 5.9], *B. terrestris* [105.1 ± 11.2], *O. bicornis* [117.7 ± 8.7], *E. balteatus* [143.5 ±  
 281 12.5]) (pollinator:  $F_{3,35} = 0.78$ ,  $P = 0.51$ ; visit number:  $F_{1,456} = 0.18$ ,  $P = 0.67$ ; pollinator:visit  
 282 number:  $F_{3,453} = 0.51$ ,  $P = 0.67$ ).

### 283 **Pollinator visitation**

284 In the orchards, 1897 insects were observed on apple blossoms: 631 honeybees, 243  
 285 bumblebees, 823 solitary bees, 76 hoverflies and 142 other, mostly Diptera individuals.  
 286 Apple variety affected the pollinator community observed visiting flowers in orchards. When  
 287 all varieties of apple were included in the analysis there was a significant effect of pollinator  
 288 ( $F_{4,445} = 35.25$ ,  $P < 0.001$ ) and a pollinator:variety interaction ( $F_{12,445} = 4.26$ ,  $P < 0.001$ ) on  
 289 visitation. No significant effect of variety on overall visit number was observed ( $F_{3,445} =$   
 290  $0.55$ ,  $P > 0.05$ ). When apple varieties were analysed separately, Cox ( $F_{4,80} = 9.08$ ,  $P <$   
 291  $0.001$ ), Braeburn ( $F_{4,240} = 26.49$ ,  $P < 0.001$ ) and Gala ( $F_{4,100} = 10.89$ ,  $P < 0.001$ ) showed  
 292 significant effects of pollinator on the number of visits observed, Bramley ( $F_{4,24} = 2.15$ ,  $P >$   
 293  $0.05$ ) did not. In Cox orchards, solitary bees were observed visiting flowers significantly  
 294 more than bumblebees and hoverflies. Hoverflies were also significantly less abundant than  
 295 all other taxa. In Braeburn, solitary bees were the most abundant followed by honeybees.  
 296 Bumblebees were also significantly more abundant than hoverflies and ‘other’ visitors. In  
 297 Gala, solitary bees and honeybees were significantly more abundant than all other taxa (Fig  
 298 2).

### 299 **Pollinator dependence**

300 Pollinator exclusion significantly affected fruit set in both Bramley and Braeburn orchards  
 301 both before apple thinning (Bramley:  $Z_{1,175} = 9.33$ ,  $P < 0.001$ ; Braeburn:  $Z_{1,94} = 6.14$ ,  $P <$   
 302  $0.001$ ) and at harvest (Bramley:  $Z_{1,175} = 7.08$ ,  $P < 0.001$ ; Braeburn:  $Z_{1,94} = 3.74$ ,  $P < 0.001$ )

303 (Fig 3). With a mean width of 97.0 (SE  $\pm$  0.9) cm compared with 93.5 (SE  $\pm$  3.4) cm, insect  
304 pollination significantly increased Bramley apple size ( $F_{1,22} = 8.61$ ,  $P = 0.008$ ). No such  
305 significant effect was seen in Braeburn apples, for which mean widths of 68.8 (SE  $\pm$  0.3) cm  
306 and 67.5 (SE  $\pm$  2.7) cm for open and pollinator excluded apples, respectively, were found  
307 ( $F_{1,31} = 3.55$ ,  $P > 0.05$ ). The number of seeds per apple was significantly affected by  
308 pollination treatment for both Bramley (Open [ $2.2 \pm 0.3$ ], Pollinators excluded [ $0.03 \pm 0.03$ ])  
309 ( $Z_{1,193} = 4.63$ ,  $P < 0.001$ ) and Braeburn (Open [ $4.7 \pm 1.2$ ], Pollinators excluded [ $1.3 \pm 0.4$ ])  
310 ( $Z_{1,160} = 9.31$ ,  $P < 0.001$ ) with seed number in the open treatment greater than in the  
311 pollinator exclusion treatment.

## 312 **Economic analysis**

313 Analysis of the economic benefits of pollination services indicates that the economic impact  
314 of insect pollination on producer profits was £14,500 per hectare for Bramley, £8,500 for  
315 Braeburn, £12,300 for Cox and £14,800 for Gala (Table 1). In total, the findings from this  
316 study and from the updated findings of Garratt et al. [8] indicate that insect pollination adds  
317 £92.1M to UK apple production for these four varieties.

## 318 **Pollinator contribution**

319 Based on effectiveness and visitation in the field, solitary bees were found to contribute to  
320 more than 50% of pollination service in three of the four varieties studied, Cox, Gala and  
321 Bramley. Bumblebees were important pollinators of Braeburn (38% of services) but  
322 otherwise accounted for <21% of services in other varieties. Honeybees consistently  
323 contributed between 23-28% of pollination services although there was often substantial  
324 variation between orchards. Due to their low visitation rates and poor pollination  
325 effectiveness, hoverflies contributed less than 3% of pollination to all varieties. Solitary bees  
326 had the most consistent presence between orchards and were never totally absent from any



327 orchard studied. By contrast, honeybee and bumblebee presence could vary greatly  
328 depending on the variety and between orchards (Table 2).

329 Extrapolating the results up to a UK scale, solitary bees are estimated to be the most  
330 economically valuable guild to the apple varieties studied increasing productivity by £51.4M  
331 ( $\pm 29.4M$ ) while hoverflies contributed the lowest benefits (£0.7M  $\pm 1.4M$ ). Honeybees were  
332 generally more valuable than bumblebees due to their greater contribution to Bramley and  
333 Gala, two widespread varieties. However, the honeybee contribution was also highly  
334 variable in these varieties (s.d.  $\sim \pm 29\%$ ), resulting in a significant variability in estimated  
335 benefits (Table 2).

336 Estimating the benefits provided by different pollinator guilds based on single visit  
337 effectiveness (Table B in S1 File) or their visitation rates alone (Table C in S1 File) has  
338 little effect on the ranked contributions, with solitary bees remaining the most important guild  
339 in all four varieties nationally. However, the monetary benefits attributed to hoverflies rise  
340 substantially (£0.7M-£4.2M nationally).

## 341 **Discussion**

342 Solitary bees, honeybees, bumblebees and hoverflies can all pollinate apples, although  
343 hoverflies were shown to be the least effective of the taxa studied. Pollinator visitation in  
344 orchards is significantly affected by apple variety and some pollinator guilds are more active  
345 on some varieties than others. This could be a result of varying nectar and pollen availability  
346 between apple varieties [29]. Using a combination of field observations and cage  
347 experiments, this study highlights the variations in relative service contribution made by four  
348 major pollinator guilds across four different varieties; this contribution is a combination of  
349 their pollination effectiveness for apples and flower visitation rates in commercial orchards,

350 as well as the dependence of these varieties on insects for pollination. The findings further  
351 demonstrate the economic benefits of insect pollination services to UK apple orchards,  
352 estimating economic benefits to producers of ~£92M across the four varieties studied.

353 The differences found between pollinator guilds and their contribution to the production of  
354 different varieties, despite spatial and temporal overlap in the surveys, indicate some varieties  
355 are better serviced by some pollinators than others. Management to maintain or enhance  
356 pollinator populations could therefore be targeted for particular varieties. Given their proven  
357 capacity to pollinate apples, as demonstrated in this study and others [10], management  
358 involving introduction of honeybees may provide a potential solution to maintain or improve  
359 apple pollination. Historically, honeybees have been widely utilised for their pollination  
360 services in UK orchards [30] but at present it remains unknown how widespread this practice  
361 is and careful management is essential to prevent honeybees from engaging in sub-optimal  
362 foraging [10,31]. The highly variable contribution made by honeybees to pollination service  
363 in some varieties suggests their utilisation could be extended. Findings from this research  
364 could guide appropriate remuneration for apiculturists providing hives for pollination services  
365 in UK apples.

366 This research shows that currently the majority of the pollination service to apples in the UK  
367 is provided by wild pollinators (£70.7M p.a.) rather than managed honeybees (£21.4M p.a.),  
368 with solitary bees in particular making a large contribution (£51.4M p.a.), both through their  
369 capacity to pollinate apple flowers effectively and flower visitation frequency. Management  
370 to increase wild pollinators often takes time to establish and produce effects. The perennial  
371 nature of apples makes local and wider landscape pollinator management practices more  
372 appropriate than in annual rotation crops, particularly given the time it takes for mitigation  
373 measures such as establishment of flower strips or altered management practices to benefit  
374 and build up wild pollinator populations. Such management will result in returns on the

375 initial investment over the lifespan of the tree crop which can often be up to 20 years. Such  
376 returns on investment in pollinator management strategies have been demonstrated in  
377 blueberry crops [32]. Wild bees require additional nectar and pollen and so planting  
378 wildflower strips in orchards can increase the abundance and reproductive success of flower  
379 visiting solitary bees [33]. Furthermore, establishment and preservation of semi-natural  
380 habitat consistently increases the diversity and abundance of wild pollinators [34] and more  
381 specifically, increased woodland habitat can benefit solitary bees in apple orchards [12,35].  
382 Similarly, providing additional artificial nesting resources can boost solitary bee populations  
383 and improve pollination service [36-38]. Such management practices could be implemented  
384 across apple varieties, all of which are heavily reliant on solitary bees. The £51.4M  
385 contribution solitary bees make to these varieties in the UK alone, highlights the potentially  
386 serious financial implications of any declines in these species and emphasises the need for  
387 effective management strategies. The relatively large contribution bumblebees make to  
388 Braeburn pollination (38%) could warrant focused management on these species in and  
389 around Braeburn orchards. Planting pollen and nectar rich species can increase local  
390 bumblebee abundance and species richness [39] while field boundaries can provide suitable  
391 nesting sites for many bumblebees [40]. Undertaking both these measures could therefore be  
392 an effective means of boosting pollination service in the long term. Increasing wild  
393 pollinator populations provides additional benefits associated with a diverse pollinator  
394 assemblage including service resilience, insurance for inter-annual variation and  
395 complimentary [41-43]. However further work will be required to assess the cost  
396 effectiveness and co-benefits of any such management plan [e.g.[32]]

397 As with a number of previous studies, estimates of the economic benefits of pollination  
398 services are limited by the assumption of constant prices and the potential complexities of  
399 extrapolating impacts from smaller scales up to a national level [44]. In particular, the

400 benefits reported here may vary depending on the presence of other inputs or ecosystem  
401 services [45]. The benefits estimated only reflect current benefits to producer profits rather  
402 than wider societal impacts (i.e. economic value); in the event of a collapse of pollination  
403 services, the benefits lost would be substantially different as prices respond and producers  
404 substitute their inputs to compensate [46]. As such these findings may over- or under-  
405 estimate the actual impacts of pollination. However, as the majority of UK apple  
406 consumption is imported [26] and there is little to indicate that imports could not be  
407 increased, the impacts on consumers are likely to be negligible. As such, despite some  
408 limitations, the economic benefits estimated in this study are likely to be the most accurate  
409 currently available.

410 Using combined findings from cage experiments, pollinator surveys and field manipulations,  
411 this study quantifies the contribution of different pollinator guilds to UK apple production  
412 which represents a significant step forward but, to do this, several assumptions have been  
413 made. In the first instance, a single pollinator species was used as a surrogate to measure and  
414 represent the pollination effectiveness of a pollinator guild but clearly the pollinator  
415 community visiting apple orchards is diverse (Table D in S1 File). In the case of *Apis*  
416 *mellifera* this is entirely appropriate as no other honeybee species are found in the UK.  
417 However other guilds are more diverse. This analysis makes the assumption that pollinator  
418 effectiveness is more similar within pollinator guilds than between pollinator guilds and,  
419 considering factors which will influence the effectiveness of pollinators when visiting  
420 flowers, including morphology, body size and pollen collecting habit, there is some  
421 justification for this assumption. For instance, *Osmia sp.* and *Andrena sp.* store pollen using  
422 scopae unlike corbiculate guilds like the bumblebees and honeybees. Also the solitary bees  
423 observed in our study orchards are all smaller than UK bumblebees. Furthermore, hoverflies  
424 will forage only for nectar and not pollen. The use of relative pollination effectiveness in the

425 analysis rather than absolute pollination effectiveness minimises the risk that conclusions  
426 drawn for one species do not reflect the pollinator guild as a whole. Despite the limitation of  
427 using a surrogate species to represent a pollinator guild, including a measure of effectiveness  
428 rather than visitation alone improves our estimate of pollinator contributions.

429 Re-estimating the economic benefits provided by each guild without weighting for pollinator  
430 effectiveness indicates that the findings change only moderately with the exception of an  
431 increase in the benefits attributed to hoverflies (Table C in S1 File) due to the low weighting  
432 afforded to their pollination effectiveness based on cage studies. The outcomes of the study  
433 would be more highly resolved if pollination effectiveness could be measured for different  
434 species within each pollinator guild and linked to visitation rates of those species in the field,  
435 but for practical reason, it is not possible to conduct a study of this scale. Nonetheless, this  
436 shortcoming highlights the need to determine appropriate proxies for pollination service  
437 analysis in future, based on shared traits within a guild.

438 In the present study, the pollination effectiveness of the four guilds on the variety  
439 Scrumptious is taken to represent their pollination effectiveness to apples as a whole. Again,  
440 the use of a relative measure of pollinator effectiveness allows for differences between the  
441 fruit set of different varieties following insect visitation and, while flower morphology  
442 invariably affects the behaviour and effectiveness of flower visiting insects (e.g. [15]), there  
443 is little variation in the floral morphology of the apple varieties studied (personal  
444 observation). Furthermore, fruit set will be strongly affected by the amount of viable  
445 polliniser pollen pollinators are carrying during floral visits. This is itself a product of each  
446 guilds visitation rate to polliniser trees and their between tree and between row movement in  
447 orchards. It is also affected by the number and distribution of polliniser trees in the orchards,  
448 as well as their compatibility with the variety in question [47]. These factors vary hugely  
449 between orchards in the UK and therefore findings from the cage experiments in the present

450 study represent accurate relative pollination efficiencies for each of the pollinator guilds,  
451 independent of variations in polliniser availability.

452 This is the first time measures of pollinator effectiveness and field abundance have been  
453 combined and compared between pollinator guilds to quantify their contribution to crop  
454 production and economic output. It is also the first time that pollinator guild contributions  
455 have been compared between different varieties of a crop. As our knowledge of the  
456 pollination efficiency of different pollinators to different crops grows and consolidates  
457 globally [48], the concepts used in this study can be applied to better quantify economic  
458 impacts of different components of the pollinator community on crop production. This can  
459 ultimately result in more holistic models of pollination service provision and facilitate better  
460 modelling of the risks of pollinator declines [44]. Specifically, this study highlights the  
461 significant contribution made by insect pollinators to UK apple production. The variable  
462 pollination effectiveness of different pollinator guilds for apples has been demonstrated and  
463 when this is combined with flower visitation in the field, the contribution of different  
464 pollinator guilds to the production of different apple varieties is pronounced. These findings  
465 have implications for the management of insect pollination services in apple orchards and  
466 highlight the potential consequences of any decline in specific taxa and advocates  
467 management targeted to specific varieties. The £92.1M insect pollinators contribute to apple  
468 production in the UK suggests that further investment in the research and implementation of  
469 insect pollinator management strategies as part of an integrated orchard management system  
470 is justified.

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603 **Table 1: Summary of the economic benefits of pollination services to UK Apple varieties**  
 604 **in 2012.**

	Cox	Gala	Bramley	Braeburn
Area (ha)	1,697	1,312	3,326	509
Price/Kg class 1 (£)	0.86	0.77	£0.83	£0.85
Price/Kg class 2 (£)	0.50	0.52	£0.53	£0.55
Total benefits/ha (£000)	£20.1	£22.9	£21.2	£18.2
Total IPB/ha (£000)	£12.3	£14.8	£14.5	£8.5
National Total IPB (£000)	£20,214.7	£19,374.3	£48,120.6	£4,339.7

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606 **Area** = the total area reported in 2012 in the Orchard Fruit Survey (Braeburn/Gala:) and in the crop year 2012/2013 (Cox/Bramley:). **Total**  
 607 **benefits/ha** = the total economic benefits of market output per hectare estimated from the open pollination treatment. **Total IPB/ha** = the  
 608 total economic benefits of insect pollination services per hectare; the difference between the value per hectare in the open and closed  
 609 treatments. **National Total IPB** = the total economic benefits of insect pollination services to the crop across the UK.

610 **Table 2: Estimated pollination services and economic benefits to each variety provided**  
 611 **by the four pollinator guilds studied based on visitation rates and effectiveness (after 3**  
 612 **visits). Measures of standard deviation are included in brackets.**

Pollinator	Variety								
	Cox		Gala		Bramley		Braeburn		Total Benefit (£M)
	Proportion of Service (%)	Benefit (£M)	Proportion of Service (%)	Benefit (£M)	Proportion of Service (%)	Benefit (£M)	Proportion of Service (%)	Benefit (£M)	
Bumblebees	21% (±13%)	£4.2 (±2.7)M	13% (±19%)	£5.3 (±5.4)M	15% (±17%)	£7.4 (±8.3) M	38% (±33%)	£1.7 (±1.4)M	£18.6M (±£17.8)
Honeybee	25% (±14%)	£5.1 (±2.8)M	28% (±28%)	£2.6 (±3.6)M	26% (±30%)	£12.7(±14.7)M	23% (±22%)	£1.0 (±0.9)M	£21.4M (± £22M)
Hoverflies	0.3% (±1%)	£0.1 (±0.1)M	2% (±5%)	£0.4 (±1.0)M	0.4% (±1%)	£0.2 (±0.3) M	1% (±1%)	£0.04(±0.06)M	£0.7M (±1.5M)
Solitary bees	54% (±21%)	£10.9 (±4.1)M	57% (±29%)	£11.0 (±5.5)M	58% (±39%)	£27.8 (±18.8)M	39% (±24%)	£1.7 (±1.0)M	£51.4M (±29.4M)

613 **Proportion of service (%)** = the average percentage contribution to total pollination services made by the taxa to the variety. **Benefits (£M)**  
 614 = the monetary benefits, in million £ of additional production, of the pollination services provided by the taxa to that specific variety.

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623 **Fig. 1. Percentage fruit set of apples (var Scrumptious) following different per flower**  
624 **visit numbers by four pollinator species**

625 **Fig. 2. Number of visits observed to different apple variety flowers by different**  
626 **pollinator taxa.** Mean  $\pm$  SE visits per minute per survey shown. Within variety, bars with  
627 different letter are significantly different ( $P < 0.05$ ) following analysis of raw count data  
628 using generalised linear mixed effects models.

629 **Fig. 3. Percentage fruit set pre and post apple thinning for Bramley and Braeburn**  
630 **apples following pollinator exclusion treatments (Mean  $\pm$  SE).**

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Fig 3