

Article (refereed) - postprint

Hutchinson, Louise A.; Oliver, Tom H.; Breeze, Tom D.; Bailes, Emily J.; Brünjes, Lisa; Campbell, Alistair J.; Erhardt, Andreas; de Groot, G. Arjen; Földesi, Rita; García, Daniel; Goulson, Dave; Hainaut, Hélène; Hambäck, Peter A.; Holzschuh, Andrea; Jauker, Frank; Klatt, Björn K.; Klein, Alexandra-Maria; Kleijn, David; Kovács-Hostyánszki, Anikó; Krimmer, Elena; McKerchar, Megan; Miñarro, Marcos; Phillips, Benjamin B.; Potts, Simon G.; Pufal, Gesine; Radzevičiūtė, Rita; Roberts, Stuart P.M.; Samnegård, Ulrika; Schulze, Jürg; Shaw, Rosalind F.; Tscharntke, Teja; Vereecken, Nicolas J.; Westbury, Duncan B.; Westphal, Catrin; Wietzke, Alexander; Woodcock, Ben A.; Garratt, Michael P.D.. 2021. **Using ecological and field survey data to establish a national list of the wild bee pollinators of crops.**

© 2020 Elsevier B.V.

This manuscript version is made available under the CC BY-NC-ND 4.0 license
<https://creativecommons.org/licenses/by-nc-nd/4.0/>



This version is available at <http://nora.nerc.ac.uk/id/eprint/530415/>

Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <https://nora.nerc.ac.uk/policies.html#access>.

This is an unedited manuscript accepted for publication, incorporating any revisions agreed during the peer review process. There may be differences between this and the publisher's version. You are advised to consult the publisher's version if you wish to cite from this article.

The definitive version was published in *Agriculture, Ecosystems and Environment*, 315, 107447. <https://doi.org/10.1016/j.agee.2021.107447>

The definitive version is available at <https://www.elsevier.com/>

Contact UKCEH NORA team at
noraceh@ceh.ac.uk

32 ¹³Agroecology Lab, Université Libre de Bruxelles (ULB), Boulevard du Triomphe CP 264/2, B-
33 1050 Brussels, Belgium

34 ¹⁴Department of Ecology, Environment and Plant Sciences, Stockholm University, 106 91
35 Stockholm, Sweden

36 ¹⁵Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, 97074 Würzburg,
37 Germany

38 ¹⁶Department of Animal Ecology, Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32,
39 D-35392 Giessen, Germany

40 ¹⁷Department of Biology, Lund University, SE-223 62 Lund, Sweden

41 ¹⁸Functional Agrobiodiversity, Department of Crop Sciences, University of Göttingen,
42 Göttingen, Germany

43 ¹⁹Nature Conservation and Landscape Ecology, Faculty of Environment and Natural
44 Resources, University of Freiburg, Freiburg, Germany

45 ²⁰Plant Ecology and Nature Conservation Group, Wageningen University,
46 Droevendaalsesteeg 3a, 6708PB, Wageningen, The Netherlands

47 ²¹Lendület Ecosystem Services Research Group, Institute of Ecology and Botany, Centre for
48 Ecological Research, Alkotmány str. 2-4, 2163 Vácrátót, Hungary

49 ²²School of Science & the Environment, University of Worcester, Worcester, United Kingdom

50 ²³Servicio Regional de Investigación y Desarrollo Agroalimentario (SERIDA). Apdo. 13, E-
51 33300 Villaviciosa, Asturias, Spain

52 ²⁴Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn,
53 Cornwall TR10 9FE, United Kingdom

54 ²⁵General Zoology, Institute for Biology, Martin Luther University Halle-Wittenberg, Hoher Weg
55 8, D-06120 Halle (Saale), Germany

56 ²⁶Molecular Evolution and Animal Systematics, Institute for Biology, Leipzig University,
57 Talstraße 33, D-04103 Leipzig, Germany

58 ²⁷Life Sciences Center, Vilnius University, Saulėtekio al. 7, LT-10223 Vilnius, Lithuania

59 ²⁸Agency for Environment and Energy Canton Basel-City, Hochbergerstr. 157, 4019 Basel,
60 Switzerland

61 ²⁹Agroecology, Dept. of Crop Sciences, University of Göttingen, Grisebachstrasse 6, 37077
62 Göttingen, Germany

63 ³⁰Plant Ecology and Ecosystems Research, University of Goettingen, Untere Karspüle 2,
64 37073 Göttingen, Germany

65 ³¹UK Centre for Ecology & Hydrology, Crowmarsh Gifford, Wallingford, Oxfordshire, United
66 Kingdom

67 *Corresponding author. E-mail: l.hutchinson@pgr.reading.ac.uk

68

69 **Abstract**

70 The importance of wild bees for crop pollination is well established, but less is known about
71 which species contribute to service delivery to inform agricultural management, monitoring
72 and conservation. Using sites in Great Britain as a case study, we use a novel qualitative
73 approach combining ecological information and field survey data to establish a national list of
74 crop pollinating bees for four economically important crops (apple, field bean, oilseed rape
75 and strawberry). A traits data base was used to establish potential pollinators, and combined
76 with field data to identify both dominant crop flower visiting bee species and other species that
77 could be important crop pollinators, but which are not presently sampled in large numbers on
78 crops flowers. Whilst we found evidence that a small number of common, generalist species
79 make a disproportionate contribution to flower visits, many more species were identified as
80 potential pollinators, including rare and specialist species. Furthermore, we found evidence of
81 substantial variation in the bee communities of different crops. Establishing a national list of
82 crop pollinators is important for practitioners and policy makers, allowing targeted
83 management approaches for improved ecosystem services, conservation and species
84 monitoring. Data can be used to make recommendations about how pollinator diversity could
85 be promoted in agricultural landscapes. Our results suggest agri-environment schemes need
86 to support a higher diversity of species than at present, notably of solitary bees. Management
87 would also benefit from targeting specific species to enhance crop pollination services to
88 particular crops. Whilst our study is focused upon Great Britain, our methodology can easily
89 be applied to other countries, crops and groups of pollinating insects.

90

91 **Key-words**

92 Agri-environment Schemes, Apple, Biodiversity, Crop pollination, Dominant Pollinators,
93 Ecosystem Services, Field Bean, Oilseed Rape, Rare Species, Strawberry.

94

95 **1. Introduction**

96 Insect pollination is key to global agricultural productivity (IPBES, 2016) due to growing
97 demand for entomophilous crops (Godfray and Garnett 2014). The nutritional and economic
98 importance of insect pollinated crops (Vanbergen et al., 2014), and the inability of managed
99 pollinators (e.g., *Apis mellifera*) to meet service demand, mean agriculture is highly dependent
100 upon wild pollinators (Aizen and Harder 2009; Breeze et al., 2014). Yet conventional
101 agricultural practices are a key driver of pollinator declines (Senapathi et al., 2015). Whilst
102 agri-environment scheme options have had positive impacts (Tonietto et al., 2018), most
103 benefit a limited suite of common species (Scheper et al., 2013) and homogeneous
104 communities provide less reliable pollination services (Grab et al., 2019). Currently agri-
105 environment schemes tend preferentially to benefit bumblebee populations (Wood et al.,
106 2015a; Wood et al., 2015b, 2016a, b), yet solitary bee species are more important pollinators
107 of some crops (Woodcock et al., 2013). As such, current agri-environment schemes may not
108 be optimally designed to increase pollination services to many crops. Identifying key pollinating
109 species to individual crops, and ones which may provide additional pollination and insurance
110 against declines in other species, would help inform agricultural management for bee
111 pollinators (Garratt et al., 2014a). Yet there is insufficient information on bee communities for
112 many crops (Kremen and Chaplin-Kramer, 2007) and no studies have attempted to establish
113 a 'national list' of crop pollinators to advise management or monitoring programmes.

114 Whilst the majority of crop flower visitation is attributed to a small proportion of bee species
115 (Kleijn et al., 2015), species-rich communities have been shown to positively influence crop
116 yields and pollination service stability (Hoehn et al., 2008; Garibaldi et al., 2011; Martins et al.,
117 2015; Dainese et al., 2019; Woodcock et al., 2019). Biodiversity conservation and ecosystem
118 service management are often seen as distinct objectives (Sutter et al., 2017), however
119 management that only targets common crop pollinators will not safeguard production if it fails
120 to encompass species that supplement service provision (Fijen et al., 2018). High species
121 turnover means that diverse communities, including rare and specialist species, are required

122 to maintain crop pollination service at regional scales (Winfree et al., 2018). With climate
123 change reducing the occupancy and richness of some wild bee species (Soroye et al., 2020),
124 supporting wider species diversity may be crucial for crop pollination service stability under
125 the substantial future environmental change that is predicted (Oliver et al., 2015; Dainese et
126 al., 2019). Additionally, different crops have distinct pollinator communities and it will be
127 beneficial to identify the pollinating taxa of individual crops and target management
128 accordingly (Garratt et al., 2014a). Furthermore, a national list of crop pollinators can inform
129 monitoring schemes to ensure they include important crop pollinating species (Carvell et al.,
130 2017; Garratt et al., 2019).

131 In order to inform pollinator management and monitoring, our study aimed to compile the bee
132 species visiting four crops: apple (*Malus domestica*), field bean (*Vicia faba*), oilseed rape
133 (*Brassica napus*) and strawberry (*Fragaria x ananassa*). Insect pollination has been shown to
134 enhance yield quantity and quality in all four crops (Bartomeus et al., 2014; Garratt et al.,
135 2014b). Additionally, they differ in flower phenology and morphology (Garibaldi et al., 2015)
136 and likely show corresponding differences in their pollinator community composition (Garratt
137 et al., 2014a). We use sites in Great Britain as a case study because its bee fauna is
138 comprehensively described and their occupancy is well recorded over a long time period
139 (Powney et al. 2019). We compiled a list of all British bee species and their available
140 physiological and ecological traits, and combined it with field survey data in order to devise an
141 approach to generate lists of (i) definite flower visitors to each crop (ii) likely flower visitors,
142 which are expected to also contribute to crop pollination (iii) possible crop flower visitors whose
143 contribution to pollination is not well understood and merits further investigation. Our aim was
144 to compile these lists for reference purposes, but not to statistically compare pollinator
145 communities between crops, due to the unstandardised nature of the datasets used to
146 generate the lists of bee species. Additionally, we identify dominant crop pollinating species,
147 and assess the contribution of wild bees compared to honey bees for crop flower visitation.

148

149 **2. Materials and Methods**

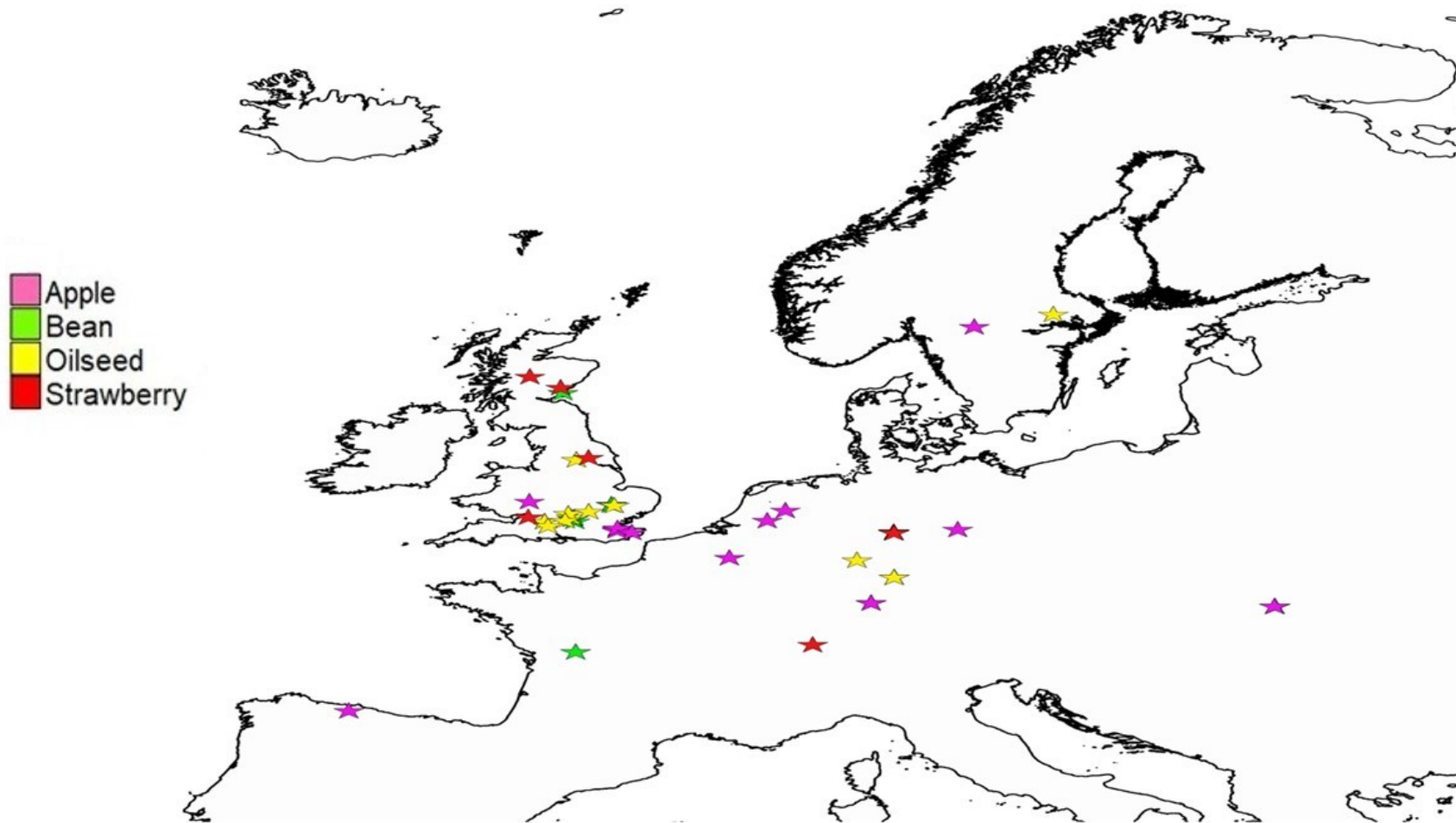
150 **2.1 Potential crop pollinators.**

151 First, a species database of all extant, resident wild bee species in Great Britain was
152 established using the most recent checklist of UK species (Else et al., 2016). For each species,
153 data on the following were collated: flight period (months); sociality (cleptoparasite, eusocial
154 or solitary); lecty (oligolectic or polylectic, including if any of the target crop plant families are
155 visited for pollen and/or nectar), tongue length (short/long), geographic coverage (distribution
156 and habitat) (based on trait information compiled by Stuart Roberts for the EU- FP6 ALARM-
157 project and BWARS, 2020) and conservation status (Webb et al., 2018). Potential crop
158 pollinators, as defined here, are those bee species which, based upon these ecological traits,
159 such as flight period, lecty, sociality and tongue length, could pollinate our target crops. Habitat
160 specialists that are not coincident with cropland were initially excluded i.e., primarily coastal,
161 heathland species. The known floral ecology of each species was then used to refine lists for
162 each crop. Cleptoparasitic species, species that are oligolectic on plant families other than the
163 target crop or polylectic, but not documented as foraging on the relevant plant family for pollen
164 or nectar and species whose flight period does not overlap with the relevant crops flowering
165 period were excluded. For field bean, only 'long-tongued' species (Michener, 2000) were
166 considered as its flowers have deep corollas and most visits by 'short-tongued' species involve
167 nectar robbing rather than legitimate visitation (Garratt et al., 2014a).

168 **2.2 Field survey data**

169 Field studies were sourced through literature searches in google scholar and existing datasets
170 held by the authors. Fifty-seven datasets from across England, Scotland and eight other
171 European countries were available to combine with the potential crop pollinator lists in order
172 to establish shortlists of crop flower visitors (Figure 1 and Table S3).

173



174

176

Figure 1: Map of Europe, showing the countries from which field studies were sourced for each crop.

177 Lists of bee species recorded in crop fields were compiled using three types of survey data:

178 i) British flower visitation studies (e.g. transect walks, observation plots).

179 ii) British pan trap studies in crop fields.

180 iii) Other European flower visitation studies (used to validate crop flower visitation for
181 species sampled in British pan traps only).

182 For every bee species the total number of reported legitimate flower visits and number of
183 studies recorded in were calculated for each crop. If studies did not include quantitative data
184 then a conservative approach was taken whereby each bee species listed was taken as
185 representing a single crop flower visit. As pan trap catches do not provide information on floral
186 associations (Westphal et al., 2008), these data were only used, in combination with trait data,
187 to generate the list of possible pollinators.

188 **2.3 Crop flower visitors**

189 The lists of potential crop pollinators were combined with the field survey data to categorize
190 bee species into one of three flower visitor categories (Figure 2; Full details in Supplementary
191 Methods 1):

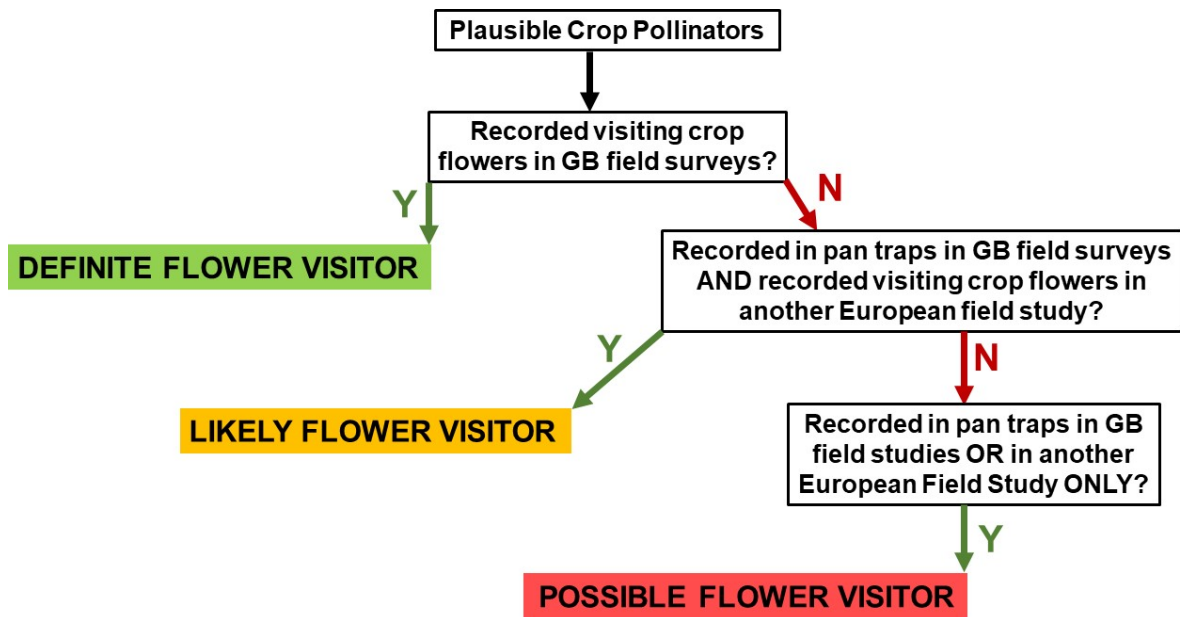
192 i) Definite Flower Visitors – Species recorded visiting crop flowers in British flower
193 visitation studies.

194 ii) Likely Flower Visitors - Species recorded in British pan trap crop studies and
195 recorded as making at least two flower visits in other European studies.

196 iii) Possible Flower Visitors - Species only recorded in British pan trap studies, or in
197 other European flower visitor studies only, and classified as a potential crop
198 flower visitor.

199

200



201

204

205

206

207 **2.4 Dominant crop flowers visitors**

208 As visitation rate to crop flowers is a good proxy of relative contribution to pollination service
 209 delivery (Vazquez et al., 2005), we identified the dominant British flower visiting bee species
 210 per crop by approximating the species attributed with a combined total of 80% of flower visits,
 211 the proportion identified as corresponding to the dominant flower visitors by Kleijn et al. (2015).
 212 Only British flower visitation datasets where bee species were either all identified to species
 213 or genus were included in the analysis (Supplementary Methods 2). Additionally, we calculated
 214 the average proportion of visits to crop flowers attributed to wild bees compared to honey bees
 215 for all crops (Supplementary Methods 2).

216

217 **3. Results**

218 **3.1 Potential crop pollinators**

219 A preliminary list of 229 extant, resident British wild bee species was compiled. Of those 132
220 species were excluded due to ecological and lecty traits that were deemed incompatible with
221 these bees being present in crop fields and/or crop flower visitors (Table S1). Four species
222 were treated as an aggregate – *Bombus terrestris* aggregate – due to the difficulties of
223 separating their workers in the field (Wolf et al., 2010; Bossert, 2015). Therefore, a total of 97
224 species were initially identified as potential crop pollinators. Accounting for their documented
225 foraging ecology and flight period, the following number of species were considered as
226 potential pollinators per crop: apple- 83, bean- 30, oilseed- 60, and strawberry – 90 (Table
227 S2).

228 **3.2 Field survey data**

229 The total number of studies sourced per crop were as follows: apple – 17; bean – 10; oilseed
230 – 19; strawberry – 11. The number of studies per survey type for each crop is provided in
231 Figure S1.

232 **3.3 Crop flower visitors**

233 Seventy-three species from ten genera were categorised as flower visitors of one or more
234 crops, 63 of which were recorded in British crop field studies (Table 1, Figure 3). Fourteen
235 species were included in flower visitor categories that were not initially identified as potential
236 crop pollinators. Ten of those were widely polylectic *Bombus* or *Lasioglossum* species, all
237 recorded in oilseed datasets, but not documented in the literature as foraging on
238 *Brassicaceae*. The remaining species were three short-tongued *Andrena* species recorded
239 visiting bean flowers, two of which are oligolectic on Fabaceae and a *Colletes* species,
240 recorded in a single strawberry dataset, that is documented as being oligolectic on another
241 plant family. The majority of species identified as potential pollinators, but not recorded in crop
242 field surveys were either rare species or polylectic species documented as having distinct

243 preferences for plant families other than the target crop. The remaining species were
 244 overwhelmingly smaller species from the genera *Hylaeus* and *Lasioglossum* or cavity nesting
 245 *Megachilidae*. Most species identified as crop flower visitors were geographically widespread
 246 (BWARS, 2020) and polylectic species. However, a quarter (n=18) of species included in
 247 flower visitor categories, currently have a designated conservation status in Britain. Full details
 248 of all species in crop flower visitor categories are given in tables S4a-d and S5a – S8d.

249

250 Table 1: Number of bee species, based upon field datasets and trait information, that were
 251 assigned to each category of flower visitor per crop

Crop	Flower Visitor Category			Total
	Definite	Likely	Possible	
Apple	19	13	25	57
Field Bean	11	0	3	14
Oilseed Rape	37	11	3	51
Strawberry	9	6	18	33

252

253 *Apple*

254 All five British apple flower visitor studies recorded every bee to species level. *Andrena* were
 255 the most speciose genus of flower visitor, both overall (n=22) and in the definite flower visitor
 256 category (n=10). *Bombus* species were the next most commonly represented genus in the
 257 latter category (n=6), but were less frequent overall (n=9) than *Lasioglossum* species (n=16).
 258 Within the definite flower visitor category 80% of flower visits were attributed to eight species,
 259 only half of which were recorded in all studies. Most likely and possible flower visitors were
 260 *Andrena* or *Lasioglossum* species.

261 *Bean*

262 Three of the five British bean flower visitor studies recorded all bee to species level, the
 263 remainder only recorded *Bombus* to species, which was both the most common genus overall
 264 (n=9) and in the definite flower visitor category (n=7). Three short-tongued *Andrena* sp. were
 265 identified as definite flower visitors, but all were recorded as very low numbers of flower visits

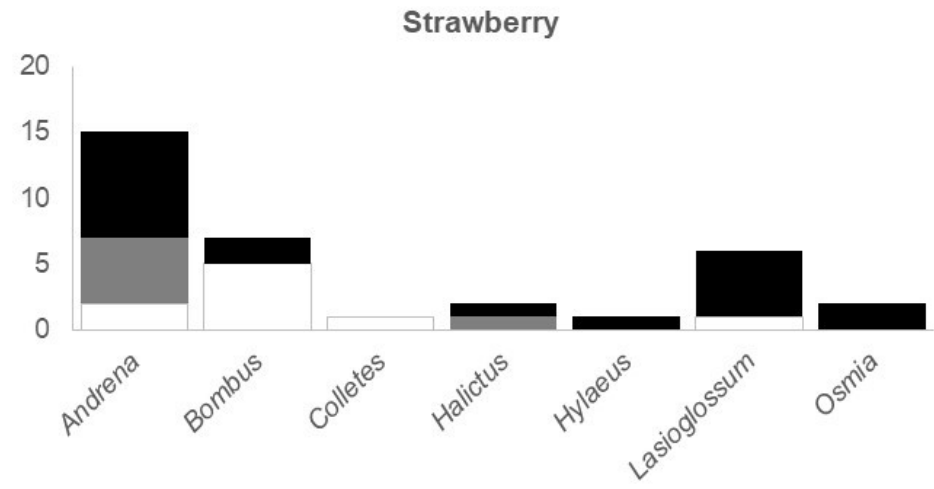
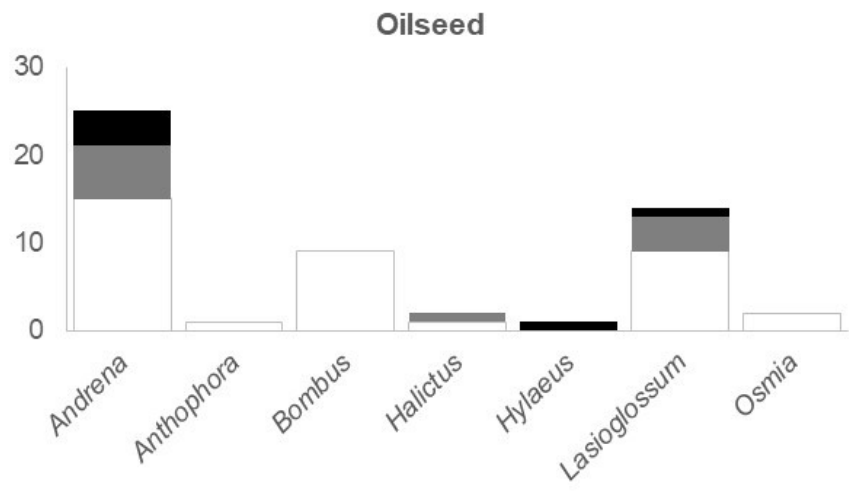
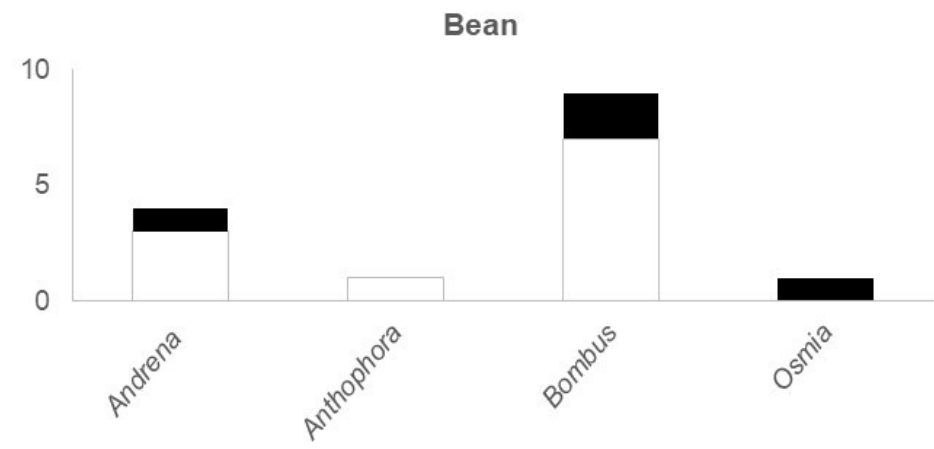
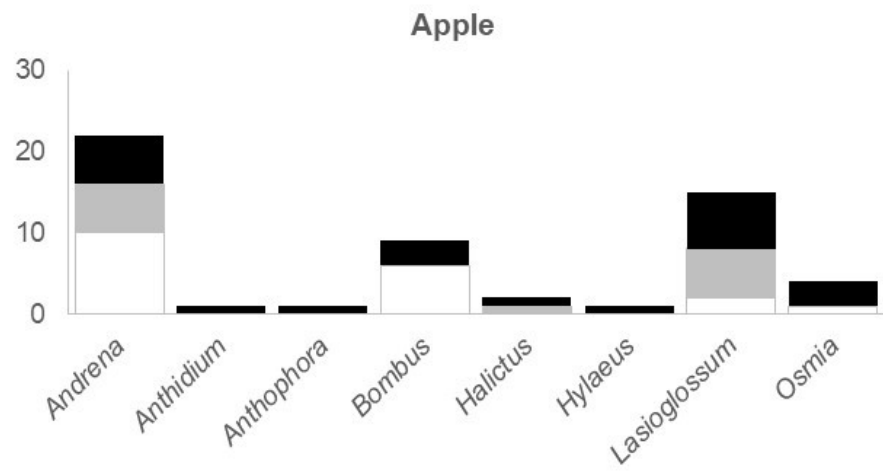
266 (≤ 10). Four *Bombus* species and *Anthophora plumipes* accounted for 95% of all visits
267 recorded in British flower visitation studies. However, all the *A. plumipes* records derived from
268 one study (Bond and Kirby, 1999) carried out at a single site. The four *Bombus* were the only
269 species recorded in four or more studies. No species met the criteria for the likely flower visitor
270 category. The possible flower visitor category included two *Bombus* and one *Osmia* species.

271 *Oilseed*

272 Six of the nine British oilseed flower visitor studies recorded bees to species level, but only
273 two included quantitative data on all bee species. *Andrena* was the most speciose genus of
274 bee, both overall ($n=27$) and within the definite flower visitor category ($n=15$). *Bombus* and
275 *Lasioglossum* species were equally represented in the definite flower visitor category ($n=9$),
276 but *Lasioglossum* were more frequent overall ($n=14$). Within the definite flower visitor category
277 80% of recorded flower visits were attributed to six species, only two of which were recorded
278 in all nine studies, with the remainder only recorded in between five and eight studies, despite
279 all being large *Andrena* or *Bombus* species, generally identified and quantified in all field
280 studies. The likely and possible visitor categories were entirely comprised of *Andrena* or
281 *Halictidae* species, two of which are oligolectic on *Brassicaceae*.

282 *Strawberry*

283 Two British strawberry flower visitor studies recorded all bees to species level. The remaining
284 three only recorded a group of large *Andrena* and *Bombus* to species. *Bombus* species were
285 the most common genus of bee within the definite flower visitor category ($n=5$), but joint
286 second as the most frequent genus overall, alongside *Lasioglossum* ($n=7$), with *Andrena*
287 species being the most prevalent genus across all categories ($n=14$). Within the definite flower
288 visitor category 80% of recorded flower visits were attributed to just two *Bombus* species,
289 which along with two other *Bombus*, were the only species recorded in more than two studies.
290 The likely visitor category was almost exclusively represented by *Andrena* species. The
291 possible visitor category was largely comprised of solitary bees from five different genera.



294 **3.4 Dominant crop flower visitors**

295 Ten bee species were attributed with 80% of flower visits across the four crops (Figure S2;
296 Figure 4). There were differences however in the number and composition of those species
297 making up the 80% of flower visits on a per crop basis. Differences in crop communities were
298 even more distinct when considering the entire suite of bee species included in the
299 characterisation of each crops' total flower visiting community (Figure 3; Figure 4). Wild bees
300 were attributed with an average of between 63 and 83 percent of crop flower visits compared
301 to honey bees (Apple: solitary bee visits = 68%; Bean: solitary bee visits = 83%; Oilseed:
302 solitary bee visits = 63%; Strawberry: solitary bee = 77%).

303

304

305

306

307

308

309

310

311

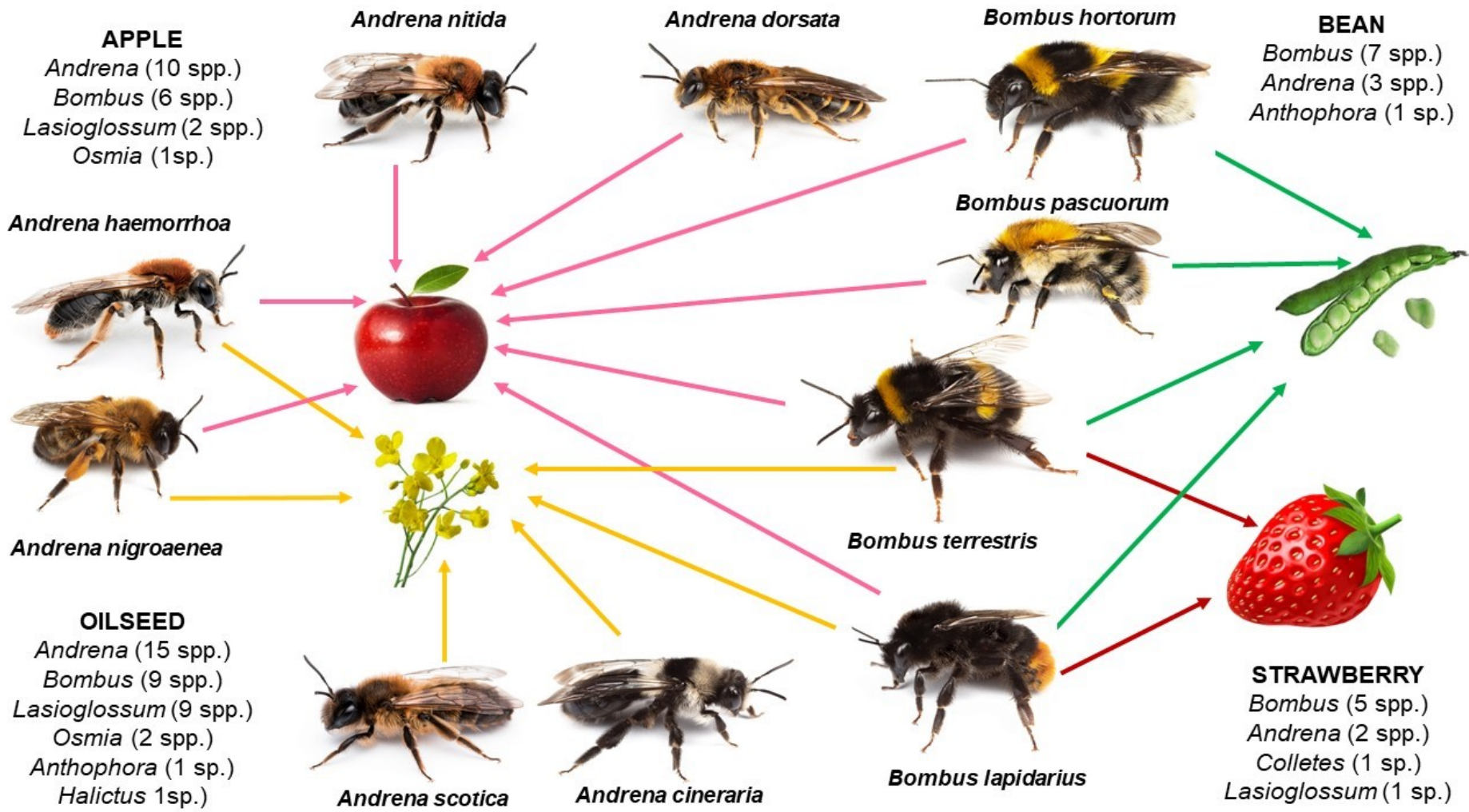
312

313

314

315

316



317

320 **4. Discussion**

321 **4.1 Crop pollinator species**

322 Our study is the one of the first to evaluate the entire wild bee community of multiple crops on
323 a national basis and can be used as model approach for other countries, crops and pollinators.
324 With the identification of bee species important for pollinating crops we build the basis to better
325 sustainably manage services with changing climate and land use. Whilst in accordance with
326 other studies (Rader et al., 2012; Kleijn et al., 2015) our results indicate that a small proportion
327 of common, generalist bee species do make the majority of crop flower visits, many more
328 species were evidenced as crop flower visitors. Additionally, our results suggest that the
329 contribution of wild bee species to crop flower visitation may be even greater than previously
330 thought. Whereas previous estimates indicate that wild bees make a similar overall
331 contribution to honey bees (Kleijn et al. 2015), when considering the entire suite of flower
332 visiting species our results indicate that wild bees make on average between 63 and 83% of
333 flower visits to our target crops. Given the benefits of biodiverse communities for current and
334 future crop pollination services (Kremen et al., 2002; Hoehn et al., 2008; Garibaldi et al., 2011;
335 Rader et al., 2012), interventions to support crop pollinators should target a more significant
336 proportion of the bee fauna than at present (Wood et al., 2015b, 2016a; Gresty et al., 2018).
337 Establishing a list of currently important, but also potentially relevant crop pollinators, is
338 necessary to help target monitoring and conservation (Carvell et al., 2017).

339 Our results also support prior evidence of distinct differences in individual crop pollinator
340 communities (Garratt et al., 2014a). The overwhelming majority of field bean and strawberry
341 flower visits were attributed to bumblebees. However, whereas field bean was visited by the
342 three longest tongued species in Britain, strawberry crops were almost exclusively visited by
343 two other bumblebee species, with relatively shorter tongues. This supports a link between
344 trait matching of bees and flowers in crop pollination (Garibaldi et al., 2015). *Bombus* species
345 were also recorded visiting apple and oilseed rape. However, due to their low abundance in
346 early spring during apple flowering (Martins et al., 2015), and lower rate of pollen transfer

347 when visiting oilseed flowers (Woodcock et al., 2013) they are less important pollinators of
348 these crops compared to solitary species. *Andrena* and *Lasioglossum* species were prevalent
349 across both apple and oilseed flower visitor categories. *Andrena* are known to be highly
350 efficient pollinators of both crops (Martins et al., 2015; Woodcock et al., 2013), especially apple
351 (*Russo et al., 2017*). Most *Lasioglossum*, species however, generally emerge later than many
352 *Andrena* species, and peak after apple flowering, whereas oilseed tends to flower later and
353 longer, and *Lasioglossum* are likely important pollinators of this crop (Perrot et al., 2018;
354 Catarino et al., 2019). Furthermore, we almost certainly significantly underestimated the
355 diversity and abundance of *Lasioglossum* bees visiting oilseed rape, given that many studies
356 did not include detailed quantitative data on this genus.

357 Our datasets also indicate that rare and specialist species may visit crop flowers when they
358 are locally abundant or are especially attracted to crop flowers (MacLeod et al., 2020). Several
359 rare species recorded in apple orchards are most common in south-east England, Britain's
360 principal apple growing region, and bee species that are oligolectic on Brassicaceae were
361 recorded in oilseed rape studies. Given that biodiversity benefits pollination (Dainese et al.,
362 2019), strategies to support biodiverse crop communities may prove critical to sustain
363 ecosystem service provision. Yet current agri-environment schemes options rarely consider
364 rare species (Senapathi et al., 2015). There is however, a significant overlap in the floral
365 resources used by common and rare crop pollinators (Sutter et al., 2017; MacLeod et al.,
366 2020), and thus there are opportunities to promote both biodiversity and conservation in
367 agricultural landscapes.

368 Our findings also offer an opportunity to anticipate potentially important future crop pollinators.
369 For example, whilst a number of European crop flower visitors not presently recorded in British
370 crop fields are currently geographically restricted, should they expand their range in the future,
371 they could ameliorate the threat of ecological mismatches between current pollinators and
372 crops due to climate change (Polce et al., 2013; Polce et al., 2014; Settele et al., 2016). Taken
373 further, this information could be used to refine existing models of bee populations used to

374 project pollinator populations at large spatial scales (e.g. Gardner et al., 2020), which can
375 assist in larger scale planning of pollinator management.

376 Identifying specific bee crop pollinating species, as we have done, can inform refinements to
377 agri-environment schemes to promote more biodiverse communities in agricultural
378 landscapes. For example, *Andrena* were the most speciose genus of bees identified across
379 flower visitor categories in three of the crops. Currently European agri-environment measures
380 to boost pollinator populations have focused on the creation of flower-rich habitats, including
381 wildflower buffer strips (Wratten et al., 2012). Yet evidence suggests these are primarily visited
382 by bumblebees, with solitary bees preferring non-sown, wild plants (Wood et al., 2015). In
383 apple orchards for example, early-flying *Andrena* species have been positively associated with
384 dandelions (*Taraxacum* agg.) rather than sown species, which often bloom later than apple
385 flowers (Campbell et al., 2017). Reduced mowing regimes in orchards, and other crop areas,
386 particularly in early spring could boost *Andrena* numbers and hence pollination. Such
387 interventions are also likely to benefit early flying *Lasioglossum*, many species of which are
388 known be attracted to yellow flowers in the family *Asteraceae*. *Osmia* species have also been
389 demonstrated as efficient pollinators of apple, oilseed and strawberry crops (Abel et al., 2003;
390 Garratt et al., 2016; Horth and Campbell, 2018), but as in this study, are frequently recorded
391 in low numbers, likely due to a lack of suitable nesting and floral resources in agricultural
392 landscapes for cavity nesting species (Gardner and Ascher, 2006; Blitzer et al., 2016).
393 Incorporating hedgerow species such as Dog Rose and Bramble, alongside, areas of old and
394 dead wood, around crop areas would provide both forage and nesting resources (Eise and
395 Edwards 2018; Gresty et al., 2018) for these and other cavity nesting bees. Future
396 management to support long-tongued solitary bees could benefit field bean pollination.
397 *Anthophora plumipes*, for example, prefers to nest in vertical soil profiles, which are not
398 currently a common feature in agricultural landscapes.

399 **4.2 Data constraints and limitations**

400 There are caveats to using foraging ecology to identify potential bee pollinators, as done here
401 and elsewhere (Ahrenfeldt et al., 2015). There is a lack of published data for many bee species
402 and others visit a wider range of flowers than can be realistically documented (Else and
403 Edwards, 2018). As such, determining the status of bee species as crop flower visitors
404 requires field survey data for confirmation. Yet comprehensive crop pollinator data is currently
405 lacking as sampling is irregular, undertaken almost exclusively as part of bespoke research
406 projects rather than systematic monitoring (Breeze et al., 2020). Furthermore, whilst census
407 methods can provide information on floral associations, they require experienced surveyors to
408 comprehensively record species richness (O'Connor et al., 2019). Across all four crops the
409 only bees which were consistently identified to species level were large, conspicuous ones
410 from the genera *Bombus* and *Andrena*. Small and inconspicuous species, particularly from
411 the genus *Lasioglossum*, were often only extensively sampled in the pan trap surveys.
412 Additionally, whilst the visitation rate of dominant species is strongly correlated to pollination
413 service delivery (Winfree et al., 2015; Fijen et al., 2018), the assumption here and elsewhere
414 that quantitative visitation data can be used to infer pollination (Kleijn et al., 2015), neglects to
415 factor in that flower visitation alone is not a perfect proxy for pollination (King et al., 2013;
416 Senapathi et al., 2015; Ollerton, 2017). Certain physiological and behavioural traits also
417 influence pollination service delivery (Martins et al., 2015). Further detailed data and research
418 is required before any definitive conclusions can be made about the contributions of individual
419 bee species to crop pollination.

420 **5. Conclusions**

421 Given the importance of wild pollinators and the detrimental impacts of conventional
422 agriculture on their populations it is unsurprising that the management of wild and managed
423 pollinating insects is considered a critical step for future food security (Garibaldi et al., 2019;
424 Kleijn et al., 2019; Rollin and Garibaldi et al., 2019; Reilly et al., 2020). Yet information on
425 which species contribute most to ecosystem service delivery has long been elusive (Kremen
426 and Chaplin-Kramer, 2007) despite its critical importance for both monitoring and conservation

427 measures. Here we combine ecological and field data to provide a uniquely comprehensive
428 overview of the crop pollinating bees of a single region, Great Britain. Whilst we have focused
429 on Great Britain, a similar approach would be applicable across Europe, and could also be
430 applied to non-bee species that have been identified as important crop pollinators (Rader et
431 al., 2016). Our research bolsters evidence that many wild bee species, including rare and
432 specialised ones, may contribute to crop pollination (Klein et al., 2003; Sutter et al., 2017;
433 Winfree et al., 2018; MacLeod et al., 2020), thus it can be argued that agri-environment
434 scheme options should not focus solely on dominant crop pollinators.

435 Future climatic changes threaten to further deplete already impoverished bee populations
436 (Soroye et al., 2020) and create spatial mismatches between crops and their pollinators, which
437 could exacerbate existing pollination deficits (Polce et al., 2014). To that end, the species
438 identified as possible crop pollinators could represent an as yet untapped pollinator resource.
439 Whilst some species may not currently visit crops due to ecological or environmental
440 constraints, they could be assisted to expand by dedicated conservation measures in
441 agricultural landscapes, allowing them to compensate for any declines in current crop
442 pollinating species. Many such species are solitary, which presently benefit much less from
443 agri-environment schemes than social species (Wood et al., 2015b, 2016a, 2016b; Gresty et
444 al., 2018). As such land managers may need to re-evaluate existing pollinator management
445 interventions and consider a broader range of species to safeguard the ecosystem service of
446 crop pollination in an uncertain future.

447 **Declaration of Competing Interest**

448 The authors declare that they have no known competing financial interests or personal
449 relationships that could have appeared to influence the work reported in this paper.

450 **Authors' contributions**

451 LH conceived the ideas, analysed the data and wrote the manuscript. MG, TB and TO
452 contributed to the conceptual development and manuscript revisions. All other authors
453 provided data and contributed to manuscript revisions.

454 **Funding**

455 LH was funded by NERC QMEE CDT. EJB was funded by a BBSRC PhD studentship under
456 grant BB/F016581/1. LB was supported by the Scholarship Program of the German Federal
457 Environmental Foundation (Deutsche Bundesstiftung Umwelt, DBU, AZ 20014/302). AJC was
458 funded by the BBSRC and Syngenta UK as part of a case award PhD (grant no. 1518739).
459 AE was funded by the Swiss National Science Foundation (grant number 405940-115642).
460 DG and A-MK were funded by grant PCIN2014-145-C02-02 (MinECo; EcoFruit project
461 BiodivERsA-FACCE2014-74). MG was supported by Establishing a UK Pollinator Monitoring
462 and Research Partnership (PMRP) a collaborative project funded by Defra, the Welsh and
463 Scottish Governments, JNCC and project partners. GAdG was funded via research projects
464 BO-11-011.01-051 and BO-43-011.06-007, commissioned by the Dutch Ministry of
465 Agriculture, Nature and Food Quality. DK was funded by the Dutch Ministry of Economic
466 Affairs (BO-11-011.01-011). AK-H was funded by the NKFIH project (FK123813), the Bolyai
467 János Fellowship of the MTA, the ÚNKP-19-4-SZIE-3 New National Excellence Program of
468 the Ministry for Innovation and Technology, and together with RF by the Hungarian Scientific
469 Research Fund OTKA 101940. MM was funded by Waitrose & Partners, Fruition PO, and the
470 University of Worcester. MM was funded by grant INIA-RTA2013-00139-C03-01 (MinECo and
471 FEDER). BBP and RFS were funded by the UK Natural Environment Research Council as
472 part of Wessex BESS (ref. NE/J014680/1). NJV was funded by the Walloon Region (Belgium)
473 Direction générale opérationnelle de l'Agriculture, des Ressources naturelles et de
474 l'Environnement (DGO3) for the "Modèle permaculturel" project on biodiversity in micro-farms,
475 FNRS/FWO joint programme EOS — Excellence Of Science CliPS: Climate change and its
476 impact on Pollination Services (project 30947854)". CW was funded by the Deutsche
477 Forschungsgemeinschaft (DFG) (Project number 405945293). BW was funded by the Natural

478 Environment Research Council (NERC) under research programme NE/N018125/1 ASSIST
479 – Achieving Sustainable Agricultural Systems www.assist.ceh.ac.uk. TB and TO are
480 supported by BBSRC, NERC, ESRC and the Scottish Government under the Global Food
481 Security Programme (Grant BB/R00580X/1). MG and data collection was funded by Insect
482 Pollinators Initiative funded jointly by a grant from BBSRC, Defra, NERC, the Scottish
483 Government and the Wellcome Trust, under the Living with Environmental Change
484 Partnership and the Sustainable Management of Orchard Pollination Services Project.

485 **Acknowledgements**

486 Thank you to Jean-Marc Molenberg for assistance in field surveys and specimen curation for
487 the apple data collection in Belgium. Thanks to Ignasi Bartomeus for providing additional field
488 survey data. Also thank you to Samantha Ardin, D.A. Bond, Hannah Feltham, Harriet Griffin,
489 E.J.M. Kirby, Jean-Noel Tasei and Verena Riedinger for published crop field survey data that
490 were used in analyses.

491 Figure 1 – Crop map courtesy of Alice Haughan, University of Reading.

492 Figure 4 – Bee photographs courtesy of Nicolas J. Vereecken and Stéphane De Greef.

493

494 **References**

495 Abel, C.A., Wilson, R.L. and Luhman, R.L., 2003. Pollinating efficacy of *Osmia cornifrons*
496 and *Osmia lignaria* subsp. *lignaria* (Hymenoptera: Megachilidae) on three Brassicaceae
497 species grown under field cages. *Journal of Entomological Science*, 38(4), 545-552.

498 Ahrenfeldt, E.J., Klatt, B.K., Arildsen, J., Trandem, N., Andersson, G.K.S., Tschardtke, T., ...
499 and Sigsgaard, L., 2015. Pollinator communities in strawberry crops—variation at multiple
500 spatial scales. *Bulletin of Entomological Research*, 105(4), 497-506.

501 Aizen, M. A. and Harder, L. D., 2009. The global stock of domesticated honey bees is
502 growing slower than agricultural demand for pollination. *Current Biology*, 19, 915–918.

503 Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissiere, B.E., Woyciechowski, M.,
504 Krewenka, K.M., ... and Bommarco, R., 2014. Contribution of insect pollinators to crop yield
505 and quality varies with agricultural intensification. PeerJ, 2, 328.

506 Blitzer, E.J., Gibbs, J., Park, M.G. and Danforth, B.N., 2016. Pollination services for apple
507 are dependent on diverse wild bee communities. Agriculture, Ecosystems & Environment,
508 221, 1-7.

509 Bond, D.A. and Kirby, E.J.M., 1999. *Anthophora plumipes* (Hymenoptera: Anthophoridae) as
510 a pollinator of broad bean (*Vicia faba major*). Journal of Apicultural Research, 38(3-4), 199-
511 203.

512 Bossert, S., 2015. Recognition and identification of species in the *Bombus lucorum*-complex-
513 A review and outlook. bioRxiv, 011379.

514 Breeze, T.D., Vaissière, B.E., Bommarco, R., Petanidou, T., Seraphides, N., Kozák, L., ...
515 and Moretti, M., 2014. Agricultural policies exacerbate honeybee pollination service supply-
516 demand mismatches across Europe. PloS one, e82996.

517 Breeze T.D., Bailey A.P., Balcombe K.G., Brereton T., Comont R., Edwards M., ... and
518 Carvell C., 2020. Pollinator Monitoring More than Pays for Itself. Journal of Applied Ecology,
519 In Press

520 BWARS., 2020. Bees, Wasps & Ants Recording Society. <https://www.bwars.com/home>

521 Campbell, A. J., Wilby, A., Sutton, P. and Wäckers, F. L., 2017. Do sown flower strips boost
522 wild pollinator abundance and pollination services in a spring-flowering crop? A case study
523 from UK cider apple orchards. Agriculture, Ecosystems & Environment, 239, 20-29.

524 Carvell, C., Isaac, N., Jitlal, M., Peyton, J., Powney, G., Roy, D., ... and Roy, H., 2017.
525 Design and testing of a national pollinator and pollination monitoring framework. Technical
526 Report. Department for Environment, Food and Rural Affairs.

527 Catarino, R., Bretagnolle, V., Perrot, T., Vialloux, F. and Gaba, S., 2019. Bee pollination
528 outperforms pesticides for oilseed crop production and profitability. *Proceedings of the Royal*
529 *Society B*, 286 (1912), 20191550.

530 Dainese, M., Martin, E.A., Aizen, M., Albrecht, M., Bartomeus, I., Bommarco, R., ... and
531 Ghazoul, J., 2019. A global synthesis reveals biodiversity-mediated benefits for crop
532 production. *bioRxiv*, 554170.

533 Else, G.R., Bolton, B. and Broad, G.R., 2016. Checklist of British and Irish Hymenoptera-
534 aculeates (Apoidea, Chrysoidea and Vespoidea). *Biodiversity Data Journal*, 4.

535 Else, G.R. & Edwards, M., 2018. *Handbook of the Bees of the British Isles: Volume 2*. Ray
536 Society.

537 Fijen, T.P., Scheper, J.A., Boom, T.M., Janssen, N., Raemakers, I. and Kleijn, D., 2018.
538 Insect pollination is at least as important for marketable crop yield as plant quality in a seed
539 crop. *Ecology Letters*, 21 (11), 1704-1713.

540 Gardner, K.E. and Ascher, J.S., 2006. Notes on the native bee pollinators in New York apple
541 orchards. *Journal of the New York Entomological Society*, 114 (1), 86-91.

542 Gardner E., Breeze T.D., Clough Y., Smith H., Baldock K., Campbell A., ... and Oliver T.,
543 2020. Reliably Predicting Pollinator Abundance: Challenges of Process Based Ecological
544 Models; *Methods in Ecology and Evolution*, In Press

545 Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R.,
546 Cunningham, S.A., ... and Holzschuh, A., 2011. Stability of pollination services decreases
547 with isolation from natural areas despite honey bee visits. *Ecology Letters*, 14 (10), 1062-
548 1072.

549 Garibaldi, L.A., Bartomeus, I., Bommarco, R., Klein, A.M., Cunningham, S.A., Aizen, M.A.,
550 ... and Morales, C.L., 2015. Trait matching of flower visitors and crops predicts fruit set
551 better than trait diversity. *Journal of Applied Ecology*, 52, 1436-1444.

552 Garibaldi, L.A., Pérez-Méndez, N., Garratt, M.P., Gemmill-Herren, B., Miguez, F.E. and
553 Dicks, L.V., 2019. Policies for ecological intensification of crop production. *Trends in ecology*
554 & *evolution*, 34(4), pp.282-286.

555 Garratt, M.P., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., ... and
556 Potts, S.G., 2014a. The identity of crop pollinators helps target conservation for improved
557 ecosystem services. *Biological Conservation*, 169, 128-135.

558 Garratt, M.P., Breeze, T.D., Jenner, N., Polce, C., Biesmeijer, J.C. and Potts, S.G., 2014b.
559 Avoiding a bad apple: Insect pollination enhances fruit quality and economic value.
560 *Agriculture, ecosystems & environment*, 184, pp.34-40.

561 Garratt, M.P.D., Breeze, T.D., Boreux, V., Fountain, M.T., Mckerchar, M., Webber, S.M., ...
562 and Biesmeijer, J.C., 2016. Apple pollination: demand depends on variety and supply
563 depends on pollinator identity. *PloS one*, 11(5), e0153889.

564 Garratt, M.P.D., Potts, S.G., Banks, G., Hawes, C., Breeze, T.D., O'Connor, R.S. and
565 Carvell, C., 2019. Capacity and willingness of farmers and citizen scientists to monitor crop
566 pollinators and pollination services. *Global Ecology and Conservation*, 20, e00781.

567 Godfray, H. C. J. and Garnett, T., 2014. Food security and sustainable intensification.
568 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369, 20120273.

569 Grab, H., Branstetter, M.G., Amon, N., Urban-Mead, K.R., Park, M.G., Gibbs, J., ... and
570 Danforth, B.N., 2019. Agriculturally dominated landscapes reduce bee phylogenetic diversity
571 and pollination services. *Science*, 363(6424), 282-284.

572 Gresty, C.E., Clare, E., Devey, D.S., Cowan, R.S., Csiba, L., Malakasi, P., ... and Willis,
573 K.J., 2018. Flower preferences and pollen transport networks for cavity-nesting solitary bees:
574 Implications for the design of agri-environment schemes. *Ecology and evolution*, 8(5), 7574-
575 7587.

576 Hoehn, P., Tschardtke, T., Tylianakis, J.M. and Steffan-Dewenter, I., 2008. Functional group
577 diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society of London*
578 *B: Biological Sciences*, 275(1648), 2283-2291.

579 Horth, L. and Campbell, L.A., 2018. Supplementing small farms with native mason bees
580 increases strawberry size and growth rate. *Journal of Applied Ecology*, 55(2), 591-599.

581 IPBES., 2016. Deliverable 3a: Thematic assessment of pollinators, pollination and food
582 production.
583 http://www.ipbes.net/sites/default/files/downloads/pdf/3a_pollination_individual_chapters_20
584 [161124.pdf](http://www.ipbes.net/sites/default/files/downloads/pdf/3a_pollination_individual_chapters_20)

585 King, C., Ballantyne, G. and Willmer, P.G., 2013. Why flower visitation is a poor proxy for
586 pollination: measuring single-visit pollen deposition, with implications for pollination networks
587 and conservation. *Methods in Ecology and Evolution*, 4(9), 811-818.

588 Klein, A.M., Steffan-Dewenter, I. and Tschardtke, T., 2003. Fruit set of highland coffee
589 increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London*.
590 *Series B: Biological Sciences*, 270(1518), 955-961.

591 Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., ... and
592 Ricketts, T.H., 2015. Delivery of crop pollination services is an insufficient argument for wild
593 pollinator conservation. *Nature Communications*, 6, 7414.

594 Kleijn, D., Bommarco, R., Fijen, T.P., Garibaldi, L.A., Potts, S.G. and van der Putten, W.H.,
595 2019. Ecological intensification: bridging the gap between science and practice. *Trends in*
596 *ecology & evolution*, 34 (2), pp.154-166.

597 Kremen, C., Williams, N.M. and Thorp, R.W., 2002. Crop pollination from native bees at risk
598 from agricultural intensification. *Proceedings of the National Academy of Sciences*, 99(26),
599 16812-16816.

600 Kremen, C. and Chaplin-Kramer, R., 2007. Insects as providers of ecosystem services: crop
601 pollination and pest control. In: *Insect conservation biology: proceedings of the royal
602 entomological society's 23rd symposium*, 349-382, Wallingford, UK: CABI Publishing.

603 MacLeod, M., Reilly, J., Cariveau, D.P., Genung, M.A., Roswell, M., Gibbs, J. and Winfree,
604 R., 2020. How much do rare and crop-pollinating bees overlap in identity and flower
605 preferences? *Journal of Applied Ecology*, 57(2), 413-423.

606 Martins, K.T., Gonzalez, A. and Lechowicz, M.J., 2015. Pollination services are mediated by
607 bee functional diversity and landscape context. *Agriculture, Ecosystems &
608 Environment*, 200, 12-20.

609 Michener, C.D., 2000. *The bees of the world* (Vol. 1). JHU press.

610 O'Connor, R.S., Kunin, W.E., Garratt, M.P., Potts, S.G., Roy, H.E., Andrews, C., ... and
611 Morris, R.K., 2019. Monitoring insect pollinators and flower visitation: the effectiveness and
612 feasibility of different survey methods. *Methods in Ecology and Evolution*, 10(12), 2129-
613 2140.

614 Oliver, T.H., Heard, M.S., Isaac, N.J., Roy, D.B., Procter, D., Eigenbrod, F., ... and Proença,
615 V., 2015. Biodiversity and resilience of ecosystem functions. *Trends in Ecology &
616 Evolution*, 30(11), 673-684.

617 Ollerton, J., 2017. Pollinator diversity: distribution, ecological function, and conservation.
618 *Annual Review of Ecology, Evolution, and Systematics*, 48, 353-376.

619 Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.L. and Bretagnolle, V., 2018. Bees increase
620 oilseed rape yield under real field conditions. *Agriculture, Ecosystems & Environment*, 266,
621 39-48.

622 Polce, C., Termansen, M., Aguirre-Gutiérrez, J., Boatman, N.D., Budge, G.E., Crowe, A., ...
623 and Somerwill, K.E., 2013. Species distribution models for crop pollination: a modelling
624 framework applied to Great Britain. *PloS one*, 8(10), e76308.

625 Polce, C., Garratt, M.P., Termansen, M., Ramirez-Villegas, J., Challinor, A.J., Lappage,
626 M.G., ... and Somerwill, K.E., 2014. Climate-driven spatial mismatches between British
627 orchards and their pollinators: increased risks of pollination deficits. *Global Change Biology*,
628 20(9), 2815-2828.

629 Powney, G.D., Carvell, C., Edwards, M., Morris, R.K., Roy, H.E., Woodcock, B.A. and Isaac,
630 N.J., 2019. Widespread losses of pollinating insects in Britain. *Nature Communications*,
631 10(1), 1018.

632 Rader, R., Howlett, B.G., Cunningham, S.A., Westcott, D.A. and Edwards, W., 2012. Spatial
633 and temporal variation in pollinator effectiveness: do unmanaged insects provide consistent
634 pollination services to mass flowering crops? *Journal of Applied Ecology*, 49(1), 126-134.

635 Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P., Howlett, B.G., Winfree, R., ... and
636 Bommarco, R., 2016. Non-bee insects are important contributors to global crop pollination.
637 *Proceedings of the National Academy of Sciences*, 113(1), pp.146-151.

638 Reilly, J.R., Artz, D.R., Biddinger, D., Bobiwash, K., Boyle, N.K., Brittain, C., ... and Ellis,
639 J.D., 2020. Crop production in the USA is frequently limited by a lack of pollinators.
640 *Proceedings of the Royal Society B*, 287(1931), p.20200922.

641 Russo, L., Park, M.G., Blitzer, E.J. and Danforth, B.N., 2017. Flower handling behavior and
642 abundance determine the relative contribution of pollinators to seed set in apple
643 orchards. *Agriculture, Ecosystems & Environment*, 246, 102-108.

644 Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G. and Kleijn,
645 D., 2013. Environmental factors driving the effectiveness of European agri-environmental
646 measures in mitigating pollinator loss—a meta-analysis. *Ecology Letters*, 16(7), 912-920.

647 Senapathi, D., Biesmeijer, J.C., Breeze, T.D., Kleijn, D., Potts, S.G. and Carvalheiro, L.G.,
648 2015. Pollinator conservation—the difference between managing for pollination services and
649 preserving pollinator diversity. *Current Opinion in Insect Science*, 12, 93-101.

650 Settele, J., Bishop, J. and Potts, S.G., 2016. Climate change impacts on pollination. *Nature*
651 *Plants*, 2(7),16092.

652 Soroye, P., Newbold, T. and Kerr, J., 2020. Climate change contributes to widespread
653 declines among bumble bees across continents. *Science*, 367(6478), 685-688.

654 Sutter, L., Jeanneret, P., Bartual, A.M., Bocci, G. and Albrecht, M., 2017. Enhancing plant
655 diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating
656 bees through complementary increase in key floral resources. *Journal of Applied*
657 *Ecology*, 54(6),1856-1864.

658 Tonietto, R.K. and Larkin, D.J., 2018. Habitat restoration benefits wild bees: A meta-
659 analysis. *Journal of Applied Ecology*, 55(2), 582-590.

660 Vanbergen, A.J., Heard, M.S., Breeze, T., Potts, S.G. and Hanley, N., 2014. Status and
661 value of pollinators and pollination services. <http://nora.nerc.ac.uk/id/eprint/505259/>

662 Vázquez, D.P., Morris, W.F. and Jordano, P., 2005. Interaction frequency as a surrogate for
663 the total effect of animal mutualists on plants. *Ecology Letters*, 8(10), 1088-1094.

664 Webb, J., Heaver, D., Lott, D., Dean, H.J., van Breda, J., Curson, ... and Foster, G., 2018.
665 Pantheon - database version 3.7.6. <https://www.brc.ac.uk/pantheon/>

666 Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., ... and
667 Vaissière, B.E., 2008. Measuring bee diversity in different European habitats and
668 biogeographical regions. *Ecological Monographs*, 78(4), 653-671.

669 Winfree, R., W. Fox, J., Williams, N.M., Reilly, J.R. and Cariveau, D.P., 2015. Abundance of
670 common species, not species richness, drives delivery of a real-world ecosystem
671 service. *Ecology letters*, 18(7), 626-635.

672 Winfree, R., Reilly, J.R., Bartomeus, I., Cariveau, D.P., Williams, N.M. and Gibbs, J., 2018.
673 Species turnover promotes the importance of bee diversity for crop pollination at regional
674 scales. *Science*, 359(6377), 791-793.

675 Wolf, S., Rohde, M. and Moritz, R.F., 2010. The reliability of morphological traits in the
676 differentiation of *Bombus terrestris* and *B. lucorum* (Hymenoptera:
677 Apidae). *Apidologie*, 41(1), 45-53.

678 Wood, T.J., Holland, J.M., Hughes, W.O. and Goulson, D., 2015a. Targeted agri-
679 environment schemes significantly improve the population size of common farmland
680 bumblebee species. *Molecular Ecology*, 24(8), 1668-1680.

681 Wood, T.J., Holland, J.M. and Goulson, D., 2015b. Pollinator-friendly management does not
682 increase the diversity of farmland bees and wasps. *Biological Conservation*, **187**, pp.120-
683 126.

684 Wood, T.J., Holland, J.M. and Goulson, D., 2016a. Providing foraging resources for solitary
685 bees on farmland: current schemes for pollinators benefit a limited suite of species. *Journal*
686 *of Applied Ecology*, 54(1),323-333.

687 Wood, T.J., Holland, J.M. and Goulson, D., 2016b. Diet characterisation of solitary bees on
688 farmland: dietary specialisation predicts rarity. *Biodiversity and Conservation*, 25(13), 2655-
689 2671.

690 Woodcock, B.A., Edwards, M., Redhead, J., Meek, W.R., Nuttall, P., Falk, S., ... and Pywell,
691 R.F., 2013. Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural
692 differences and diversity responses to landscape. *Agriculture, Ecosystems &*
693 *Environment*, 171, 1-8.

694 Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J., ...
695 and Jauker, F., 2019. Meta-analysis reveals that pollinator functional diversity and abundance
696 enhance crop pollination and yield. *Nature Communications*, 10(1) 1-10.

697 Wratten, S.D., Gillespie, M., Decourtye, A., Mader, E. and Desneux, N., 2012. Pollinator
698 habitat enhancement: benefits to other ecosystem services. *Agriculture, Ecosystems &*
699 *Environment*, 159, pp.112-122.