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Using ecological and field survey data to establish a national list of the wild bee pollinators of crops.

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69 Abstract

The importance of wild bees for crop pollination is well established, but less is known about 70 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 substantial variation in the bee communities of different crops. Establishing a national list of 81 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 would also benefit from targeting specific species to enhance crop pollination services to 87 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.

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91 Key-words

92 Agri-environment Schemes, Apple, Biodiversity, Crop pollination, Dominant Pollinators,

93 Ecosystem Services, Field Bean, Oilseed Rape, Rare Species, Strawberry.

95 **1. Introduction**

96 Insect pollination is key to global agricultural productivity (IPBES, 2016) due to growing demand for entomophilous crops (Godfray and Garnett 2014). The nutritional and economic 97 importance of insect pollinated crops (Vanbergen et al., 2014), and the inability of managed 98 pollinators (e.g., Apis mellifera) to meet service demand, mean agriculture is highly dependent 99 upon wild pollinators (Aizen and Harder 2009; Breeze et al., 2014). Yet conventional 100 agricultural practices are a key driver of pollinator declines (Senapathi et al., 2015). Whilst 101 agri-environment scheme options have had positive impacts (Tonietto et al., 2018), most 102 103 benefit a limited suite of common species (Scheper et al., 2013) and homogeneous communities provide less reliable pollination services (Grab et al., 2019). Currently agri-104 environment schemes tend preferentially to benefit bumblebee populations (Wood et al., 105 106 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 against declines in other species, would help inform agricultural management for bee 110 111 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 a 'national list' of crop pollinators to advise management or monitoring programmes. 113

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 management that only targets common crop pollinators will not safeguard production if it fails 119 120 to encompass species that supplement service provision (Fijen et al., 2018). High species turnover means that diverse communities, including rare and specialist species, are required 121

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 species visiting four crops: apple (Malus domestica), field bean (Vicia faba), oilseed rape 132 133 (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 et al., 2014a). We use sites in Great Britain as a case study because its bee fauna is 137 comprehensively described and their occupancy is well recorded over a long time period 138 139 (Powney et al. 2019). We compiled a list of all British bee species and their available physiological and ecological traits, and combined it with field survey data in order to devise an 140 approach to generate lists of (i) definite flower visitors to each crop (ii) likely flower visitors, 141 which are expected to also contribute to crop pollination (iii) possible crop flower visitors whose 142 contribution to pollination is not well understood and merits further investigation. Our aim was 143 to compile these lists for reference purposes, but not to statistically compare pollinator 144 communities between crops, due to the unstandardised nature of the datasets used to 145 146 generate the lists of bee species. Additionally, we identify dominant crop pollinating species, and asses the contribution of wild bees compared to honey bees for crop flower visitation. 147

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149 **2. Materials and Methods**

150 **2.1 Potential crop pollinators.**

First, a species database of all extant, resident wild bee species in Great Britain was 151 152 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 visited for pollen and/or nectar), tongue length (short/long), geographic coverage (distribution 155 156 and habitat) (based on trait information compiled by Stuart Roberts for the EU- FP6 ALARMproject and BWARS, 2020) and conservation status (Webb et al., 2018). Potential crop 157 158 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 specialists that are not coincident with cropland were initially excluded i.e., primarily coastal, 160 161 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 target crop or polylectic, but not documented as foraging on the relevant plant family for pollen 163 or nectar and species whose flight period does not overlap with the relevant crops flowering 164 period were excluded. For field bean, only 'long-tongued' species (Michener, 2000) were 165 166 considered as its flowers have deep corollas and most visits by 'short-tongued' species involve nectar robbing rather than legitimate visitation (Garratt et al., 2014a). 167

168 2.2 Field survey data

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



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:

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 for181 species sampled in British pan traps only).

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

188 **2.3 Crop flower visitors**

The lists of potential crop pollinators were combined with the field survey data to categorize
bee species into one of three flower visitor categories (Figure 2; Full details in Supplementary
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.
- iii) Possible Flower Visitors Species only recorded in British pan trap studies, or in
 other European flower visitor studies only, and classified as a potential crop
 flower visitor.
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Figure 2: Methodology by which bee species were categorised as definite, likely and possible flower visitors.

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207 2.4 Dominant crop flowers visitors

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

217 **3. Results**

218 **3.1 Potential crop pollinators**

A preliminary list of 229 extant, resident British wild bee species was compiled. Of those 132 219 220 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 separating their workers in the field (Wolf et al., 2010; Bossert, 2015). Therefore, a total of 97 223 species were initially identified as potential crop pollinators. Accounting for their documented 224 225 foraging ecology and flight period, the following number of species were considered as potential pollinators per crop: apple- 83, bean- 30, oilseed- 60, and strawberry - 90 (Table 226 S2). 227

228 3.2 Field survey data

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

232 3.3 Crop flower visitors

Seventy-three species from ten genera where categorised as flower visitors of one or more 233 crops, 63 of which were recorded in British crop field studies (Table 1, Figure 3). Fourteen 234 species were included in flower visitor categories that were not initially identified as potential 235 crop pollinators. Ten of those were widely polylectic Bombus or Lasioglossum species, all 236 recorded in oilseed datasets, but not documented in the literature as foraging on 237 Brassicaceae. The remaining species were three short-tongued Andrena species recorded 238 239 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

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

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Table 1: Number of bee species, based upon field datasets and trait information, that were

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assigned to each category of flower visitor per crop

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

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253 Apple

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

261 Bean

Three of the five British bean flower visitor studies recorded all bee to species level, the remainder only recorded *Bombus* to species, which was both the most common genus overall (n=9) and in the definite flower visitor category (n=7). Three short-tongued *Andrena* sp. were identified as definite flower visitors, but all were recorded as very low numbers of flower visits (≤10). Four *Bombus* species and *Anthophora plumipes* accounted for 95% of all visits recorded in British flower visitation studies. However, all the *A. plumipes* records derived from one study (Bond and Kirby, 1999) carried out at a single site. The four *Bombus* were the only species recorded in four or more studies. No species met the criteria for the likely flower visitor 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 bee, both overall (n=27) and within the definite flower visitor category (n=15). Bombus and 274 275 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 80% of recorded flower visits were attributed to six species, only two of which were recorded 277 278 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 guantified in all field studies. The likely and possible visitor categories were entirely comprised of Andrena or 280 Halictidae species, two of which are oligolectic on Brassicaceae. 281

282 Strawberry

Two British strawberry flower visitor studies recorded all bees to species level. The remaining 283 284 three only recorded a group of large Andrena and Bombus to species. Bombus species were the most common genus of bee within the definite flower visitor category (n=5), but joint 285 286 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. The likely visitor category was almost exclusively represented by Andrena species. The 290 possible visitor category was largely comprised of solitary bees from five different genera. 291



Figure 3: The number of bee species from each genus which were categorised as definite likely or possible flower visitors per crop

3.4 Dominant crop flower visitors

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

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Figure 4: Dominant crop visiting bee species (attributed with ~80% of flower visits in field studies per crop) shown as photographs, with

number of bee species in each genus that are 'definite' flower visitors for each crop.

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

339 Our results also support prior evidence of distinct differences in individual crop pollinator communities (Garratt et al., 2014a). The overwhelming majority of field bean and strawberry 340 flower visits were attributed to bumblebees. However, whereas field bean was visited by the 341 342 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 trait matching of bees and flowers in crop pollination (Garibaldi et al., 2015). Bombus species 344 were also recorded visiting apple and oilseed rape. However, due to their low abundance in 345 346 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 resources used by common and rare crop pollinators (Sutter et al., 2017; MacLeod et al., 365 2020), and thus there are opportunities to promote both biodiversity and conservation in 366 agricultural landscapes. 367

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

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

376 Identifying specific bee crop pollinating species, as we have done, can inform refinements to agri-environment schemes to promote more biodiverse communities in agricultural 377 landscapes. For example, Andrena were the most speciose genus of bees identified across 378 flower visitor categories in three of the crops. Currently European agri-environment measures 379 to boost pollinator populations have focused on the creation of flower-rich habitats, including 380 wildflower buffer strips (Wratten et al., 2012). Yet evidence suggests these are primarily visited 381 382 by bumblebees, with solitary bees preferring non-sown, wild plants (Wood et al., 2015). In apple orchards for example, early-flying Andrena species have been positively associated with 383 dandelions (Taraxacum agg.) rather than sown species, which often bloom later than apple 384 385 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 dead wood, around crop areas would provide both forage and nesting resources (Else and 394 Edwards 2018; Gresty et al., 2018) for these and other cavity nesting bees. Future 395 management to support long-tongued solitary bees could benefit field bean pollination. 396 Anthophora plumipes, for example, prefers to nest in vertical soil profiles, which are not 397 398 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 from the genera Bombus and Andrena. Small and inconspicuous species, particularly from 410 the genus Lasioglossum, were often only extensively sampled in the pan trap surveys. 411 412 Additionally, whilst the visitation rate of dominant species is strongly correlated to pollination service delivery (Winfree et al., 2015; Fijen et al., 2018), the assumption here and elsewhere 413 that quantitative visitation data can be used to infer pollination (Kleijn et al., 2015), neglects to 414 factor in that flower visitation alone is not a perfect proxy for pollination (King et al., 2013; 415 416 Senapathi et al., 2015; Ollerton, 2017). Certain physiological and behavioural traits also influence pollination service delivery (Martins et al., 2015). Further detailed data and research 417 is required before any definitive conclusions can be made about the contributions of individual 418 bee species to crop pollination. 419

420 **5. Conclusions**

Given the importance of wild pollinators and the detrimental impacts of conventional agriculture on their populations it is unsurprising that the management of wild and managed pollinating insects is considered a critical step for future food security (Garibaldi et al., 2019; Kleijn et al., 2019; Rollin and Garibaldi et al., 2019; Reilly et al., 2020). Yet information on which species contribute most to ecosystem service delivery has long been elusive (Kremen 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 specialised ones, may contribute to crop pollination (Klein et al., 2003; Sutter et al., 2017; 432 433 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 (Sorove et al., 2020) and create spatial mismatches between crops and their pollinators, which could exacerbate existing pollination deficits (Polce et al., 2014). To that end, the species 437 438 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 interventions and consider a broader range of species to safeguard the ecosystem service of 445 446 crop pollination in an uncertain future.

447 Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personalrelationships 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.

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