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6		threats to wild insect pollinators			
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51	Contents	
52	1. Importance of Insect Pollination	3
53	1.1 Providing an Ecosystem Service	3
54	1.2 Brief Introduction to Pollination Ecology and the Importance of Wild	
55	Pollinators	8
56	2. Major Threats to the Pollination Service Provided by Insects	13
57	3. Steps in the Right Direction to Protect Insect Pollinator Services: Policy Actions	19
58	4. Understanding and Mitigating Specific Threats to Wild Insect Pollinators to Protect	
59	Pollinator Services	21
60	4.1 Understanding the Stability of Insect Pollinator Communities	22
61	4.2 Using Molecular Approaches to Monitor Insect Pollinators	24
62	4.3 How Do Parasites Shape Wild Insect Pollinator Populations?	29
63	4.4 Understanding Insect Pollinator Population Responses to Resource Availability	31
64	4.5 Engineering Flowering Field Margins as Habitats to Attract Insect Pollinators	35
65	4.6 How Might We Improve the Wider Countryside to Support Insect Pollinators	39
66	4.7 Insect Pollinators in Urban Areas	41
67	5. Considerations When Developing Future Research and Mitigation Strategies	45
68	Acknowledgements	47
69	Appendix	48
70	References	52
71		

- 72 Abstract
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74 Insect pollination constitutes an ecosystem service of global importance, providing 75 significant economic and aesthetic benefits as well as cultural value to human society, 76 alongside vital ecological processes in terrestrial ecosystems. It is therefore important to 77 understand how insect pollinator populations and communities respond to rapidly changing 78 environments if we are to maintain healthy and effective pollinator services. This paper 79 considers the importance of conserving pollinator diversity to maintain a suite of functional 80 traits to provide a diverse set of pollinator services. We explore how we can better understand 81 and mitigate the factors that threaten insect pollinator richness, placing our discussion within 82 the context of populations in predominantly agricultural landscapes in addition to urban 83 environments. We highlight a selection of important evidence gaps, with a number of 84 complementary research steps that can be taken to better understand: i) the stability of 85 pollinator communities in different landscapes in order to provide diverse pollinator services; 86 ii) how we can study the drivers of population change to mitigate the effects and support 87 stable sources of pollinator services; and, iii) how we can manage habitats in complex 88 landscapes to support insect pollinators and provide sustainable pollinator services for the 89 future. We advocate a collaborative effort to gain higher quality abundance data to 90 understand the stability of pollinator populations and predict future trends. In addition, for 91 effective mitigation strategies to be adopted, researchers need to conduct rigorous field-92 testing of outcomes under different landscape settings, acknowledge the needs of end-users 93 when developing research proposals and consider effective methods of knowledge transfer to 94 ensure effective uptake of actions.

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## 1. Importance of insect pollination

- 98
- 99 1.1 Providing an ecosystem service
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101 Insects show an astonishing taxonomic diversity and are abundant in almost all 102 environments across the globe (ca. 1 million described species, with an estimated >4 million 103 undescribed; Stork et al., 2015). Their importance for the functioning of ecosystems cannot 104 be overstated, contributing to fundamental ecosystem processes including soil turnover, 105 decomposition and nutrient cycling, and play key roles in local food webs (Schwartz et al., 106 2000). These processes have direct implications for human welfare by providing critical 107 'ecosystem services', which were defined by Fisher and colleagues as "the aspects of 108 ecosystems utilized (actively or passively) to produce human well-being" (Fisher et al., 2009: 109 modified from Boyd and Banzhaf 2007). For example, predatory and parasitoid insects play 110 the role of natural enemies of pest herbivores and so help to control the pests of agricultural 111 crops grown to feed the human population.

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113 Of the multiple roles that insects play, pollinating flowering plants is a process that is 114 of the upmost importance in terrestrial environments and one which provides vital ecosystem services for human wellbeing (Carpenter et al., 2006; Garibaldi et al., 2011a, 2014). Over 115 116 85% of described flowering plant species are dependent, to some degree, on animal 117 pollination (Ollerton et al., 2011), with mobile foraging insects accounting for the vast 118 majority of this activity (Kremen et al., 2007). Insect pollination maintains genetic diversity 119 in plant populations (Kearns et al., 1998), and provides advantages such as increased fruit 120 quality and quantity, and seed production and fertility, leading to greater vigour of the next generation (Albrecht et al., 2012; Barrett, 2003). Thus, ecologically, insect pollination is 121

crucial in sustaining diverse and healthy populations of wild plants and this in turn underpins trophic networks (Memmott, 1999). Insect pollination also has high economic value to humans (Allsopp et al., 2008, Hein, 2009; Palomo et al., 2015; Winfree et al., 2011b), significantly increasing the yield and health of cultivated crops (see Table 1), placing the value of insect pollination for world agriculture >  $\in$ 150bn (Gallai et al., 2009; Lautenbach et al., 2012), as well as being of high aesthetic and cultural value through supporting florally diverse landscapes (Lovell and Sullivan, 2006; Wratten et al., 2012).

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130 A growing global human population (9bn by 2050) and increases in the average 131 calorific intake per person, places rising demands for food security under rapidly changing 132 environments (Godfray et al., 2010). As much as 75% of agricultural crop species are, to 133 some degree, reliant on animal pollination (Table 1), with the suggestion that a complete loss 134 of this service could reduce yields by ca. 40% and 16% for fruit and vegetables, respectively 135 (Klein et al., 2007). Furthermore, most lipids and micronutrients important for the human diet 136 and public health are obtained from plants requiring animal pollination (Chaplin-Kramer et 137 al., 2014; Eilers et al., 2011). With insects constituting the vast majority of animal 138 pollination, we should recognise our duty to help maintain sustainable and healthy insect 139 pollinator populations and take full advantage of this 'free' ecosystem service effectively. 140 Reports of insect pollinator declines in many parts of the world suggest, however, that we 141 may not have lived-up to this responsibility (see section 2) increasing the risk of future 142 pollination deficits in areas requiring high, and increasing, pollination demands (Aizen et al., 143 2008a; Aizen and Harder, 2009; Lautenbach et al., 2012; Polce et al., 2014).

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Areas experiencing drastic transitions in land-use from natural habitats to large scale intensive agriculture, may find that native resident pollinators are unable to provide the level 147 Table 1. Selected recent studies showing the effects of wild or managed pollinators on commercially important crops. Studies consist of reviews 148 of primary literature that present an overview of the global picture (1-3) and recent studies showing experimental manipulations that did not 149 focus exclusively on honeybees (4-9). Pollinators were either allowed open access to inflorescence (OP) or excluded while still allowing wind 150 and self-pollination (WS) to occur. The studies were chosen as examples and the table is not an exhaustive coverage of the literature.

	Major insect pollinator(s)	Plant host(s)	Quality measure(s)	Description	Authors
1	Various	Various	Various	Review of 252 crop species showing that majority of important crops benefit from animal (overwhelmingly insect) pollination by increasing either seed production, fruit set or fruit number	(Klein et al., 2007)
2	Apis mellifera, Various	Various	Fruit set	Study of 41 global crop systems, showing general trend for i) fruit set to increase with visitations from wild pollinators, ii) magnitude of increase in fruit set to be significantly greater for plants visited by wild pollinators relative to honeybees.	(Garibaldi et al., 2013)
3	Various	Various	Economic impact	Review of 90 studies of crop visiting pollinators using data from 1394 global field sites, concluding that crop visits from bees provided pollination service that contributed ca. \$3,251ha <sup>-1</sup>	(Kleijn et al., 2015)
4	Apis mellifera, Bombus spp. Hoverflies	Oilseed rape (Brassica napus)	Seed set, seed quality, market value	Experimental manipulation using ten spring oilseed rape (canola) fields that were either OP or WS, showing OP comparatively increased seed weight and quality but had no effect on seed set (estimated increase in market value of crop by ca. 20%).	(Bommarco et al., 2012b)
5	Various	Gala & Cox Apple (Malus domestica)	Fruit set, seed set, fruit quality, economic impact	Experimental manipulation of pollination across six orchards in two commercial apple varieties. OP treatment produced significant increase in fruit set and seed number compared to WS (economic benefits ca. £11,900 and £14,800ha <sup>-1</sup> for Cox and Gala varieties respectively).	(Garratt et al., 2014a)
6	<i>Apis mellifera,</i> Wild bees Hoverflies	Blueberry ( <i>V. corymbosum</i> )	Fruit set, seed set, fruit weight	Experimental manipulation using ten paired sites with either wildflower planted (WF) or mowed field (MF) margins across four years. WF increased fruit set, average berry weight and seed set but for only 3 of 4 years after planting; increase corresponded to increase in abundance of wild bees and hoverflies in same years.	(Blaauw and Isaacs, 2014a)
7	Apis mellifera, Osmia bicornis	Strawberry (Fragaria x ananass)	Fruit set, fruit weight, Economic value	Experimental manipulation of ten plots in areas with established communities of commercially available pollinators. Inflorescences receiving OP produced higher prop. of marketable fruit, higher fruit weight and longer shelf life compared with WS (increased commercial value per fruit by 38.6%).	(Klatt et al., 2014)
8	Apis mellifera, Bombus spp.	Field bean ( <i>Vicia faba</i> )	Seed set, Seed weight	Experimental manipulation at 10 sites, with OP produced twice the seed and contained beans that were approximately 9% heavier than the WE treatment	(Nayak et al., 2015)
9	Apis mellifera Various	Apple ( <i>M. domestica</i> )	Fruit set	Study of 47 orchards with managed honeybee colonies either present or absent, reporting proportion of fruit set was higher in OP compared to WS. Fruit set was not significantly affected by honeybee presence but did increase with wild bee species richness.	Mallinger and Gratton (2015)

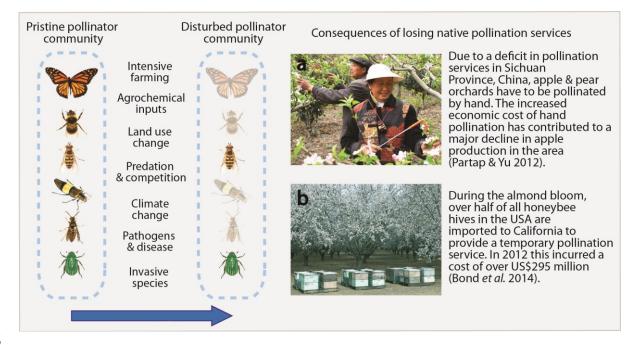
151 of pollination service required (Astegiano et al., 2015; Klein et al., 2012; Kremen et al., 2002, 152 2004). For example, in the state of California, USA, half of the country's domesticated 153 honeybee hives are transported to the region to pollinate large scale cultivations (such as 154 Almonds: Aizen and Harder, 2009), a tactic similarly adopted by other countries across the 155 globe (Crane, 1990; Klein et al., 2007; Palomo et al., 2015). In the apple and pear orchards of 156 the Sichuan province of China, apparent reductions in wild bee populations, have led to a 157 dependency on flowers having to be pollinated by hand (Figure 1; Partap & Partap, 2002; 158 Partap and Ya, 2012). Instead of receiving a free and rapid pollination service from a healthy 159 insect community (Morandin and Winston, 2006), it has been replaced by comparatively 160 expensive human labour. Apple and pear cultivation in the area has now declined 161 significantly (Partap and Ya, 2012), and it thus seems that in the long-term, crops which are 162 less dependent on insect pollinators (such as plum, loquat, walnut, and other cereal crops), 163 will be grown instead. Such action may only exacerbate the problem to local insect pollinator 164 populations as this could further reduce nutritional resource availability in those landscapes, 165 especially as many self-compatible plants produce low (or zero) nectar content and can produce less nutritious pollen that may also be harder for insects to collect (Zimmerman, 166 167 1988; Johnson & Bond, 1997).

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### 169 **1.2 Brief introduction to pollination ecology and the importance of wild pollinators**

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171 Many angiosperm species possess relatively open flower morphologies, allowing a 172 range of insect pollinator species access to the nectar and pollen rewards within. Such plant-173 pollinator mutualisms are often generalised involving many species interactions (Willmer, 174 2011). Whilst the dynamics of mutualistic networks can be relatively complex, we can make 175 the broad theoretical prediction that generalist species may be more resistant to



177 Figure 1| Combined and interactive set of environmental stressors can threaten pollinator 178 communities. Persistently induced stress may lead to pollinator population declines resulting 179 in the composition and stability of pollinator communities to be affected with potential loss of 180 species richness and reduced pollination insurance. Loss of pollinator services can impact on human welfare in many ways, but a major concern is that native resident pollinator 181 182 communities are no longer able to keep-up and meet demands leading to ineffective pollination of agricultural crops and wildflowers. For example, inadequate local pollination 183 184 services have led to the implementation of extreme measures, including costly replacement 185 by: a) employing human labour to hand pollinate flowers (Partap and Yu, 2012; photo taken 186 and provided with permission by Uma Partap), or b) manage domesticated pollinators such as honeybees (Bond et al., 2014). Many insect taxa constitute a pollinator community all of 187 188 which visit flowers for nectar and pollen rewards, but certain Orders constitute the vast 189 majority of insects providing a pollination service: the Coleoptera (beetles), Diptera (flies), 190 some Hemiptera (true bugs), Hymenoptera (bees, many wasps & some ants), Lepidoptera 191 (butterflies & moths) and Thysanoptera (thrips).

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196 environmental perturbations, depending on its extent, and their presence may contribute to 197 greater redundancy in pollination function and community resilience to global change 198 (Astegiano et al., 2015; Lever et al., 2014). For example, if environmental changes extirpate 199 or reduce the abundance of the primary pollinator of a plant, or vice versa, then other 200 generalist species depending on their functional traits may be able to fulfil the role of 201 mutualist by engaging in flower visits (Figure 2; Aizen et al., 2012; Ashworth et al., 2015; 202 Burkle et al., 2013; Memmott et al., 2004; Mitchell et al., 2009b; Waser et al., 1996; but see 203 Kaiser-Bunbury et al., 2010; Winfree et al., 2014). Communities of generalist species, 204 sharing similar functional traits, may have high inter-specific competition between pollinators 205 for shared floral resources or between plants for pollinator functional groups (Johnson and 206 Steiner, 2000; Mitchell et al., 2009a; Rosas-Guerrero et al., 2014; Figure 2), especially under 207 scenarios of declining wildflower or pollinator populations (see sections 2 & 4). There is, 208 however, some evidence from empirical data coupled with simulation modelling that 209 increased network nestedness (high fraction of shared interactions) may facilitate an increase 210 in the number of species constituting the community (Bastolla et al., 2009; Lever et al., 211 2014). In contrast, some plant species have floral traits that have co-evolved to be 212 specifically adapted to the feeding apparatus of one or a minority of insect pollinator species, 213 thereby representing a relatively exclusive mutualism. For example, the secretion of nectar at 214 the base of a deep corolla or spur is associated with visitation by long-tongued insects (Arditti 215 et al., 2012), or flowers whose anthers require pollen release by vibration (sonication) are 216 pollinated by insects whose thoracic flight muscles can vibrate at an appropriate resonant 217 frequency – process known as buzz pollination (De Luca and Vallejo-Marin, 2013).

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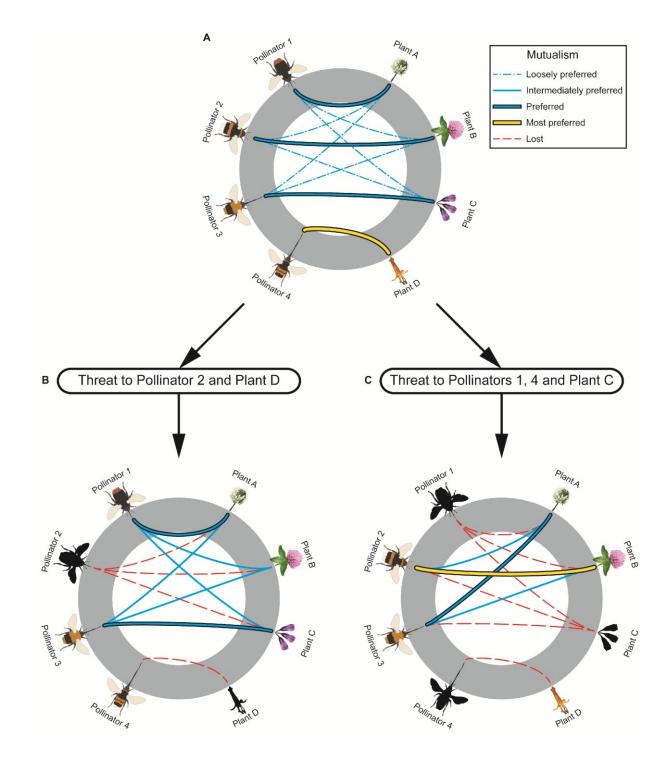


Figure 2| Simplified and hypothetical plant-pollinator network, showing a community of four insect pollinator species and four flowering plant species and the potential consequences of localised species extinction(s) to network structure. Scenario A) Pollinators 1-3 and plants A-C show a generalist mutualism, where each pollinator and plant has a preferred relationship (shown by line thickness and colour), but will also visit / receive other inter-specifics to subsidise their nectar or pollen intake / pollen transport. The strength of the mutualism may be dependent on pollinator competition, for instance: pollinator 1 has a preference for plant A 229 and can theoretically competitively exclude (to some degree) pollinators 2 and 3 from visiting 230 plant A (Brosi and Briggs, 2013; Sauve et al., 2014). Pollinator 4 has a longer tongue 231 compared to the other pollinators, and a specialised mutualism with plant D with no 232 competition from the other pollinators as they are unable to reach the nectar reward at the 233 base of plant D's long corolla. Thus, pollinator 4 has a high preference, or dependency, on 234 plant D. Scenario B) Loss of pollinator 2 (i.e. local extinction) changes the preference (or 235 dependency) of the other two pollinators due to competitor release: plant B receives higher 236 visitation rates from pollinator 1 and 3 compared to when pollinator 2 was previously present. 237 This shows that the generalist network has a level of redundancy where other pollinators with 238 similar functional traits (i.e. tongue length) can fill the role of pollinator 2 and maintain a 239 population of plant B in the community an example of network re-wiring. In contrast, loss of 240 plant D is likely to affect pollinator 4 more significantly, and dependent on the ability to visit 241 short corolla flowers, will reduce population size, showing there is lower redundancy in this 242 specialist network. Scenario C). If pollinator 4 were to be lost this would cause localised 243 extinction of plant D. Loss of pollinator 1 will cause competitive release for pollinators 2 and 244 3, but with loss of plant D, it will likely change preferences (or dependency) for plant A and 245 B as well. It will likely strengthen the preference between pollinator 2 and plant B as less 246 floral resources are available. Pollinator 3 will have to change its preference to plant A as it 247 will encounter high competitive exclusion when visiting plant B.

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249 Having numerous specialist mutualisms within a plant-pollinator community, 250 whereby the plant and pollinator are specialised on each other (and interact with fewer other 251 species) may increase overall functional trait diversity. However, this may result in low 252 functional redundancy at the community network level due to a lack of substitutable species 253 traits or, in other words, there are a small number of pollinators and/or plant species 254 possessing compatible functional traits to fill the functional gap should either mutualist 255 decline (Figure 2; Mouillot et al., 2013; Weiner et al., 2014). The spectrum of interactions 256 spanning generalist to specialist interactions is important in determining how some plant-257 pollinator relationships remain relatively stable under environmental change, whilst others 258 may not (Burkle and Alarcon, 2011; Burkle et al., 2013; Dalsgaard et al., 2013). Moreover,

when floral resources are limited generalist species may gradually replace specialists due to their ability to forage on a range of resources (Carre et al., 2009; Scheper et al., 2014; Waser et al., 1996). At a habitat scale, we would expect maintenance of pollinator species richness to be linked to maintenance of high floral trait diversity, and vice versa. This highlights the importance of conserving bio-diverse habitats to maintain ecosystem functioning and importantly the provision of ecosystem services (Balvanera et al., 2006; Bartomeus et al., 2013; Cardinale et al., 2006; Daily, 1997).

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267 Bees are frequent and effective pollinators of wildflowers and agricultural crops 268 (Kleijn et al., 2015). Social bees (e.g. honeybees, bumblebees, stingless bees), in particular, 269 have become a focus of insect pollinator studies, in which the numerical abundance of 270 workers per colony make them a dominant 'pollination service provider' in many landscapes. 271 The domestication of honeybees has allowed humans to exploit their pollination service by 272 transporting colonies in man-made hives to sites with high pollination demand (Breeze et al., 273 2011; Potts et al., 2010b; for bumblebee and solitary bee management see: Palomo et al. 274 2015; Pitts-Singer and Cane, 2011; Velthuis and van Doorn, 2006). The significant loss of 275 honeybee colonies each year (Lee et al., 2015; Neumann and Carreck, 2010; Oldroyd, 2007; 276 Potts et al., 2010b), has raised concern, in both the food production industry and the public 277 domain, for the effect on the overall pollination service that honeybees provide (Aizen and 278 Harder, 2009; Polce et al., 2014).

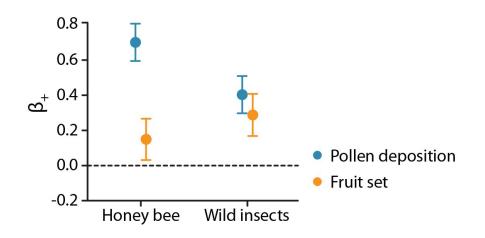
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Compared to the large number of wild insect pollinators, pollinator research on the honeybee has received relatively high attention, with particular emphasis being placed on the current threats posed by parasites and disease (Brown, 2015; Genersch et al., 2010; Ratnieks and Carreck, 2010). Whilst there is little doubt that honeybee losses are of concern, the 284 importance of all remaining wild pollinators and the threats they face should not be 285 overlooked (Figure 3; Ollerton et al., 2012; Winfree et al., 2007). Indeed, to have a 286 sustainable pollination service we cannot rely on one or a few domesticated species. Rather, 287 we must maintain a community constituting a diverse set of mobile pollinating organisms 288 with a broad suite of functional traits to maintain pollinators with 'insurance values' to meet 289 multiple pollination demands and prevent future pollination deficits (Albrecht et al., 2012; 290 Breeze et al., 2014; Gagic et al., 2015; Garratt et al., 2014b; Hoehn et al., 2008; Isbell et al., 291 2011; Mallinger and Gratton, 2015; Martins et al., 2015; Orford et al., 2015; Winfree et al., 292 2007; but see: Winfree et al., 2015). Crop pollination services can be enhanced when having 293 a diverse community of insect pollinators (Brittain et al., 2013a, 2013b; Greenleaf and 294 Kremen, 2006; Hoehn et al., 2008). Moreover, native and/or wild pollinators are more 295 efficient at pollinating certain plant species than honeybees (Figure 3; Garibaldi et al., 2014; 296 Jauker et al., 2012; Rader et al., 2013; Stanley et al., 2013; Thomson and Goodell, 2001; 297 Vicens and Bosch, 2000; Woodcock et al., 2013), and that long tongued wild pollinators can 298 effectively pollinate plants that may not be accessible for short-tongued pollinators such as 299 honeybees (Willmer, 2011). Yet despite the clear importance of wild pollinators, we have as 300 yet: i) a limited understanding of their population status; ii) major gaps in our knowledge of 301 the factors that threaten them and the subsequent impairment to the services they provide; and 302 iii) still much to learn about how we can change our actions and refine our approaches to help 303 maintain healthy pollinator populations and sustain valuable pollinator services.

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309 Figure 3 Figure taken and adapted from Garibaldi and colleagues (2013) who performed an 310 analysis to investigate the pollination service of honeybees versus wild insect pollinators in 311 41 animal pollinated crop systems across the globe. Plot shows the difference between the average regression coefficients ( $\beta$ +, ±95% CI) for pollen deposition and fruit set. The figure 312 313 shows that whilst foraging honeybees deposit a higher amount of pollen on con-specific 314 flowers compared to wild insect pollinators, they are less effective at pollinating the plant as 315 measured by the level of fruit set which was higher in wild insect pollinators. This supports 316 the importance of conserving a healthy community of native pollinators in these agricultural 317 areas.

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319 This paper posits that to sustain pollinator services and meet increasing pollination 320 demands (Aizen et al., 2008a), we must understand how to support and maintain healthy 321 pollinator populations and communities. The aim of this paper, therefore, is to provide a 322 perspective on the research advances required for us to better understand the risks posed to 323 wild pollinators and the services they provide, whilst detailing approaches we could adopt to 324 better mitigate such threats. We touch on most of the factors previously implicated as threats 325 to wild insect pollinators (see section 2) and consider the implications of our arguments to 326 relate to the status of insect pollinators in agricultural and urban landscapes. We further place

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much of our discussion in the context of the developed world where rural settings are often dominated by intensive farming, and urban areas have well-developed infrastructures. Whilst we also reference the global literature for our discussion of current knowledge and evidence gaps, we concentrate on the schemes and initiatives taking place within Europe, and especially the UK, for our case-studies to support future action plans and approaches. However, the concepts, knowledge and perspectives we discuss here have broad implications for the conservation of pollinators and their services worldwide.

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## 336 2. Major threats to the pollination service provided by insects

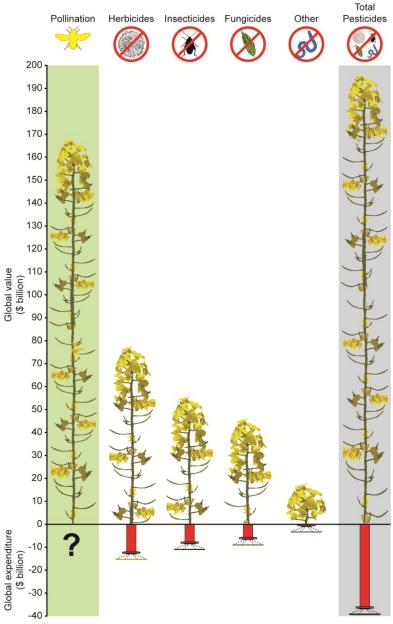
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338 Multiple factors likely act in combination to impose an overall level of stress on insect 339 pollinator populations (Bryden et al., 2013; Goulson et al., 2015; Perry et al., 2015; 340 Vanbergen et al., 2013). Implicated factors include climate change, habitat fragmentation, 341 land-use change and associated chemical inputs to the environment (i.e. agrochemicals), 342 invasive species and the added pressures of predation and competition (Godfray et al., 2014; 343 Gonzalez-Varo et al., 2013; Goulson et al., 2015; Kerr et al., 2015; Morales et al., 2013; Potts 344 et al., 2010a; Vanbergen et al., 2013, 2014a). Infection by parasites (and pathogens) also 345 poses a particular biotic threat, for example wild populations of the western honey bee, Apis 346 *mellifera*, have largely disappeared across Europe and N. America which may be attributed to 347 the parasitic mite Varroa destructor (Rosenkranz et al., 2010) and the viruses it transmits (Le 348 Conte et al., 2010; Sumpter and Martin, 2004). Managed honey bee colonies survive due to 349 significant prophylactic and reactive management techniques, and wild bumblebees are also 350 threatened by a range of emerging diseases (see section 4.3; N. America: Cameron et al., 351 2011; UK: Fuerst et al., 2014; McMahon et al., 2015; S. America: Arbetman et al., 2013; 352 Schmid-Hempel et al., 2014). Given that many parasites appear to be both generalists and 353 transmitted via flowers, it is likely that solitary bees and other insect pollinators are also at 354 risk, but we currently lack the appropriate data to gauge such threats.

355

356 Whilst efforts have been made to quantify the effect of each factor alone, gaining 357 reliable measures of their overall impact, particularly interactions, has proven difficult 358 because of large differences in morphology and life-history among taxa. Theoretical studies 359 suggest that a combination of stressors may be sufficient to trigger failure of social bee 360 colonies (Bryden et al., 2013; Perry et al., 2015), yet empirical studies looking at interactive 361 effects are typically limited to two (or few) factors (Baron et al., 2014; Becher et al., 2013; 362 Doublet et al., 2015; Fauser-Misslin et al., 2014; Gill et al., 2012; Gonzalez-Varo et al., 2013; 363 Hoover et al., 2012; Kennedy et al., 2013; Kleijn and van Langevelde, 2006; Oliver et al., 364 2012; Pettis et al., 2013; Schweiger et al., 2010; Vanbergen et al., 2013). Land-use change 365 and management is seen as one of the leading drivers of insect pollinator declines (Garibaldi 366 et al., 2014; Ollerton et al., 2014; Vanbergen, 2014). The rapid habitat transformation over 367 recent decades, predominantly due to anthropogenic activity, appears correlated with reported 368 declines in insect pollinator species richness (Potts et al., 2010a; Senapathi et al., 2015). 369 Taking the UK as an example, we have seen at least a 97% loss of wild flower meadows 370 since the 1930s (Fuller, 1987) at the same time as a significant increase in the levels of 371 agricultural intensification and urbanisation (National Ecosystem Assessment 2011, 372 www.gov.uk/ecosystems-services). During this period, the UK has seen contractions in the 373 geographic ranges of a number of insect pollinator species, as well as declines in species 374 richness at local scales and species extinctions at the national scale (Biesmeijer et al., 2006; 375 Carvalheiro et al., 2013; Goulson et al., 2005; Nieto et al., 2014; Ollerton et al., 2014; 376 Senapathi et al., 2015; Thomas et al., 1994, 2004), although the rate of these declines may

379 With increasing demands for food security and consumer pressure for affordable 380 produce, extensive areas of previously natural landscapes have been transformed to intensive 381 crop monocultures providing little nutritional resource to support insect pollinators if non-382 flowering, or little nutritional diversity and/or quality if it is (Bates et al., 2011; Decourtye et 383 al., 2010; Garibaldi et al., 2011b; Jha and Kremen, 2013a; Kennedy et al., 2013; Kremen et 384 al., 2002; Raine and Gill, 2015; Steffan-Dewenter and Westphal, 2008; Tscharntke et al., 385 2005; Winfree et al., 2011a). Accelerating agricultural intensification across the globe over 386 the past five decades is deemed a major cause of biodiversity loss (Batary et al., 2011; Foley 387 et al., 2011). Land clearance and removal of hedgerows for intensive agriculture decreases 388 overall wildflower diversity and abundance (Carvell et al., 2006; Holzschuh et al., 2008; 389 Rundlöf et al., 2008) and can restrict suitable nesting sites (Goulson et al., 2010; Knight et al., 390 2009; Williams et al., 2010). To protect crops against pest species, agrochemicals such as 391 pesticides are applied (Figure 4; Meehan et al., 2011), which may be having inadvertent 392 detrimental effects on insect pollinator behaviour, physiology, brood rearing and foraging 393 performance (Desneux et al., 2007; Exley et al., 2015; Fischer et al., 2014; Gill and Raine, 394 2014; Gill et al., 2012; Palmer et al., 2013; Whitehorn et al., 2012), leading to potential harm 395 of wild pollinator populations (Brittain et al., 2010; Rundlöf et al., 2015). This highlights one 396 of the ironies of modern agricultural practice; that by intensively growing flowering crops we 397 degrade the natural landscape that supports healthy pollinator populations and subsequently 398 degrading the very pollination service that the flowering crops benefit from (Figure 4). 399 Consequently, stress induced impairment to pollinator foraging ability could be having 400 negative impacts on the efficacy of the pollination service they provide (Gill and Raine, 401 2014), however to our knowledge, this expectation has not been explicitly tested. Viable



402 Figure 4| Relative value (financial income) and financial expenditure of pollination services 403 and various pesticides. Value of pollination (green bar) was estimated to be worth \$168.75bn 404 in 2009 (re-valuated from €153bn estimation by Gallai et al., 2009). Cost of these services, 405 considered to be money invested into action to protect and promote pollinators through land-406 use management and health related interventions, however, is unknown. The cost of various 407 pesticides was extracted from the United States Environmental Protection Agency for 2006-408 2007 Market Estimates. The value of each of these groups was then crudely calculated as an 409 upper estimate of 500% return (Pimentel et al., 1993). The total value and expenditures of the 410 four pesticides categories were summed for "Total Pesticides" (grey bar). "Other" pesticides include the nematicides, molluscicides and alternative chemicals (e.g. sulphur). 411

413 options to practice lower intensity farming and / or maintaining larger areas of semi-natural 414 habitats is likely to provide a more sustainable option in supporting insects for their 415 pollination service (see Section 4.6; Andersson et al., 2012; Bartomeus et al., 2014; Bohan et 416 al., 2013; Garibaldi et al., 2011b; Holzschuh et al., 2008; Kennedy et al., 2013; Kleijn and 417 van Langevelde, 2006; Ricketts et al., 2008).

418

419 For most insect pollinator groups, species richness has been reported to be in decline 420 across much of Europe (Biesmeijer et al., 2006; Bommarco et al., 2012a; Carvalheiro et al., 421 2013; Conrad et al., 2006; Nilsson et al., 2013; Ollerton et al., 2014; Senapathi et al., 2015; 422 Wenzel et al., 2006) and N. America (Burkle et al., 2013; Cameron et al., 2011) over the last 423 several decades. Other areas of the globe may have also suffered from similar declines over 424 this time scale, but to date we have limited data to investigate this with any certainty. Our 425 understanding of major changes in insect pollinator species richness at broad spatial scales is 426 improving, yet we are still limited in what we can conclude from the data due to it being 427 either: i) at a low spatial resolution (coverage across large regional scales is patchy); ii) of 428 variable accuracy of location and sampling area (i.e. range from  $\pm 100s$  to  $\pm 10,000s$  of 429 meters), which is problematic given that pollinators vary in dispersal ability; iii) limited to a 430 number of repeated measures at standardised times both within and across seasons / years; iv) 431 uses non-standardised sampling methods, making data comparison from multiple sources 432 difficult; v) obtained from multiple, different sources, which can introduce methodological 433 artefacts; vi) inconsistent in the level of taxonomic identification (i.e. down to family, genus 434 or species level); and, vii) perhaps most crucially, a general lack of data on species 435 abundance (at given spatial and temporal scales).

436

437

Identifying the drivers that shape insect pollinator population abundance requires both

438 high resolution data and universally standardised methods (Maes et al., 2013). The resulting 439 datasets should also be complemented by research focused on more localised population 440 changes. Whilst this type of data is missing for most insect pollinator groups, we can learn a 441 lot from data collected for butterflies, from databases such as for the UK Butterfly 442 Monitoring Scheme in which long term population data can allow powerful standardised 443 estimation of abundance in order to explore population trends and impacts of environmental 444 change (Oliver et al., 2010; Thomas, 2005; Thomas et al., 2011). Encouragingly this kind of 445 approach, further incorporating 'citizen scientists', is being adopted more widely, for 446 example by the National Pollinator Strategy for England (Figure 5) and the France-wide 447 monitoring scheme Spipoll (http://www.spipoll.org; Deguines et al., 2012). Gaining a greater 448 coverage of pollinator abundances, and thus pinpointing of localised population changes in 449 multiple locations across different geographic regions, enables a more coherent 450 understanding of the likely drivers of population change and consequent effects on ecosystem 451 services.

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453

454 3. Steps in the right direction to protect insect pollinator services: policy
455 actions

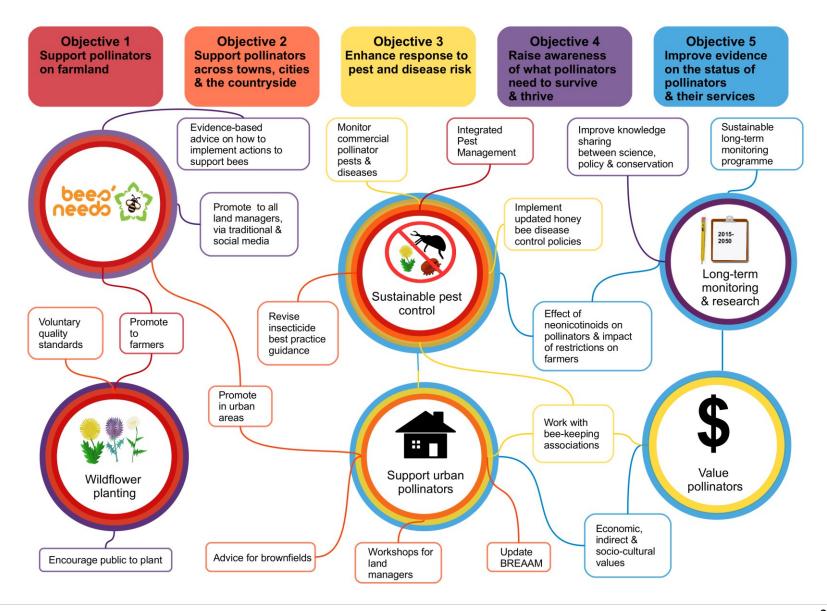
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457 Mitigating threats to insect pollinator services has become an important issue for 458 policy and the public. A range of conservation initiatives have been developed to improve 459 understanding of the risks posed, and how to deliver a sustainable pollination service at 460 global, regional and national scales (Table 2). Advancing ecological research into insect 461 pollinators requires an understanding of where current policy stands and how research 462 approaches can answer or inform stated objectives. At the global stage, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES; est.2012 and with 124 member states), recognises the need to provide policy-relevant knowledge to inform decision making. Identified as a globally important thematic topic, the assessment of "*Pollinators, pollination and food production*" (incl. insect pollinators) is being conducted on the basis that 'pollination services' are of fundamental significance. National pollinator initiatives / schemes require robust evidence if stated objectives are to be well justified, achievable, transparent, and critically to be of high societal relevance (see Table 2 in Appendix).

470

471 The recently launched National Pollinator Strategy for England (Defra, 2014) 472 provides an exemplary case study, in which an independent review of the "status and value of 473 pollinators and pollination services" was commissioned to provide a framework for future 474 action (Vanbergen et al., 2014a). This led to the declaration of four main objectives to: i) support pollinators on a variety of land types; ii) enhance responses to pest and disease risk; 475 476 iii) raise awareness of what pollinators need to survive and thrive; and, iv) improve the 477 evidence on the status of pollinators and the service they provide. These objectives were 478 accompanied by statements of approach for how they should be achieved, by: a) developing 479 and field testing a new monitoring framework to provide abundance data for insect 480 pollinators and to integrate citizen science; b) assessing economic, social and cultural values 481 of pollinators; and, c) to better understand how agricultural practices, in particular crop 482 protection, affect insect pollinator populations (see Section 4 and Figure 5). The strategy also 483 encourages the research community to carry out longer-term studies that policy-makers need, 484 and policy makers to maintain a continuity of policy approach across different parliaments, 485 negating the traditional short-term government view that can often hinder conservation 486 actions (Pullin et al., 2009).

487



489 Figure 5 Recently launched National Pollinator Strategy for England (Defra 2014) 490 highlights five objectives to maintain sustainable pollinator services. Although each objective 491 addresses a particular key area, and has actions targeted to that area, many of the issues 492 addressed in the Strategy are interlinked, and each objective supports the other. Addressing 493 one action (open boxes) will in many cases contribute to another either directly or through 494 one of six main themes. Here, the actions of the Strategy are shown colour coded and 495 connected to allow navigation and an intuitive overview. Coloured rings show which 496 objectives are linked to a particular theme.

497

498 To support wild insect pollinators, agricultural land can be managed to deliver a broad 499 array of public goods, by combining food production alongside other ecosystem services such 500 as maintaining culturally valuable insect pollinator habitats. Within the EU, for instance, the 501 Common Agricultural Policy (CAP) can compensate agricultural land managers (i.e. farmers) 502 for direct losses to income when altering the intensity of farming practices to better support 503 biodiversity and public goods. Through agri-environment schemes (AES) financial 504 compensation is provided to help offset loss of income from setting-aside land that could 505 otherwise be cultivated ('opportunity cost'), and estimated implementation costs such as the purchase of flowering plant-seed or costs of additional management (see sections 4.5 & 4.6; 506 507 Batary et al., 2011; Garibaldi et al., 2014; Rundlöf et al., 2013). AES can be used to target 508 ecosystem services that generate yield benefits in agriculture, such as insect pollination, 509 although this objective should be clearly separated from their use to conserve biodiversity, 510 because the necessary actions are likely to be different (Ekroos et al., 2014, Kleijn et al., 511 2015). In England, the new AES launched in 2015, named Countryside Stewardship, includes the 'Wild Pollinator and Farm Wildlife Package' designed to incentivise farmers to provide 512 513 additional resources for insect pollinators.

514

515

Pesticides used for crop protection pose a potential risk to non-target beneficial

516 insects, with foragers coming into contact with residues in the environment (Desneux et al., 517 2007; Osborne, 2012). Particular concerns have been raised about the application of plant-518 systemic neonicotinoid insecticides to flowering crops attractive to insect pollinators 519 (primarily bees). Reactions to the viewpoint that neonicotinoids place insect pollinators at an 520 unacceptable risk, the EU placing a restriction on the use of three neonicotinoids as seed 521 treatments (EFSA Commission Implementing Regulation (EU) no. 485/2013), and moves 522 haven been made in some states of Canada and the United States to reduce neonicotinoid use. 523 However, whilst restrictions may be viewed by some as a step-in-the-right-direction in 524 protecting insect pollinators, it has also been the subject of criticism, with questions being 525 raised over the assessment of the evidence underpinning this decision (Eisenstein, 2015) by 526 intensively growing flowering crops we degrade the natural landscape that supports healthy 527 pollinator populations and subsequently degrading the very pollination service that the 528 flowering crops benefit from. Whichever standpoint is taken, understanding the balance 529 between the benefit of crop protection and costs of impairment to a pollination service should 530 be the overall objective to achieve a pragmatic solution (Figure 4). Any review should 531 consider what the alternative methods of crop protection would be in order to sustain 532 adequate crop yields, to minimise off-site contamination to organisms other than insect 533 pollinators, and to be of low hazard to humans (Godfray et al., 2014; Raine and Gill, 2015).

534

# 535 4. Understanding and mitigating specific threats to wild insect pollinators

- 536 to protect pollinator services
- 537

538 Understanding the responses of insect pollinators to environmental stressors is 539 important in understanding how we can manage a sustained pollinator service for the future, 540 making it a major priority for both research and policy (Vanbergen et al., 2014a). Given the 541 complexity of these biological systems, we must avoid approaching pollinator management in 542 a naïve or overly simplistic manner otherwise our chances of meeting targets for pollinator services may be compromised. For example, engineering areas of land set-a-side to support 543 544 pollinators cannot be assumed to be effective if landscape context and land-use type have not 545 been considered. Whilst the objective is to increase biodiversity, many actions will only 546 support increased numbers of common pollinator species rather than re-establishing 547 endangered species (Scheper et al., 2013). It would be unfortunate if advisory actions to 548 support pollinators were communicated to end users based on poorly informed decisions 549 resulting in little practical and conservation impact, as the ramifications are likely to result in 550 a loss of confidence in policy advice along with unwarranted financial costs (Pe'er et al., 551 2014).

552

Key questions include how should we structure and maintain habitats to support insect 553 554 pollinators and increase subsequent services, and at what scale should this be implemented if 555 stakeholders are going to benefit, whilst ensuring that subsidies are not wasted. Here we 556 highlight some key evidence gaps, to refine our research efforts and ensure we better 557 understand how to maintain stable insect pollinator populations and structured communities 558 that are resilient to imposed stress. We consider seven primary themes, and for each we 559 discuss the evidence gaps and the research steps we can take to advance our understanding. 560 The steps raised within each theme are not in competition with each other, and in many cases 561 represent complimentary approaches in providing a generalised framework to direct future 562 research in addressing the evidence gaps...

563

#### 564 **4.1 Understanding the stability of insect pollinator communities**

565

566 The stability of ecosystem functioning requires ecological resilience, which is the 567 capacity of a population, community or ecosystem to buffer environmental perturbations and 568 re-organise whilst undergoing change without loss of structure or functioning (Cardinale et 569 al., 2012; Folke et al., 2004; Holling, 1973). The key question is what level of perturbation 570 can be buffered when extreme events occur, such as an acute local pollution episode, severe 571 habitat disturbance or rapid climate change? Plant-pollinator mutualisms are embedded 572 within a wider network of community interactions (Memmott, 1999; Pocock et al., 2012). 573 While plant-pollinator interactions are dynamic, the topology or structure of the network is 574 thought to confer a degree of stability or robustness upon the community (Bascompte et al., 575 2003; Kaiser-Bunbury et al., 2010; Memmott et al., 2004; Olesen et al., 2007; Ramos-576 Jiliberto et al., 2012; Thebault and Fontaine, 2010; Tylianakis et al., 2010; Valdovinos et al., 577 2013; Vieira and Almeida-Neto, 2015). There is, however, much debate over the extent that 578 different properties of network architecture confer stability or robustness to species loss 579 (Rohr et al., 2014). For example, species that are highly abundant and well connected to 580 many other species in the network, typically generalists, may increase overall network 581 robustness (Winfree et al., 2014). However, other evidence suggests that increased network 582 connectance (the proportion of possible links between species) may lead to a greater chance 583 of extinction cascades following species loss (Vieira et al., 2015), and the structuring of these 584 connections appears important with predictions that increased network nestedness imparts 585 stability (Allesina & Tang 2012; James et al., 2012). Moreover, behavioural plasticity means 586 that a pollinator species can potentially 'rewire' the network by switching to alternate plant 587 species following extirpation of a partner pollinator species, thereby maintaining the overall 588 community cohesion (Figure 2; Kaiser-Bunbury et al., 2010; Ramos-Jiliberto et al., 2012; 589 Valdovinos et al., 2013). Hence, this highlights the importance of ensuring we have a diverse 590 set of insect pollinators to maintain taxonomic or functional trait diversity (i.e. species

complementarity or functional redundancy), which serves to deliver a diverse set of
pollination services even in the face of species losses (Bartomeus et al., 2013; Moretti et al.,
2009; Woodcock et al., 2014; also see Kleijn et al. 2015).

594

595 Despite this apparent potential for an intrinsic stability to pollinator-plant networks, 596 there is increasing evidence of parallel declines in species richness of flowering plants and 597 their pollinators (Biesmeijer et al., 2006; Burkle et al., 2013; Cameron et al., 2011; 598 Carvalheiro et al., 2013; Ollerton et al., 2014). These declines may be linked to ecological 599 traits like diet specialisation or particular habitat requirements that predispose particular 600 pollinator species to extinction risk under environmental change (Aizen et al., 2012; 601 Biesmeijer et al., 2006; Williams et al., 2010). For example, in areas experiencing significant 602 transitions to more homogenous landscapes such as intensive arable monocultures, short 603 tongued generalist species of insect pollinators may be less affected than long tongued 604 specialists due to the concomitant loss of habitat(s) that maintain specific plants (Figure 2; 605 Goulson et al., 2005). Simulation modelling of empirical data shows that if the most 606 connected species in plant-pollinator networks are lost, then this may trigger a cascade of 607 secondary extinctions of plants or pollinators (Kaiser-Bunbury et al., 2010; Memmott et al., 608 2004; Vieira and Almeida-Neto, 2015). The implication is that if environmental change 609 reaches a level sufficient to extirpate these highly linked species then there is a risk that the 610 whole plant-pollinator network could disassemble and jeopardise the continued delivery of 611 insect pollination in that ecosystem (Lever et al., 2014). Other research shows these highly 612 connected species tend to also be the most abundant and hence among the least vulnerable to 613 extinction under environmental change (Winfree et al., 2014). Recent advances in such co-614 extinction modelling that incorporates variable dependences of different mutualistic partners, 615 and hence greater biological realism, should improve our ability to predict the likelihood of extinction cascades and the role of network structure in community stability (Vieira andAlmeida-Neto, 2015).

618

619 There remain several notable research challenges. First, we need to better understand 620 how networks are assembled or disassemble under rapid environmental change or in response 621 to agricultural land management (Devoto et al., 2007; Vanbergen, 2014; Vanbergen et al., 622 2014b). Second, we need to identify, through coupled experimental and predictive modelling 623 approaches the extent that different network properties (nestedness, connectance, modularity) 624 contribute to community dynamics or stability (Astegiano et al., 2015; Tylianakis et al., 625 2010). Third, how can extinction-driven alteration of network structure affect the delivery of 626 crop pollination services and wild plant reproduction (Bohan et al., 2013; Tixier et al., 2013). 627 It is increasingly being recognised that species interactions, such as pollination, and the 628 services derived from them are an important measure of biodiversity that has been largely 629 overlooked due to the disproportionate emphasis on the species (nodes) within ecological 630 networks, rather than their links (Ings et al., 2009). For example, at what point does the 631 erosion or reorganisation of plant-pollinator networks by anthropogenic drivers lead to loss of 632 the links that confer functional redundancy upon the system and what is the magnitude of the 633 impact on pollination services and plant reproduction (Aizen et al., 2008b, 2012; Burkle et 634 al., 2013; Devaux et al., 2014; Stout, 2014; Vanbergen et al., 2014b)? To answer such 635 questions we need to explore the mechanistic linkages between network assembly and 636 pollination processes across replicated environmental gradients and experimentally 637 manipulate field systems. Coupled with this, we should consider how other scientific 638 disciplines have transformed our understanding and ability to quantify network structure and 639 function (Heleno et al., 2014). For example, pollinator network ecology is currently 640 underpinned by traditional field approaches (e.g. visitation transects) and taxonomic expertise

641 that provide data on the identity and frequency of mutualists but which are time-consuming. Recent advances in molecular techniques has given rise to the possibilities of rapidly 642 643 analysing field collections to enable measures of taxonomic diversity and a high-throughput 644 quantification of species abundance (Bohmann et al., 2014; Keller et al., 2015; Richardson et 645 al., 2015), to re-construct with high precision and accuracy the structure of different plant-646 pollinator assemblages (see next section 4.2; Vacher et al., 2015). These molecular approaches will also enhance our ability to robustly monitor pollinator populations (Dicks et 647 648 al., 2013; Lebuhn et al., 2013), and quantify pollinator community structure under different 649 environmental stresses or contexts.

650

## 651 **4.2 Using molecular approaches to monitor insect pollinators**

652

653 Obtaining data to study insect pollinator population sizes and pollinator network 654 ecology are reliant on taxonomic identification of species and counts of individuals. For 655 monitoring purposes, quantitative surveys (recording richness and abundances of organisms) 656 are preferable to qualitative surveys (establishing only presence of species per locality: Kerr 657 et al., 2015), but both suffer from time consuming sorting, identifying and counting plant and 658 pollinator diversity, making it slow and financially costly for active management (Lebuhn et 659 al., 2013). Moreover, taxonomic experts are needed regularly but this may not be possible if 660 experts are few and in high demand. Researchers are therefore exploring the developments of 661 novel molecular tools to aid the efforts in both identification and quantification (Kuhlmann, 662 2015), with the aim of providing greater taxonomic precision, a robust method of monitoring 663 aspects of pollinator populations and to quantify pollinator community structure under 664 different environmental conditions (Tang et al., 2015). The overall objective is to monitor reliably across multiple sites to gain spatial aspects of pollinator community structure 665

repeatedly over time to assess trends and react adaptively to protecting insect pollinatorservices.

668

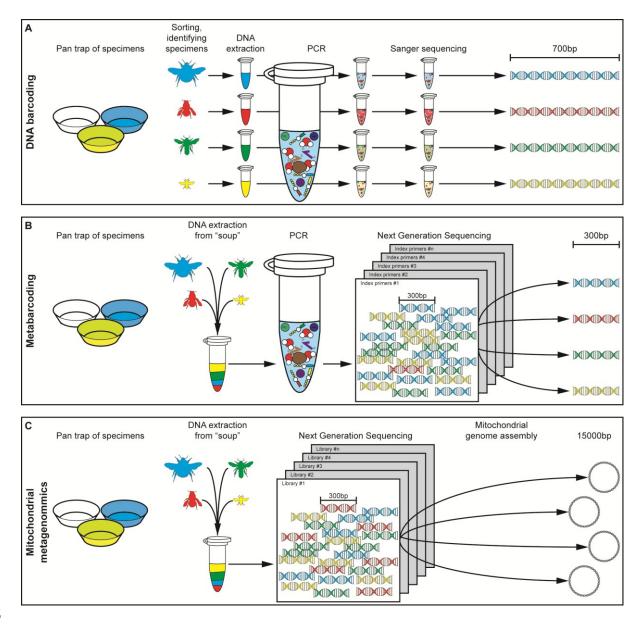
669 Employing molecular taxonomy through 'DNA barcoding' using the mitochondrial 670 cytochrome oxidase (COI) marker (particularly for insects) has now become relatively 671 commonplace (Hebert et al., 2003; Magnacca and Brown, 2012; Schmidt et al., 2015). By 672 cross-referencing sequences obtained from collected tissue samples to the growing global 673 database of barcodes that are linked to taxonomically well-studied specimens, we can use 674 these short, standardised gene regions to identify species rapidly and reliably (Figure 6). 675 Furthermore, such molecular identification is not limited by the state of the specimen, for 676 instance an insect pollinator specimen can be identified at any developmental life-stage or 677 even from non-living remains in the environment (eDNA) (Taberlet et al., 2012), or ingested 678 by predators. However, the frequently low differentiation between species and high 679 geographic variation within a species means we need to understand how well the COI marker and its genetic variation capture the species limits. Thus, judicious use of COI-based genetic 680 681 clusters (sometimes referred to as Operational Taxonomic Units (OTUs)) is usually 682 acceptable for monitoring purposes, but these entities should be backed up by careful and 683 accurate morphological examination (Meyer and Paulay, 2005).

684

DNA barcoding of European bees has now progressed to the point where COI sequences are available for many species (Schmidt et al., 2015) and are accessible through the global Bee Barcode of Life Initiative (Bee-BOL) (http://www.bee-bol.org). Similarly, there is a well-populated DNA barcode database for butterfly species (including all 59 British spp.), but to date no orchestrated effort has been made to complete a DNA barcode database for other pollinator groups. The practicality of populating these databases is aided by the 691 possibility to generate sequence data from preserved specimens, as those in museum 692 collections, which can establish the link to known vouchers of taxonomic relevance or to 693 monitor change over time against historical specimens (Hebert et al., 2013; Timmermans et 694 al., 2015). The resulting database of reference sequences then becomes part of a growing 695 framework of genotypes from wider surveys that extend the biogeographic, ecological and 696 taxonomic scope of pollinator studies.

697

698 Despite this power, DNA barcoding is time-consuming because it requires working 699 with individual specimens, and so next-generation sequencing (NGS) technology may be 700 preferred, which can potentially survey specimens in bulk and circumvent the need to 701 separate and sort samples (e.g. captured insect pollinators in a pan trap). The most 702 straightforward and cost efficient approach is 'metabarcoding' that applies the principle of 703 DNA barcoding to a bulk sample by conducting PCR and sequencing on the mixture allowing 704 an indiscriminate field collection to be analysed (Figure 6; Creer et al., 2010; Gibson et al., 705 2014; Taberlet et al., 2012; Vacher et al., 2015; Yu et al., 2012). Massively parallel NGS 706 technologies produce numerous independent sequence reads, each corresponding to a 707 separate PCR amplicon, which may originate from any species in the mixture. In addition, 708 primer indexing permits the simultaneous sequencing of numerous samples (e.g. from 709 multiple pan traps), keeping costs low. However, this methodology is associated with various 710 problems such as biases in amplification success across different taxa, which may create false 711 negatives (Clarke et al., 2014; Tang et al., 2015), contamination risk and potential co-712 amplification of mitochondrial pseudogenes (Song et al., 2008), and the comparatively short 713 sequence achievable with the current NGS technology, which limits the analysis of the COI 714 gene to roughly a half-length 'minibarcode' and hence reduces discriminatory power (Tang et 715 al., 2015).



717 Figure 6 DNA barcoding, metabarcoding and mitochondrial metagenomics pipelines. A) 718 Specimens collected (e.g. pan trap) must first be identified by expert taxonomists. For DNA 719 barcoding, specimens and all downstream processes must be kept separate. The DNA from 720 each representative specimen is extracted separately, amplified by PCR at specific loci (i.e. 721 COI) and Sanger sequenced, to produce a reference database for use for metabarcoding (B) 722 and mitochondrial metagenomics (C). B) Metabarcoding does not require the sorting of bulk 723 samples. Whole samples are homogenised into a 'soup' and DNA is extracted directly from 724 this. PCR is performed on this bulk DNA extract with primers designed for a shorter read 725 length to accommodate the possible sequencing output of the next generation sequences. 726 Multiple bulk samples can be analysed simultaneously if differently indexed primers are used 727 for each sample; these indexed primers can be used to sort the samples out bioinformatically

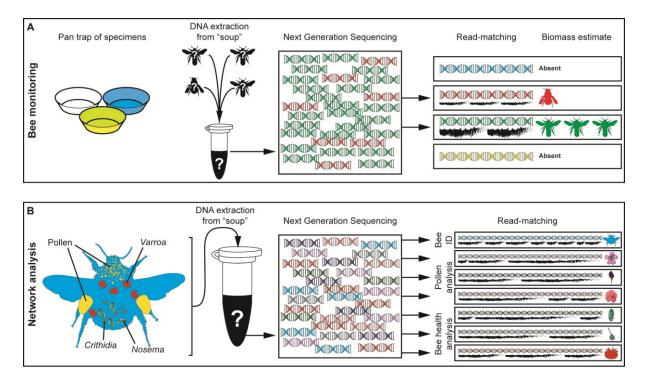
728 after sequencing. Next generation sequencing of the PCR products is performed after which 729 bioinformatics pipelines are used to extract unique sequence reads. These reads are 730 retrospectively identified using the DNA barcode reference database. C) Mitochondrial 731 metagenomics is also performed on bulk samples. DNA extracted from homogenised soups 732 do not undergo a PCR step, instead the raw DNA from the DNA extract is shotgun 733 sequenced. Different samples can be sequenced simultaneously if they are prepared in 734 differently labelled libraries. The sequence output is bioinformatically cleaned, quality 735 checked, parsed into mitochondrial DNA, and assembled into mitochondrial genomes. These 736 mitochondrial genomes are then identified using the reference database.

737

738 Given these drawbacks, the use of PCR-free methods is desirable. Current approaches 739 similarly analyse mitochondrial genomes, but exploit the fact that mitochondria are abundant (ca. 200 copies per nuclear genome; Correa et al., 2012) and thus are naturally enriched over 740 741 other markers. Total DNA is extracted from a bulk sample of specimens and subjected to 742 shotgun sequencing to produce millions of short reads. Genome assembly from these reads 743 produce full or partial mitochondrial genomes for each of the species present in the mixed 744 sample. This approach, known as mitochondrial metagenomics (Crampton-Platt et al., 2015), 745 was recently applied to bee communities and provides powerful 'super-barcodes' used as a 746 reference library (Tang et al., 2015). These reference mitochondrial genomes are used to profile any number and mixture of specimens that may be collected (for example in field pan 747 748 traps that attract and collect flying insect pollinators). Shotgun sequences from the bulk 749 sample are matched against the reference library thus revealing the presence and absence of 750 species from the read-matches. Crucially, this analysis requires many fewer reads than the 751 initial assembly of generating the mitochondrial genome references. Profiling success using 752 this approach has been high (>95%, taking into account false presences and absences 753 combined: Gómez-Rodríguez et al., 2015), and much higher than using metabarcoding (Tang 754 et al., 2015). In addition, studies have established the correlation of read number with 755 abundance and biomass (Gómez-Rodríguez et al., 2015; Tang et al., 2015; Zhou et al., 2013),

756 and thus read matching can potentially be used for assessment of species abundance (we 757 therefore can obtain both qualitative and quantitative survey results; Figure 7). Tang et al. (2015) calculated that for large-scale monitoring of pollinator communities using the read 758 759 mapping approach which is approximately 50% less labour intensive than the conventional 760 survey work based on morphological identifications. Alternative approaches for abundance 761 measures may come from rapid barcoding techniques conducted by PCR directly on the specimens (no DNA extraction) and short reads that could potentially sequence tens of 762 763 thousands of specimens whose identification is based on sequence data on which to base the 764 specimen count (Meier et al., 2015; Tang et al., 2015; Wong et al., 2014).

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766

**Figure 7** Read-matching of sequences. **A)** Specimens caught in a pan trap of unknown identity and quantity can be homogenised and shotgun sequenced. In this example, the only sequences present in the sample match to two of the four species in the DNA reference library. Furthermore, given that the number of sequences matching the amount of representative DNA in the extract, the number of sequence reads should correlate with the amount of DNA in the original sample, and given that the amount of DNA present per specimen should correlate with the biomass of the specimen, obtaining a quantification of the

number of specimens per species is possible with an appropriate calibration. B) Commensals of the specimen can be elucidated with the read-matching approach. DNA from the carried pollen, parasites and pathogens, as well as that from the pollinator, are present in the DNA extract. In this example, the identity of the bee, the pollen from three plant species and the disease agents are shown using a read-matching approach.

779

780 Beyond the estimates of abundance, the advantage of metagenomic sequencing is that 781 the sequence reads are mostly a complete reflection of the entire ecosystem, including those 782 organisms associated to the pollinator specimens (Bohmann et al., 2014). These methods 783 offer the potential to study plant-pollinator networks as DNA from bulk samples contains not 784 only pollinator DNA, but also any associated organic material such as pollen, parasites and 785 pathogens (Figure 7). Using a read-matching approach, matching DNA from pollen would 786 allow the practitioner to populate plant-pollinator networks in a more direct fashion than 787 studies using visitation as a proxy (King et al., 2013), and more rapidly, reliably and to a 788 higher resolution than microscopy methods (Kraaijeveld et al., 2015). Presently plant 789 identification via molecular approaches still rely on several short chloroplast barcodes but 790 whole chloroplast genome sequencing is expanding rapidly, which will overcome the 791 problem of low chloroplast abundance in the pollen, currently addressed with sequencing of 792 the nuclear ITS region (Bohmann et al., 2014; Keller et al., 2015; Richardson et al., 2015; 793 Sickel et al., 2015). Matching parasites and disease agents (section 4.3), and the associated 794 pollinator microbiome, would allow assessment of pollinator community health as well as its 795 diversity and abundance. Metagenomics could be used to detect EIDs in wild pollinators, a 796 largely unknown and neglected system or even the spill-over of these diseases from managed 797 to wild pollinators (Goulson and Hughes, 2015). While molecular approaches have been 798 tested to screen bees for disease agents (Fürst et al., 2014; Graystock et al., 2014), these are 799 PCR based and therefore target specific diseases with primers that need to have close affinity 800 with the targets. A metagenomics approach does not suffer from a primer biases and so it

801 would be possible to detect all of the diseases simultaneously.

802

### 803 **4.3 How do parasites shape wild insect pollinator populations?**

804

805 Wild pollinators exist in complex and diverse assemblages. In unperturbed 806 assemblages, endemic parasites may control populations of individual species when showing 807 host specialisation, or, if they are multi-host parasites act through apparent competition to 808 modulate the relative abundance of different species (Dobson, 2004; Holt and Pickering, 809 1985). In perturbed assemblages, where the abundance of subsets of species is depressed 810 through human impacts, effects of reservoirs (where one host acts as the major carrier of the 811 parasite) and spill-overs (where the parasite is transmitted from reservoir to non-reservoir 812 hosts) may drive host species with anthropogenically reduced populations to extinction 813 (Daszak 2000; de Castro and Bolker, 2005; Dobson 2004). Emerging infectious diseases, which are not confined to pollinators, may also threaten population declines or species 814 815 extinction if they spread rapidly and have high impacts on individual fitness (de Castro and 816 Bolker, 2005). Hence, understanding the top-down pressure placed on insect pollinator 817 populations by endemic and emerging parasites, alongside infectious diseases (EIDs), is 818 important given that maintaining healthy populations is a prerequisite for a healthy 819 pollination service (Brown, 2015). For example, concerns have been raised over the effect 820 that parasites and infectious diseases are having on the overall pollination service provided by 821 honeybees, as individual infection can impair individual foraging performance (Wolf et al., 822 2014), and high prevalence in colonies can lead to significant problems (Dainat et al., 2012; 823 Higes et al., 2008; Martin, 2001; Nazzi et al., 2012).

824

825

Our understanding of endemic parasites and EIDs in wild pollinators is largely limited

826 to bumblebees, although parasites and disease in managed honey bees are also well known 827 (Genersch et al., 2010). Our knowledge of the situation in wild solitary bees, hoverflies, and 828 other pollinators, is limited to point samples of individuals in space and time (Evison et al., 829 2012; Singh et al., 2010). Whilst our knowledge of endemic parasites in bumblebees is 830 relatively broad and deep (Schmid-Hempel, 1998), we know almost nothing about how they 831 interact with the population dynamics of their hosts. This is a specific example of the larger 832 issue, in that we simply do not understand the relative importance of the putative drivers of 833 wild pollinator population dynamics in the field. Similarly, we have only a vague idea of the 834 distribution and abundance patterns of endemic parasites, although studies using regional 835 (Durrer and Schmid-Hempel, 1995), and continent-scale (Cordes et al., 2012) approaches are 836 starting to fill this gap. In contrast, studies of EIDs in wild bumblebees have explicitly taken 837 large-scale geographical approaches, with parasites, some associated with population 838 declines, being mapped in N. America (Cameron et al., 2011), S. America (Schmid-Hempel 839 et al., 2014) and the United Kingdom (Fürst et al., 2014; McMahon et al., 2015).

840

841 If we are to understand the impact of endemic parasites and EIDs on wild pollinator 842 populations and its subsequent effect on pollinator services, a number of key questions need 843 to be addressed. First, we need to map the drivers of population dynamics and identify the 844 relative importance of endemic parasites and EIDs within this larger picture. This requires 845 studies of population dynamics within and across years at the same site (see next section 4.4), 846 and the quantification of potential limiting resources, predators, and parasites. Second, the 847 directionality of EIDs needs to be confirmed - who is giving what to whom across the 848 season? And the degree of impact of EIDs on wild pollinators needs to be determined in 849 laboratory studies (Graystock et al., 2013). Third, we need to understand the drivers of 850 parasite population and epidemic dynamics within and across species. This will require a range of approaches, including eco-immunology, field observation and landscape analyses. Specifically, we should be attempting to map the 'parasite exposure landscape', that is, the distribution and abundance of parasites in the environment (both in hosts and on flowers; Anderson et al., 2013), and how this relates to the probability of becoming infected. This is likely to vary over spatial and temporal scales across the landscape, but by identifying key 'hubs of transmission' we may be able to focus our conservation efforts, and investigate whether such hubs geographically overlay with hotspots of high pollination demand.

858

#### 4.4. Understanding insect pollinator population responses to resource availability

860

861 Meeting local pollination demands reliably and throughout the year requires large 862 insect pollinator populations to provide numerical and functional responses to temporal 863 changes (Lautenbach et al., 2012; Polce et al., 2014), and to be stable with long-standing 864 residency in local areas (Klein et al., 2012). A realistic concept of a stable population is one 865 that shows resilience to environmental perturbation by rapidly recovering from induced 866 reductions in population size (a 'bounce back'; Holling, 1973; Steiner et al., 2006). It is 867 therefore important we understand how populations respond to imposed stress to protect 868 populations from reaching tipping points that trigger population crashes (Bryden et al., 2013; 869 Dai et al., 2012; Drake and Griffen, 2010; Lever et al., 2014). Population resilience is largely 870 dependent on population size, with small populations being vulnerable to bottleneck events 871 with proportional losses of individuals, compared to large populations, likely having a higher 872 impact on effective population size (Fagan et al., 2001; Hanski and Saccheri, 2006; Shaffer, 873 1981), increasing population susceptibility to future stress and chances of inbreeding 874 depression (Frankham, 1995a, b) and ultimately local extinctions (Lawton and May, 1995; 875 Saccheri et al., 1998). We therefore need to understand what habitat requirements are

876 important for pollinator life-histories, and how variation in resource availability impacts on877 population dynamics (Yamamura et al., 2006).

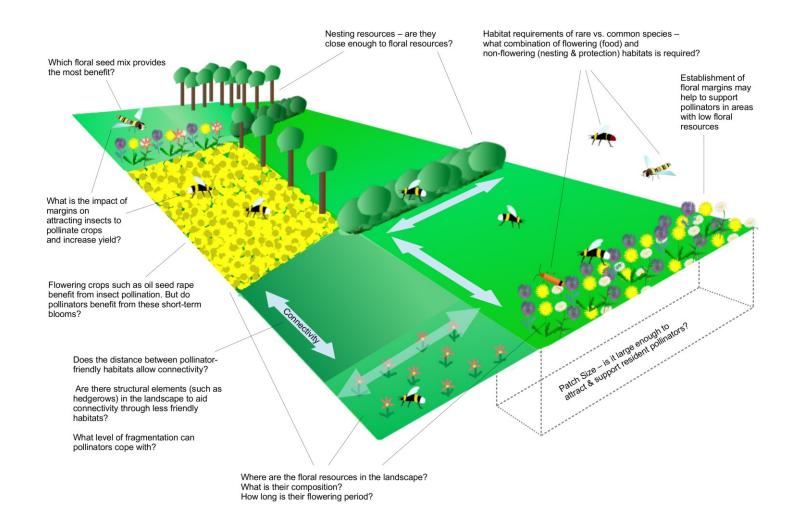
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879 We can start by first targeting research to help conserve key species or groups that 880 provide a highly valued pollinator service (Kleijn et al., 2015, Winfree et al., 2015). In 881 designing and managing supportive habitats, we need to understand a habitat's carrying 882 capacity for the pollinator(s) in question, taking into consideration habitat size (which can 883 influence resource diversity, potentially resource quality, and positively correlates with 884 absolute resource abundance although not necessarily resource density) and compositional 885 heterogeneity (Blaauw and Isaacs, 2014b; Fahrig et al., 2011; Tscharntke et al., 2002). 886 Importantly, we must consider particular habitat features that meet fundamental life-history 887 requirements (Blaauw and Isaacs, 2014a, Dicks et al., 2015). For an insect pollinator, the 888 primary habitat requirements are likely to be: i) floral and other nutritional resources, ii) nest 889 (breeding) sites, and iii) levels of protection (Figure 8; Fortel et al., 2014; Williams and 890 Kremen, 2007; Wray and Elle, 2015). The floral preferences of a large diversity of insect 891 pollinators have been well studied (see section 4.6; Willmer, 2011), and significant advances 892 have been made in understanding how to attract species or communities to engineered or 893 enhanced floral rich habitats (although other predatory or parasitic insects require other 894 available organisms to survive). However, we understand little of whether such habitats are 895 able to 'retain' resident populations in the long term with any constancy. Therefore, shifting 896 some of the research focus towards better understanding requirements ii and iii, can help us to 897 understand the 'retention capability' of habitats. To do this we need to understand more about 898 the micro-habitat requirements for nesting (breeding) sites and where these sites are spatially 899 and temporally located. Though our knowledge base on wild bees is improving significantly 900 (Goulson et al., 2010; Knight et al., 2009; Williams et al., 2010), we rarely find nests that fail.

901 Furthermore, we understand even less about what composite features of a habitat provide 902 protection from threats such as predators and weather conditions (Boggs and Inouye, 2012).

903

904 Spatial and temporal variation of resources will have impacts on the basic properties 905 underpinning population dynamics, namely: i) the basic demography (birth and death rates) 906 and age structure of a population; and, ii) the immigration and emigration of individuals in 907 and out of local (sub-)populations. Although assessment of simple birth rates appears at first-908 glance a basic task, it is in actuality rather challenging, as insect pollinators are often small 909 and hard to track (Hagler and Jackson, 2001), with nest sites often being inconspicuous. 910 Unlike honeybees where close monitoring of colonies has provided detailed insights into 911 social colony dynamics (Becher et al., 2013, 2014; Khoury et al., 2011, 2013; Naug, 2008), 912 there is a comparative lack of data on the levels of successful hatching, rearing and adult 913 development for most insect pollinators. Gaining knowledge on seasonal emergence times 914 and dispersal behaviour would inform us of the best times for sampling pollinators to provide 915 indirect data on hatching successes. Furthermore, development of methods to help find and 916 identify nests aided by local knowledge of pollinator natural history, would be advantageous. 917 Pollinator fecundity and hatching success is likely to be related to the availability of 918 nutritional resources (O'Brien et al., 2003; Vaudo et al., 2015), which may be increased by 919 providing enhanced floral resources in the landscape (Dicks et al., 2015; Holland et al., 2015; 920 Morandin and Winston, 2006). But to effectively support a population throughout the season 921 comprehensive knowledge of plant-pollinator phenologies are required to ensure that 922 resources are available for crucial stages of the life-cycle (Memmott et al., 2010), as biasing 923 resources towards specific age sector(s) of the population may leave other sectors vulnerable.



924

925 Figure 8| Representation of a rural scene, depicting a typical patchwork of habitat types across the landscape (not to scale). This highlights some

926 of the factors that influence residency and movement of pollinators across the landscape.

928 Susceptibility to different environmental pressures is likely to vary at different life 929 cycle stages of an insect pollinator. Gaining a better understanding of this will enable 930 implementation of habitat features that can increase protection at different times of the year. 931 Floral resource availability, for example, is not only important leading up to laying, but also 932 crucial to build nutritional reserves in preparation for species that hibernate (i.e. storing fats) 933 if starvation is to be avoided (Beekman et al., 1998; Brown et al., 2003; Leather et al., 1993), 934 and flowers should be located relatively close geographically to hibernation sites. Moreover, 935 the overwintering sites need to be suitable to enable individuals to overcome the demands and 936 exigencies of hibernation. Hence, efforts should be refined to aid individuals at critical life 937 stages in order to mitigate populations experiencing severe 'demographic pinch points'.

938

939 Repeated and long term monitoring of species at specified sites, including employing 940 mark-recapture methods, will be key to understanding the population biology of insect 941 pollinators (see sections 2, 3 and all sub-sections of section 4; Drag et al., 2011; Hagler and 942 Jackson, 2001). However, observation of individuals in a habitat patch may represent a 943 temporary immigration, instead of a permanent population enhancement (Jonsson et al., 944 2015), a tactic used by pollinators to access requirements that may be limited in other 945 neighbouring patches – a process known as 'habitat complementation' (Dunning et al., 1992; 946 Mandelik et al., 2012; Tarrant et al., 2013). Hence, dispersal ability is likely to determine 947 how well such meta-populations can cope with increasing habitat fragmentation (Fahrig, 948 2001), an area that would benefit from further research (Jauker et al., 2009; Rands, 2014). 949 Studies have shown that foraging abilities of flying insect pollinators range widely (Cant et 950 al., 2005; Carvell et al., 2012; Gathmann and Tscharntke, 2002; Greenleaf et al., 2007; 951 Knight et al., 2005; Osborne et al., 1999; Pasquet et al., 2008), and this will be further

927

952 influenced by climatic variables, such as temperature and wind-speed. To inform habitat 953 management practices, efforts should be focused on advancing our understanding on the 954 foraging / dispersal abilities in different landscape complexities for a diverse set of 955 pollinators (Figure 9), taking into consideration the combination of size and eco-956 physiological strategies (Gathmann and Tscharntke, 2002; Niitepold et al., 2009; Pawar et al., 957 2012), and how such demands may influence susceptibility to other threats. In a rapidly 958 changing world, it is important to understand how meta-populations ranging from numerous 959 small (and fragmented) local populations showing low connectivity (low gene flow), through 960 to fewer large and well-connected populations (high gene flow) can cope under different 961 environmental settings and landscape structural complexity (Figure 8; Tscharntke et al., 962 2002; Weibull et al., 2000), and crucially how this has a consequent effect on pollination 963 service (Holland and DeAngelis, 2001).

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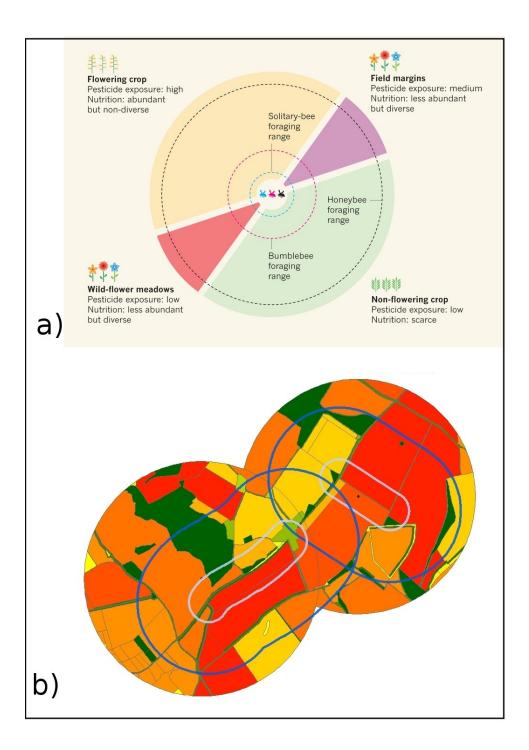
### 966 **4.5 Engineering flowering field margins as habitats to attract insect pollinators**

967

968 Engineering of certain habitats can increase the delivery of floral resources, nesting 969 areas and protection to support a greater insect pollinator abundance and richness of insect 970 pollinators which can in turn provide a pollination service to improve crop yields, including 971 its reliability and quality (Klatt et al., 2014; Kleijn et al., 2006). Unfortunately, understanding 972 how to engineer the 'optimal' agricultural field margin has not proved to be simple to 973 achieve. Crops differ in the level of pollination and the community of insect pollinators 974 required (Albrecht et al., 2012; Fruend et al., 2013), and pollinator species may also differ in 975 their resource requirements throughout the year (Olesen et al., 2008). Wild insect pollinators 976 also differ in their mobility and foraging strategies (Greenleaf et al., 2007) and consequently 977 the amount and spatial configuration of engineered habitats should determine their 978 effectiveness (Brosi et al., 2008). Furthermore, engineered margins are not necessarily always 979 needed or desirable; a farmer growing predominantly non-flowering crops does not 980 necessarily need a pollination service, so if they were to invest in engineering a pollinator 981 supportive margin the purpose would be for ecological (rather than economic) reasons. The 982 requirement of engineered margins, therefore, needs to be determined with guidance on 983 regional or landscape specific pollinator community abundance or on-farm monitoring 984 schemes. Moreover, relying on engineered margins alone is risky because establishment of 985 the sown species can fail and this requires removing land from production. Therefore, a 986 better option may be to supplement existing habitats that also support insect pollinator 987 communities (Franzen and Nilsson, 2008; Ricketts et al., 2008; Wood et al., 2015a). Thus 988 when managing floral rich habitats we should consider whether it will compliment, rather 989 than conflict, with other blooming periods from other floral sources nearby (Williams et al., 990 2010), and acknowledge that this will differ in areas where crops are non-flowering versus 991 flowering (Figure 9; Raine and Gill, 2015). The value of such natural or semi-natural habitats 992 in agricultural areas remains largely undefined although national and international projects 993 (www.quessa.eu) are underway to address this gap.

994

The first step in designing engineered margins is to identify whether a pollination deficit exists for crops, and the extent to which this deficit varies between regions with different landscape complexities (Marshall et al., 2006). Variation is expected because existing habitats will differ in the floral resources they provide and in their abundance and distribution across landscapes. The level of deficit is known for some crops (Aizen and Harder, 2009; Lautenbach et al., 2012; Polce et al., 2014), although varietal differences exist and are not well understood (Klein et al., 2007). Information about landscape-scale provision



1003

**Figure 9** Foraging options to central place foragers (such as bees) is dependent on their foraging range. **A)** Taken from Raine & Gill (2015) this is a conceptual diagram showing some general types, and typical proportions, of habitats that are available to foraging pollinators in rural landscapes. Pollinator species show a wide range in dispersal abilities which can limit the total amount of suitable habitats that can be viably visited. Evidence shows that individual honeybees have a much larger foraging range than either bumblebees

or solitary bees (see section 4.4). B) Foraging ranges of solitary bees drawn around the 1010 1011 location of an engineered floral field margin strip (black line). Map depicts the real cropping 1012 and semi-natural habitats found on a farm in Dorset, UK, with 160m representing the 1013 minimum (grey line) foraging range and 600m the maximum (blue line) (Gathmann and 1014 Tscharntke, 2002). Ranges allow a visualisation of: i) which areas the field margins are likely 1015 to have an effect on, regarding attraction of resident solitary bees; ii) which areas bees are 1016 able to reach were they to nest or reside in one of the field margins and act as a central 1017 forager. Pollinators with small foraging ranges have the potential to be isolated from 1018 neighbouring populations; intriguingly even at a maximum foraging distance, solitary bees 1019 may be unable to travel between field margins and thus connecting habitats are likely 1020 required in such a setting (the landscape map was generated for the QuESSA project funded 1021 by the EU and provided with permission from John Holland).

1022

1023 is scarce (Richards, 2001; Steffan-Dewenter et al., 2002), but is needed if the requirement for 1024 additional floral or nesting resources is to be identified spatially and temporally (Figure 8). 1025 Engineered margins have typically been designed to support bumblebees by planting their 1026 most preferred foraging plants (Fabaceae), however, evidence is now emerging about the 1027 value of other insects that have different foraging preferences (Wood et al., 2015b; 1028 Woodcock et al., 2013). Data are limited but a few studies suggest that perennial wildflower 1029 mixes may support a wider range of pollinators (Dicks et al., 2010), and floral richness is as 1030 important as floral abundance, with insect pollinators shown to have increased growth rates 1031 and immuno-competence from being fed diverse diets (Di Pasquale et al., 2013; Vaudo et al., 1032 2015). Achieving the desired habitat, however, does present challenges because sown plant 1033 species may not always establish and can depend on soil type, the plant's establishment 1034 method, competition between sown and unsown plants and subsequent management (Pywell 1035 et al., 2011).

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We next need to understand how such engineered habitats are utilised by insect

1038 pollinators and whether they can realistically subsidise nearby crop pollination. The value of 1039 flower-rich habitats is typically measured through assessment of pollinator abundance and species richness relative to other habitats (Carvell et al., 2007), and is likely influenced by the 1040 1041 composition and complexity of the landscape (Scheper et al., 2013; Shackelford et al., 2013). 1042 Surprisingly, it is still poorly understood whether the attraction of pollinators to flowering 1043 crops is enhanced with nearby engineered habitats, although the positive influence of semi-1044 natural habitats has to some extent been demonstrated (Chacoff and Aizen, 2006; Kleijn and 1045 Sutherland, 2003; Klein et al., 2003; Kremen et al., 2004; Morandin and Winston, 2006). 1046 Even where the level of crop pollination has been quantified it is usually measured by proxies 1047 such as pollinator abundance in the field or resulting crop yield, rather than pollen transfer, 1048 visitation rates or plant fitness (King et al., 2013; Liss et al., 2013).

1049

1050 Quantifying the measures needed to achieve the desired pollinator community, is 1051 important, whether these are enhancement of existing habitats or establishment of new 1052 flower-rich and nesting areas. Guidelines on the proportion of flower-rich habitats needed in 1053 the landscape are appearing (Holland et al., 2015; Morandin and Winston, 2006), but also 1054 with evidence of redistribution rather than population enhancement that require further 1055 investigation (see section 4.4; Jönsson et al., 2015). To maximise the potential of engineered 1056 margins and minimise the amount of land removed from production to support pollinators 1057 (Figure 10), the following steps could be adopted. i) For each flowering crop and main 1058 varieties identify whether pollination is needed and which pollinators are likely to provide 1059 this service. ii) Assess the landscapes in which the crops are produced for alternative floral 1060 and nesting resources through the pollinator activity period to identify potential resource gaps 1061 (see section 4.4). iii) Engineer margins using plant species that will not encourage crop pests 1062 or diseases. iv) Carry out small-scale trials of engineered margins to compare different

1064 1065 1066 Identify pollination Survey landscapes Design engineered need and which for existing floral and habitat(s) to supplement pollinators are important nesting resources existing resources 1067 1068 1069 1070 Guidelines on establishment. Large-scale trials to assess Small-scale trial to refine 1071 management and where to if pollinators enhanced and seed mixes, optimise deploy to ensure maximum management and assess pollination improved. Cost-1072 farm coverage by pollinators benefit analysis usage by pollinators 1073 1074 1075

**Figure 10** Six primary steps to maximise the potential of engineered margins to support wild pollinators whilst minimising the amount of land removed from production. Between the Design and Small-scale-trial stages feedback will be required to 'optimise' management towards the target pollinator(s). Scaling up from Small-trial to Large-trials may have different and unforeseen outcomes, therefore, the dashed line represents feeding this information back to the design stage if this were to occur.

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1084 establishment methods across a range of soil and climatic conditions, and measure usage by 1085 pollinators and how this is enhanced within adjacent crops. v) Conduct larger-scale trials of 1086 engineered habitats across the landscape. vi) Evaluate the economic implications (a type of 1087 cost-benefit analysis) of removing land from production to provide the service in comparison 1088 to the increase in crop value. Step v should address spatial scales that consider abundance 1089 decay curves (estimated time of disappearance) from engineered habitats, requirements for 1090 corridors and existing resources provided by other non-crop and cropped habitats, and it 1091 should also evaluate whether crop pollination is improved relative to that in control areas.

1092 Such an approach could be conducted in conjunction with habitat development for natural 1093 enemies that also function as pollinators (e.g. certain hoverflies) or require similar resources 1094 (e.g. parasitoids that require nectar; Wratten et al., 2012).

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### 1096 **4.6 How might we improve the wider countryside to support insect pollinators**

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1098 A number of mitigation strategies are being implemented to conserve or enhance 1099 threatened biodiversity in agricultural landscapes. These often integrate conservation 1100 objectives with extensive farming practices in the same landscape, although many of these 1101 actions target more generic provision of resources for a range of wildlife rather than 1102 pollinators per se (Pywell et al., 2012). Specific actions of the AES for pollinators, such as 1103 retaining patches of uncropped flower-rich habitat and of planting floral resources (e.g. for 1104 declining bumblebee species), can increase the local abundance and species richness of 1105 foraging pollinators (Scheper et al., 2013; Wood et al., 2015b). In England, there is also now 1106 a Wild Pollinator and Farm Wildlife Package in the Countryside Stewardship that aims to 1107 support pollinators through provision of flower-rich and nesting habitats. A few studies show 1108 that such actions also enhance pollination services to nearby crops (see section 4.5; Garibaldi 1109 et al., 2014), but whether this reflects genuine increases in numbers or pollinators moving 1110 around with consequent dilution of densities elsewhere is largely unknown (Carvell et al., 1111 2014). So far, there is very little evidence that these actions make pollinator communities 1112 more resilient, which the underlying policy aim. From a policy perspective, the key questions 1113 are: i) what area and extent of land should be dedicated to such actions; ii) how should they 1114 be deployed spatially to have the best chance of success; and, iii) how does it work in practice 1115 (Dicks et al., 2015).

1116

1117 To date, the main focus for pollinator conservation actions has been on the design and 1118 provision of mixtures of flowers, whilst largely ignoring other potentially limiting factors, 1119 especially in temperate regions. These actions have traditionally focused on providing 1120 particular taxa with specific floral needs: for example, the response of declining, longer-1121 tongued bumblebees to the creation of legume-rich margins has received considerable 1122 attention (Heard et al., 2007). More recent studies have tried to tackle the question of how 1123 much flower-rich habitat is needed across different landscapes (Holland et al., 2015), 1124 including detailed studies of how bumblebees respond to flower provision (Carvell et al., 1125 2012; Heard et al., 2007), or how they alter their foraging patterns (Carvell et al., 2014), by 1126 estimating how much pollen and nectar some common species need to raise their larvae 1127 (Dicks et al., 2015). This has direct relevance as to whether the encouraged minimum area of 1128 land set aside within the AES is sufficient, as evidence suggests that only common species 1129 may benefit from current guidelines (Holland et al., 2015; Wood et al., 2015b). Therefore, the 1130 question is whether we need to achieve some threshold percentage area before we will see 1131 any significant effects on supporting stable insect pollinator assemblages? However, without 1132 long-term pollinator trend data it is difficult to identify target levels.

1133 Whilst the wider pollinator community can respond positively to local habitat floral 1134 management (Heard et al., 2012; Knop et al., 2006), there have been few studies of diversity 1135 and abundance responses at the farm scale or above. This is important since agricultural 1136 intensification influences biodiversity and ecosystem processes by reducing the 1137 heterogeneity, composition and configuration of habitats at difference spatial scales 1138 (Tscharntke et al., 2012). This is expected to have distinct effects on different pollinator 1139 guilds and pollination services but remains largely unexplored (Carvell et al., 2011; 1140 Holzschuh et al., 2007). There is still debate as to whether currently available AES are 1141 enhancing farmland biodiversity efficiently (Kleijn et al., 2011), especially pollinators 1142 (Scheper et al., 2013). In addition, there is concern that AES may suppress yields (e.g. 1143 through land-use costs), thereby increasing pressure on non-cropped habitats, with 1144 unintended negative environmental consequences. There is thus a clear need to understand 1145 and predict how wild pollinator community structure and functional attributes are altered by 1146 AES delivery and landscape configuration, especially if a balance must be struck between 1147 reducing the effects of multiple pressures and the wider need for more sustainable agriculture. 1148 The pollinator communities associated with different habitat types, landscapes and regions 1149 are being documented in various research projects and monitoring programmes (e.g. EU 1150 project QuESSA, UK project Agriland) are now under development (Baldock et al., 2015; 1151 Carvell et al., 2014). The relative importance of different specific resources or their spatial 1152 layout to pollinator communities could be estimated using existing ecological knowledge of 1153 many pollinators. These approaches could be combined in either highly parameterised 1154 process-based models or more generic conceptual models to explore to what extent different 1155 actions deployed in different scenarios at landscape scales meet biodiversity protection goals 1156 or alter the delivery of more sustainable agriculture (Kremen et al., 2007; Lonsdorf et al., 1157 2009; see: www.naturalcapitalproject.org/InVEST.html).

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- 1159 4.7 Insect pollinators in urban areas
- 1160

Pollinators in urban areas are relatively understudied in comparison to those in rural habitats, although interest in how urban areas might sustain pollinator populations and provide pollinator services has increased in recent years (Baldock et al., 2015; Bates et al., 2011; Bonaszak & Zmihorski, 2012; Geslin et al., 2013; Hernandez et al., 2009; Ireneusz-Hennig & Ghazoul, 2012; Sirohi et al., 2015). Pollinator services provided by insects in urban areas include pollination for urban food production (i.e. subsistence growing of vegetables 1167 and fruits) and pollination of native plant species that grow in urban areas, as well as 1168 providing aesthetic value to people desiring interaction with nature on their doorstep. Urban 1169 habitats can harbour important insect pollinator diversity, with the pollinator fauna of our 1170 towns and cities being at least as diverse as those of the surrounding countryside (Baldock et 1171 al., 2015; Sirohi et al., 2015). Considering that urbanised land cover in many countries has 1172 greatly expanded in the past few decades (for example, across UK (National Ecosystem 1173 Assessment 2011) and Europe (Gerard et al., 2010)), and that globally the proportion of 1174 people living in urban areas now exceeds 50% (UNFPA 2007), it is perhaps surprising that 1175 we know relatively little about the impact of towns and cities on insect pollinator populations, 1176 communities and networks (Geslin et al., 2013). Moreover, how should we manage urban 1177 areas most effectively to benefit pollinators? Given the recent policy interest in pollinator 1178 conservation (see section 3), practitioners require information and advice on how to manage 1179 public and private urban land to benefit pollinators. This is challenging, because perhaps 1180 more than any other habitat type, urban areas represent a matrix of different land use types 1181 (Wray and Elle, 2015), from car parks to allotments. Larger areas with more pollinator 1182 friendly habitat, such as nature reserves, parks, allotments and gardens, are connected by 1183 strips of potentially pollinator friendly habitat including roadside verges, hedgerows, river 1184 banks and canal towpaths, railway cuttings and embankments (Figure 11). Understanding 1185 how pollinator populations develop within such a 'grainy' landscape requires understanding 1186 of how habitat diversity, patch size and connectivity influences their meta-population 1187 dynamics (Cane et al., 2006; Perovic et al., 2015).

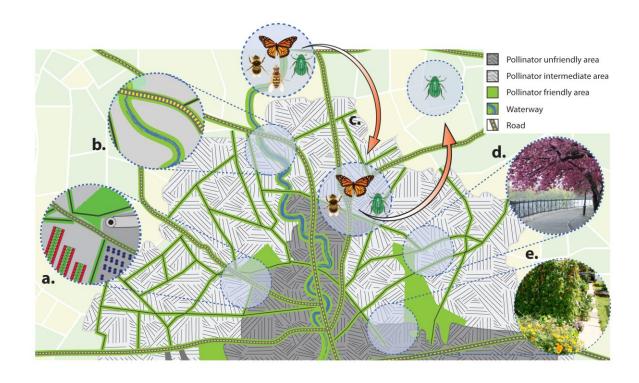
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We currently have a limited understanding of whether urban areas act as sources or sinks for pollinator populations, either in terms of population numbers or genetic diversity. We know that urban habitats can support high abundance and species richness of some 1192 pollinator taxa (bees) but not others (hoverflies) relative to farmland and nature reserves 1193 (Baldock et al., 2015), yet we know very little of the connectivity of pollinator populations 1194 across habitat types. Quantifying the scale and extent of pollinator movement into and out of 1195 cities is crucial to understanding the role of urban pollinator populations in regional 1196 ecosystem service provision. This issue is also linked to the roles of landscape features that 1197 allow population dispersal – particularly linear features such as hedgerows, roadside verges 1198 and waterways. It is important to know how habitat connectivity is influenced by pollinator 1199 traits, such as levels of generality in plant associations, population structure (e.g. social vs 1200 solitary bees) and observed relationships between body size and dispersal ability (Greenleaf 1201 et al., 2007; Hagen et al., 2012). Questions associated with population structure can be 1202 addressed using genetic analyses across urban-rural gradients, and across contrasting urban 1203 habitat types, replicated in a range of towns and cities of different sizes. In addition, more 1204 mark-release-recapture studies are required for direct estimation of dispersal and foraging 1205 distances over single generation, ecological timescales (Chapman et al., 2003).

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Little is known about the role of urban pollinators in mediating gene flow between 1207 1208 plant populations within and outside cities (Roberts et al., 2007). This will require a greater 1209 understanding of the intricacies of pollen transport, for example by linking pollinator 1210 dispersal with estimates of gene flow (Figure 11). On a landscape scale, rare long-range 1211 pollen dispersal events may be more important for maintaining the genetic diversity of 1212 populations than frequent but local pollen dispersal (Wilcock and Neiland, 2002). We also 1213 need to understand the efficacy and impact of pollen flow between the many cultivars of 1214 native or naturalised plant species grown in urban environments and native provenances in 1215 surrounding non-urban habitats. Such gene flow has the potential to maintain genetic 1216 diversity in native populations, or could harm them through outbreeding depression or

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1221 Figure 11 Representation of an urban landscape showing a dynamic environment a) Can 1222 insect pollinators be permanent residents in such habitats? A matrix of different land-use 1223 types that may be deemed as pollinator friendly (e.g. allotments, gardens, or hedgerows), or 1224 unfriendly (e.g. high density industrial, commercial or housing) areas. b) Are features such as 1225 verges of roads and waterways (and railways) important in allowing pollinator movement to 1226 connect patches of suitable resources within cities, as well as providing corridors for 1227 pollinator and plant gene flow? c) Species richness in some urban areas can be comparable 1228 with some rural areas (Baldock et al., 2015), and so we need to establish if urban areas act as 1229 pollinator sinks, drawing in pollinators from surrounding rural areas, or as sources, 1230 replenishing perturbed pollinator communities in rural areas. Either way, migration between 1231 urban and rural areas may be important in mediating plant gene flow between visited flowers. 1232 d) Bringing aesthetic value to urban areas by: observing pollinators on your doorstep, and 1233 benefitting from their pollination service such as increasing the health of visually beautiful 1234 flowering plants in parks, allotments and gardens. e) Increasing interest in urban food 1235 production (such as garden beans pictured), both domestically and commercially, requires a

healthy pollinator community in urban areas in a similar way to agriculture practices in ruralareas.

1238 The growing of food in cities has increased dramatically in recent times; worldwide, urban 1239 agriculture involves an estimated 100 million people (Eigenbrod and Gruda, 2015), covers an 1240 area of at least 68 million hectares, and accounts for around 16% of lands devoted to crops 1241 (Thebo et al., 2014). Previous studies have demonstrated that urban agriculture can support 1242 diverse communities of bees and butterflies (Matteson et al., 2008; Matteson and Langellotto, 1243 2010), but the value of the pollination services provided by pollinators in urban environments 1244 remains unquantified (Lin et al., 2015). To understand the economic value of pollinators in 1245 urban areas we need to identify the range and abundance of crops grown in urban areas, and 1246 the role of insect-mediated pollen flow for these crops (Van Rossum, 2009, 2010). 1247 Assessment of the ecosystem service value of urban pollinators requires estimation of the 1248 economic value of their contributions both to urban agriculture, and crop production in 1249 surrounding non-urban areas.

1250

1251 Management of urban habitats for pollinators requires understanding of how to 1252 improve habitat quality, and of how to link good quality habitat patches in ways that best 1253 support pollinator populations. Habitat connectivity is crucial to the maintenance of viable 1254 populations and pollinator species richness; urban areas are thought to restrict gene flow in 1255 some bumblebees (Jha, 2015; Jha and Kremen, 2013b) and some solitary bees (Davis et al., 1256 2010). However, it is very likely that different urban habitat types vary markedly in their 1257 impacts on dispersal and gene flow. We would expect pollinators to move more easily along 1258 flowering linear features than across large areas of flower-free man-made surfaces (though 1259 bees and butterflies will follow non-rewarding linear routes between flower patches; Cranmer 1260 et al., 2012). Flower-rich road verges, for example, not only support pollinators, but also 1261 provide potential dispersal routes, highlighting the need to develop management best practices for these and other linear features (Dicks et al., 2013; Hanley and Wilkins, 2015; Henriksen and Langer, 2013; Hopwood, 2008; Noordijk et al., 2009; Wojcik and Buchmann, 2012). The growing popularity of planted wildflower meadows in cities will increase food resources for pollinators, and perhaps more than any other single effect, individual human behaviour (in terms of the way we plant and manage gardens and other green spaces, such as parks and allotments) can exert significant impact on habitat quality for plants and pollinators.

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1270 To date, few studies have examined the effect of management approaches on urban 1271 pollinators, and those that have been carried out focus primarily on single sites (Blackmore 1272 and Goulson, 2014; Garbuzov et al., 2015). To guide management practice, future work 1273 needs to consider societal impacts as well as effects on biodiversity. We need to understand 1274 and quantify the impact on public health and well-being from enhancing public green-space 1275 for pollinators, and need to better understand the relationships between these benefits and the 1276 cost and frequency of management interventions in urban areas (such as mowing or pesticide 1277 application). Identification of general patterns, whilst appropriately accounting for site and/or 1278 year characteristics, requires longitudinal studies monitoring insect pollinators to elucidate 1279 the impacts of alternative management regimes and interventions over multiple sites and 1280 years.

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1283 5. Considerations when developing future research and mitigation
1284 strategies

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1286 A major goal in supporting insect pollinators is to get the right balance between land-

1287 use for anthropogenic activities, such as food production or urbanisation, versus the 1288 responsibility we have in conserving healthy and diverse insect pollinator populations and 1289 communities. To ensure we achieve this goal, a key approach to land management strategies 1290 is to enact evidence-based decision making rather than adopting uniform responses to 1291 political agendas. Policy initiatives designed to support excellent research to understand 1292 pollinator sustainability, with the intention of using research outputs to better inform decision 1293 making, should therefore be both applauded and supported. However, the challenges put 1294 forward to the research community often comprise very broad questions and goals that may 1295 not be straightforward to tackle or simple to implement. It is important that researchers 1296 communicate and feedback with both clarity and transparency about their intended and 1297 ongoing research, so that objectives can be developed in ways that are useful for researchers, 1298 policy and practice, as by doing so any mitigation actions requiring development can be 1299 achieved more rapidly and effectively.

1300

1301 It is also important that we align research developments by considering the concerns 1302 raised by stakeholders and identify areas which are suffering (or are at future risk) from 1303 pollination deficits. Consequently, researchers should look to co-develop proposals with the 1304 right balance of all stakeholders, from academic, conservation, industry, policy and 1305 practitioner backgrounds, with their needs considered in order to apply research to the 1306 practical world (Dicks et al., 2013; Turnhout et al., 2012). For instance, a common criticism 1307 is the ambiguity of the term, 'ecosystem service', when describing the process of pollination. 1308 When researchers use this term, it is important they consider the distinct difference between 1309 the study of ecosystems functions and ecosystem services, by considering how their research 1310 (for example on insect pollinators) also provides a direct or indirect socio-economic benefit, 1311 and how actions might then be implemented by land managers to deliver pollination services,

1312 especially in the specific case of improving flowering crop production or the health of wild 1313 flower populations. Furthermore, although understanding the specific risks posed to insect 1314 pollinators is no doubt crucial, it is only one piece of the whole puzzle. The remaining pieces 1315 required are to understand the actions required to mitigate such threats. To achieve this we 1316 require knowledge about the likely uptake of certain schemes and the behaviours of end-users 1317 that hopefully results in them taking action. Research needs to thus be tailored towards 1318 informing effective management to better inform viable management of the land to support 1319 insect pollinators. This latter point is critical because we need to consider wider values, such 1320 as how we might best meet the needs of farmers / land owners in rural areas, or perhaps 1321 planners, green space designers and residents in urban areas and consider providing the 1322 aesthetic and cultural values to the public.

1323

1324 Kennedy et al (2013), suggested that for each 10% increase in area of high-quality 1325 habitat (for bees), for instance a conversion of intensively farmed agricultural land to a more 1326 natural habitat land-use, could return around a 37% increase in species abundance and 1327 richness (for wild bees). Achieving this goal, however, may prove difficult because economic 1328 interests may conflict with conserving suitable habitats which is an issue of high relevance to 1329 large scale agriculture that relies on efficient land-use. Land managers appear to be relatively 1330 open to discussing the potential of managing land for pollinators, but they are looking for 1331 clear, concise and balanced advice about how to most effectively do this with as little cost 1332 and time incurred as possible. Thus, to most effectively deliver advice we must be 1333 considerate of the pressures placed on them. Farmers can be classed as custodians of the 1334 countryside, yet they are also businessmen and are under pressure to make a profit whilst 1335 meeting consumer demands for the countryside. For farmers to heed to specific advice, 1336 therefore, we should be attempting to provide a demonstrable, specific action, applicable to

their businesses (a 'true' not hypothetical ecosystem service). If we perceive an action as being an ecological enhancement of the land (in this case increasing stable pollinator communities and / or pollinator diversity) we need to make this relatively cost effective and make the link clear to how such an ecosystem service can provide potentially economic and / or even aesthetic enhancement. Similarly, the same principle approach should be taken when encouraging the general public to support insect pollinators, for instance, in designing garden habitats to support a diverse set of insect pollinators.

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1345 It is of further importance that the implementation of specific actions considers what 1346 the short versus long-term effects will be (Blaauw and Isaacs, 2014a). For example, when 1347 engineering habitats to help conserve insect pollinators, how long might it take for an 1348 agricultural field margin or urban flower bed sown with a 'pollinator friendly' plant seed mix 1349 to establish? How long does this plant community remain in flower and does the composition 1350 of flower species change over time? How long does the floral community remain attractive to 1351 insect pollinators, and how regularly does it need to be managed to keep it free of invading 1352 non-flowering plants? As we have discussed, concerted research efforts and knowledge 1353 exchange to determine and recommend the best implementation methods are thus required 1354 (Arlettaz et al., 2010), but this must be followed up with close monitoring to determine 1355 whether such recommendations actually benefit target insect pollinators (Stem et al., 2005).

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- 1357

## 1358 Contribution

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1360 The order of author appearance broadly depicts the level of contribution to the paper:1361 RJG administered the development, organised and put together the paper; RJG and SGP

initiated the collaboration; RJG, KCRB through to GW, and SGP contributed to conceiving
ideas, acted as champions of identified evidence gaps and were involved in writing the paper;
ANA provided significant input into putting the paper together; ANA through to PBS
contributed to conceiving ideas and comments on the paper. Figures were conceived and
produced by RJG, LAG, JMH, CQT and ANA.

1367

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1369

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## Appendix

**Table 2:** Selected global, regional and national initiatives relevant to pollinators and pollination service.

	Initiative name	Scale	Description
1	Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES)	Global	Independent intergovernmental body established to strengthen the science- policy interface for biodiversity and ecosystem services conservation and sustainable use of biodiversity, long-term human well-being and sustainable development. The "Pollinators, pollination and food production" assessment aims at enhancing policy responses to pollinator declines, and deficits in pollination.
2	Convention on Biological Diversity (CBD)	Global	CBD programme on agricultural biodiversity has an International Initiative for the Conservation and Sustainable Use of Pollinators. In addition the CBD Aichi Biodiversity Targets cover pollinators and pollination services.
3	International Pollinator Initiative (IPI)	Global	International Initiative for the Conservation and Sustainable Use of Pollinators Plan of Action consists of four basic elements: Assessment, Adaptive Management, Capacity Building, and Mainstreaming. FAO has been coordinating and facilitating the implementation of the IPI by undertaking, in collaboration with numerous partners, activities that contribute to the implementation of these four elements.
4	Sustainable Development Goals (SDGs)	Global	SDGs will replace the Millennium Development Goals with a change in paradigm with biodiversity now having its own goal. Goal 15: "Protect, restore and promote sustainable use of terrestrial ecosystemsand halt all biodiversity loss" which will help underpin Goal 2: "End hunger, achieve food security and adequate nutrition and promote sustainable agriculture".
5	Global Pollination Project	Global	Global Environment Facility (GEF) funded project to consolidate the knowledge base to inform good agricultural practices to improve food security, nutrition and livelihoods through enhanced conservation and sustainable use of pollinators (Brazil, Ghana, India, Kenya, Pakistan, Nepal and South Africa). The project is coordinated by the Food and Agriculture Organization of the United Nations, with implementation support from the United Nations Environment Programme (UNEP).
6	Prevention of honeybee Colony Losses (COLOSS)	Global	COLOSS is an international, non-profit association headquartered in Bern, Switzerland focussed on improving the well-being of bees at a global level. COLOSS is composed of scientific professionals incl. researchers, veterinarians, agriculture extension specialists, and students from 69 countries.
7	Global Biodiversity Information Facility (GBIF)	Global	GBIF is an international open data infrastructure, funded by governments that allows anyone, anywhere to access data about all types of life on Earth, incl. many pollinator species, shared across national boundaries via the web.
8	International Commission for Pollinator Plant Relationships (ICCPR)	Global	ICCPR has the following objectives to: (i) Promote and coordinate research on relationships between plants and bees; (ii) Organise meetings, colloquia or symposia related to the above topics, and to publish and distribute the proceedings; (iii) Collaborate closely with national and international institutions interested in the relationships between plants and bees, particularly those whose objectives are to expand scientific knowledge of animal and plant ecology, and fauna protection.
9	Status and Trends of European Pollinators (STEP)	Regional (Europe)	Large scale research project funded by the EC which is assessing the status and trends of pollinators in Europe, quantifying the relative importance of various drivers and impacts of change, identifying relevant mitigation strategies and policy instruments, and disseminate this to a wide range of stakeholders.
10	Sustainable pollination in Europe - joint research on bees & other pollinators (SUPER-B)	Regional (Europe)	SUPER-B is a knowledge exchange network bringing together scientific and societal communities involved in the conservation and sustainable management of ecosystem services mediated by pollinators

11	North American	Regional	NAPPC's mission is to encourage the health of resident and migratory
12	Pollinator Protection Campaign (NAPPC) African Pollinator	(N. America) Regional	pollinating animals in N. America to: (i) Raise public awareness and education and promote constructive dialogue about pollinators' important to agriculture, ecosystem health, and food supplies; (ii) Encourage collaborative, working partnerships among participants and federal, state and local government entities. This will strengthen the network of associated organizations working on behalf of pollinators; (iii) Promote conservation, protection and restoration of pollinator habitat; (iv) Document and support scientific, economic and policy research - creating the first-ever, international data bank (library) of pollinator information API has two main purposes to: (i) facilitate African country participation in
	Initiative (API)	(Africa)	the International Pollinator Initiative's (IPI) global pollinator project; and (ii) improve pollinator biodiversity conservation, and the pollination of crops and wild plants through networking.
13	Oceania Pollinator Initiative (OPI)	Regional (Oceania)	Key functions of the OPI are to: (i) 1.Monitor pollinator decline, its causes and its impact on pollination services; (ii) Address the lack of taxonomic information on pollinators; (iii) Assess the economic value of pollination and the economic impact of any decline; (iv) Promote conservation, restoration, and sustainable use of pollinators in agriculture and ecosystems.
14	England's National Pollinator Strategy (NPS)	National (England, UK)	NPS vision is to see pollinators thrive, so they can carry out their essential service to people of pollinating flowers and crops, while providing other benefits for our native plants, the wider environment, food production and overall human welfare.
15	Brazilian Pollinator Initiative (BPI)	National (Brazil)	BPI focuses on national policies, research, scientific meetings and learning activities. A national evaluation on pollinator and pollination status in Brazil is under construction, and strategies and actions are underway to consolidate the Brazilian Pollinators Network.
16	White House – Pollinator Research Action Plan	National (USA)	As part of a larger Federal strategy to ensure pollinator health, President Obama issued the Presidential Memorandum "Creating a Federal Strategy to Promote the Health of Honey Bees and Other Pollinators." The memorandum called on the Federal government to draft a pollinator research action plan
17	Wales Action Plan for Pollinators	National (Wales, UK)	Welsh Government has worked with industry and stakeholders to look in more detail at the evidence and issues around pollinators and their conservation in Wales. Following consultation the Action Plan for Pollinators sets the strategic vision, outcomes and areas for action to improve conditions for pollinators and work to halt and reverse their decline in Wales.
18	Canadian Pollination Initiative (CANPOLIN)	National (Canada)	CANPOLIN was a large scale research project addressing the growing problem of pollinator decline in agricultural and natural ecosystems in Canada.
19	French National Action Plan	National (France)	A ten point action plan for pollinators
20	Insect Pollinators Initiative (IPI)	National (UK)	UK research funders invested £10m in an Insect Pollinator Initiative which supported multiple research projects aiming to understand the causes and consequences of threats to insect pollinators.