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**Protecting an ecosystem service: approaches to understanding and mitigating  
threats to wild insect pollinators**

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## Abstract

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

## 1. Importance of insect pollination

### 1.1 Providing an ecosystem service

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

Of the multiple roles that insects play, pollinating flowering plants is a process that is of the utmost importance in terrestrial environments and one which provides vital ecosystem services for human wellbeing (Carpenter et al., 2006; Garibaldi et al., 2011a, 2014). Over 85% of described flowering plant species are dependent, to some degree, on animal pollination (Ollerton et al., 2011), with mobile foraging insects accounting for the vast majority of this activity (Kremen et al., 2007). Insect pollination maintains genetic diversity in plant populations (Kearns et al., 1998), and provides advantages such as increased fruit 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

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 > €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).

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

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



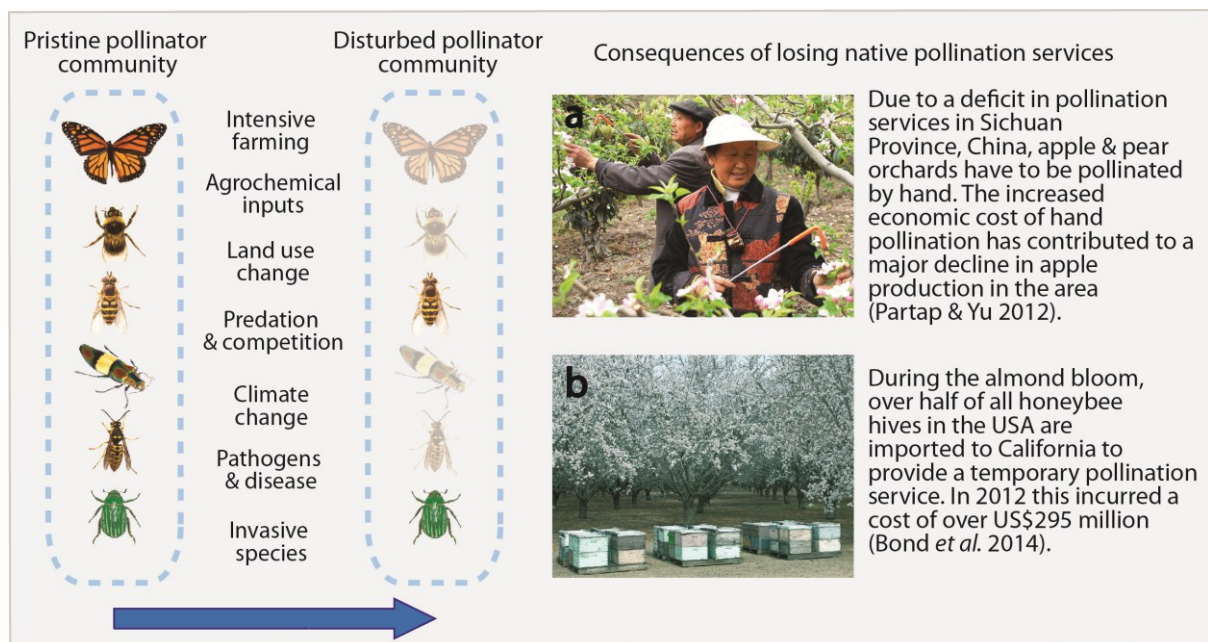
147 **Table 1.** Selected recent studies showing the effects of wild or managed pollinators on commercially important crops. Studies consist of reviews  
148 of primary literature that present an overview of the global picture (1-3) and recent studies showing experimental manipulations that did not  
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	<i>Apis mellifera</i> , 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	<i>Apis mellifera</i> , <i>Bombus</i> spp. Hoverflies	Oilseed rape ( <i>Brassica napus</i> )	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 ( <i>Malus domestica</i> )	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	<i>Apis mellifera</i> , <i>Osmia bicornis</i>	Strawberry ( <i>Fragaria x ananass</i> )	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	<i>Apis mellifera</i> , <i>Bombus</i> 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	<i>Apis mellifera</i> 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)

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

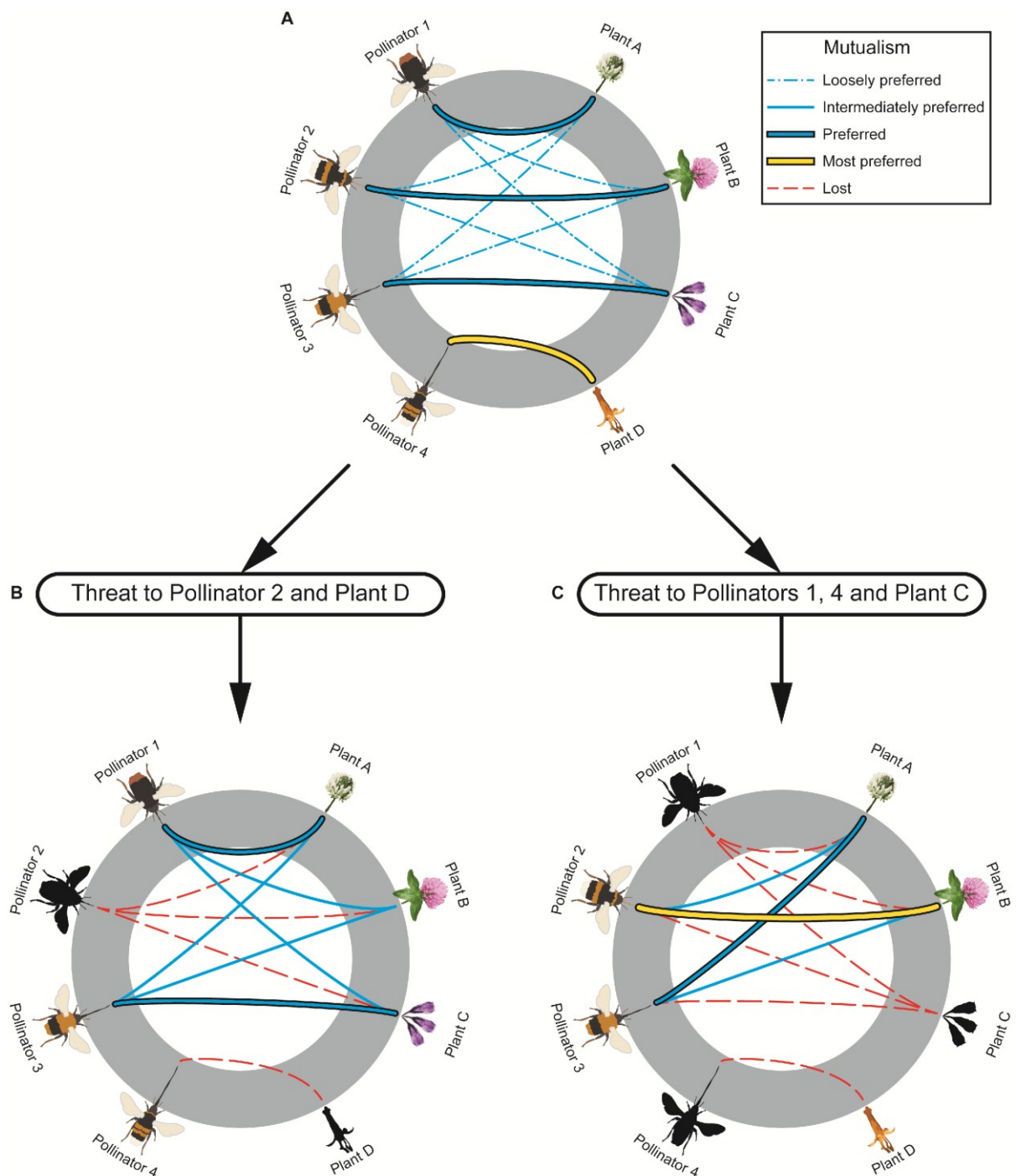
## **1.2 Brief introduction to pollination ecology and the importance of wild pollinators**

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



**Figure 1|** Combined and interactive set of environmental stressors can threaten pollinator communities. Persistently induced stress may lead to pollinator population declines resulting in the composition and stability of pollinator communities to be affected with potential loss of 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 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 services have led to the implementation of extreme measures, including costly replacement by: a) employing human labour to hand pollinate flowers (Partap and Yu, 2012; photo taken 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 which visit flowers for nectar and pollen rewards, but certain Orders constitute the vast majority of insects providing a pollination service: the Coleoptera (beetles), Diptera (flies), some Hemiptera (true bugs), Hymenoptera (bees, many wasps & some ants), Lepidoptera (butterflies & moths) and Thysanoptera (thrips).

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



221

222 **Figure 2**| Simplified and hypothetical plant-pollinator network, showing a community of four  
 223 insect pollinator species and four flowering plant species and the potential consequences of  
 224 localised species extinction(s) to network structure. Scenario A) Pollinators 1-3 and plants A-  
 225 C show a generalist mutualism, where each pollinator and plant has a preferred relationship  
 226 (shown by line thickness and colour), but will also visit / receive other inter-specifics to  
 227 subsidise their nectar or pollen intake / pollen transport. The strength of the mutualism may  
 228 be dependent on pollinator competition, for instance: pollinator 1 has a preference for plant A

and can theoretically competitively exclude (to some degree) pollinators 2 and 3 from visiting plant A (Brosi and Briggs, 2013; Sauve et al., 2014). Pollinator 4 has a longer tongue compared to the other pollinators, and a specialised mutualism with plant D with no competition from the other pollinators as they are unable to reach the nectar reward at the base of plant D's long corolla. Thus, pollinator 4 has a high preference, or dependency, on plant D. Scenario B) Loss of pollinator 2 (i.e. local extinction) changes the preference (or dependency) of the other two pollinators due to competitor release: plant B receives higher visitation rates from pollinator 1 and 3 compared to when pollinator 2 was previously present. This shows that the generalist network has a level of redundancy where other pollinators with similar functional traits (i.e. tongue length) can fill the role of pollinator 2 and maintain a population of plant B in the community an example of network re-wiring. In contrast, loss of plant D is likely to affect pollinator 4 more significantly, and dependent on the ability to visit short corolla flowers, will reduce population size, showing there is lower redundancy in this specialist network. Scenario C). If pollinator 4 were to be lost this would cause localised extinction of plant D. Loss of pollinator 1 will cause competitive release for pollinators 2 and 3, but with loss of plant D, it will likely change preferences (or dependency) for plant A and B as well. It will likely strengthen the preference between pollinator 2 and plant B as less floral resources are available. Pollinator 3 will have to change its preference to plant A as it will encounter high competitive exclusion when visiting plant B.

Having numerous specialist mutualisms within a plant-pollinator community, whereby the plant and pollinator are specialised on each other (and interact with fewer other species) may increase overall functional trait diversity. However, this may result in low functional redundancy at the community network level due to a lack of substitutable species traits or, in other words, there are a small number of pollinators and/or plant species possessing compatible functional traits to fill the functional gap should either mutualist decline (Figure 2; Mouillot et al., 2013; Weiner et al., 2014). The spectrum of interactions spanning generalist to specialist interactions is important in determining how some plant-pollinator relationships remain relatively stable under environmental change, whilst others 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).

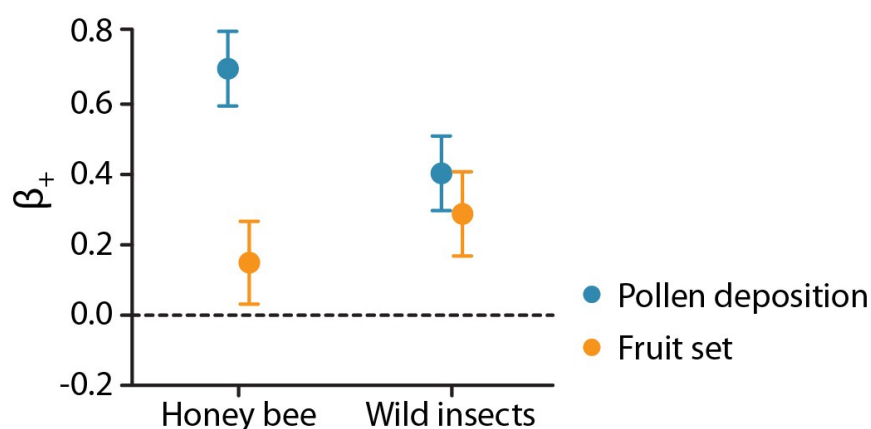
Bees are frequent and effective pollinators of wildflowers and agricultural crops (Kleijn et al., 2015). Social bees (e.g. honeybees, bumblebees, stingless bees), in particular, have become a focus of insect pollinator studies, in which the numerical abundance of workers per colony make them a dominant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

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

importance of all remaining wild pollinators and the threats they face should not be overlooked (Figure 3; Ollerton et al., 2012; Winfree et al., 2007). Indeed, to have a sustainable pollination service we cannot rely on one or a few domesticated species. Rather, we must maintain a community constituting a diverse set of mobile pollinating organisms with a broad suite of functional traits to maintain pollinators with ‘insurance values’ to meet multiple pollination demands and prevent future pollination deficits (Albrecht et al., 2012; Breeze et al., 2014; Gagic et al., 2015; Garratt et al., 2014b; Hoehn et al., 2008; Isbell et al., 2011; Mallinger and Gratton, 2015; Martins et al., 2015; Orford et al., 2015; Winfree et al., 2007; but see: Winfree et al., 2015). Crop pollination services can be enhanced when having a diverse community of insect pollinators (Brittain et al., 2013a, 2013b; Greenleaf and Kremen, 2006; Hoehn et al., 2008). Moreover, native and/or wild pollinators are more efficient at pollinating certain plant species than honeybees (Figure 3; Garibaldi et al., 2014; Jauker et al., 2012; Rader et al., 2013; Stanley et al., 2013; Thomson and Goodell, 2001; Vicens and Bosch, 2000; Woodcock et al., 2013), and that long tongued wild pollinators can effectively pollinate plants that may not be accessible for short-tongued pollinators such as honeybees (Willmer, 2011). Yet despite the clear importance of wild pollinators, we have as yet: i) a limited understanding of their population status; ii) major gaps in our knowledge of the factors that threaten them and the subsequent impairment to the services they provide; and iii) still much to learn about how we can change our actions and refine our approaches to help 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  
 312 average regression coefficients ( $\beta_+$ ,  $\pm 95\%$  CI) for pollen deposition and fruit set. The figure  
 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.

318

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

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.

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

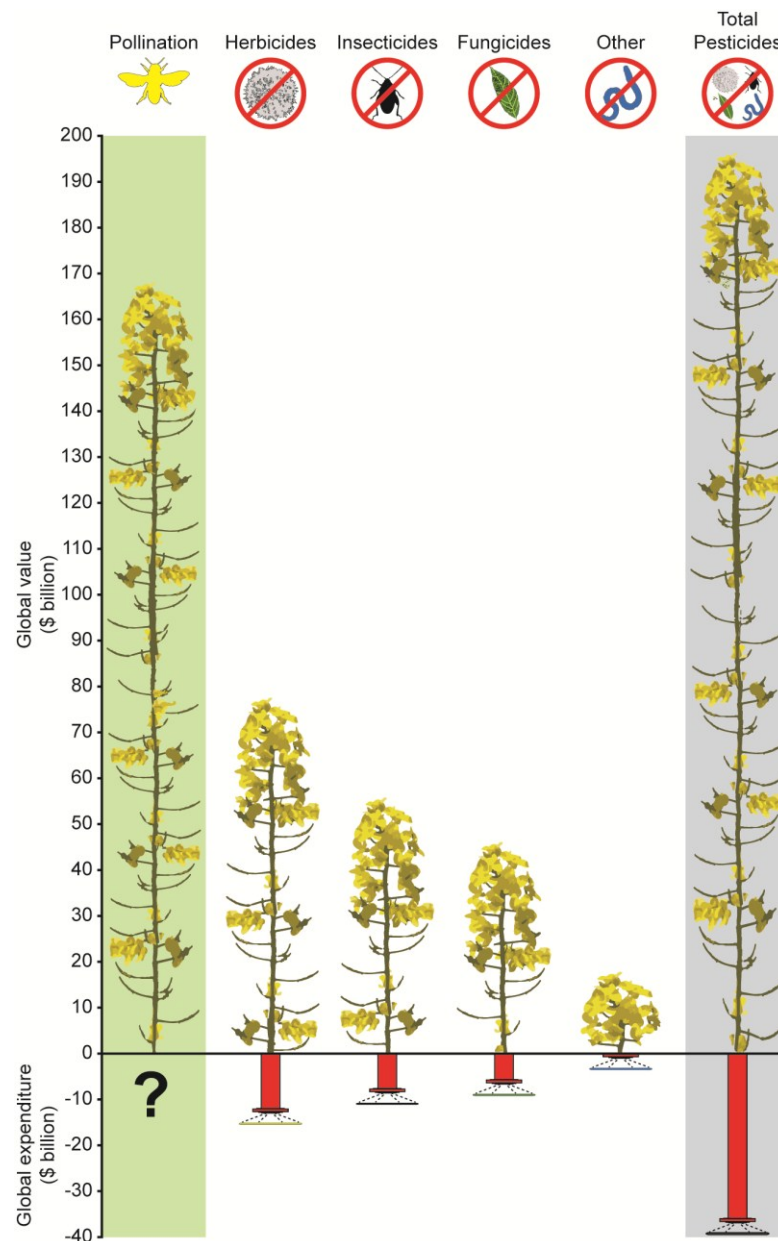
Multiple factors likely act in combination to impose an overall level of stress on insect pollinator populations (Bryden et al., 2013; Goulson et al., 2015; Perry et al., 2015; Vanbergen et al., 2013). Implicated factors include climate change, habitat fragmentation, land-use change and associated chemical inputs to the environment (i.e. agrochemicals), invasive species and the added pressures of predation and competition (Godfray et al., 2014; Gonzalez-Varo et al., 2013; Goulson et al., 2015; Kerr et al., 2015; Morales et al., 2013; Potts et al., 2010a; Vanbergen et al., 2013, 2014a). Infection by parasites (and pathogens) also poses a particular biotic threat, for example wild populations of the western honey bee, *Apis mellifera*, have largely disappeared across Europe and N. America which may be attributed to the parasitic mite *Varroa destructor* (Rosenkranz et al., 2010) and the viruses it transmits (Le Conte et al., 2010; Sumpter and Martin, 2004). Managed honey bee colonies survive due to significant prophylactic and reactive management techniques, and wild bumblebees are also threatened by a range of emerging diseases (see section 4.3; N. America: Cameron et al., 2011; UK: Fuerst et al., 2014; McMahon et al., 2015; S. America: Arbetman et al., 2013;

Schmid-Hempel et al., 2014). Given that many parasites appear to be both generalists and transmitted via flowers, it is likely that solitary bees and other insect pollinators are also at risk, but we currently lack the appropriate data to gauge such threats.

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

have decreased more recently (Carvalho et al., 2013).

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



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

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

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

Identifying the drivers that shape insect pollinator population abundance requires both

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

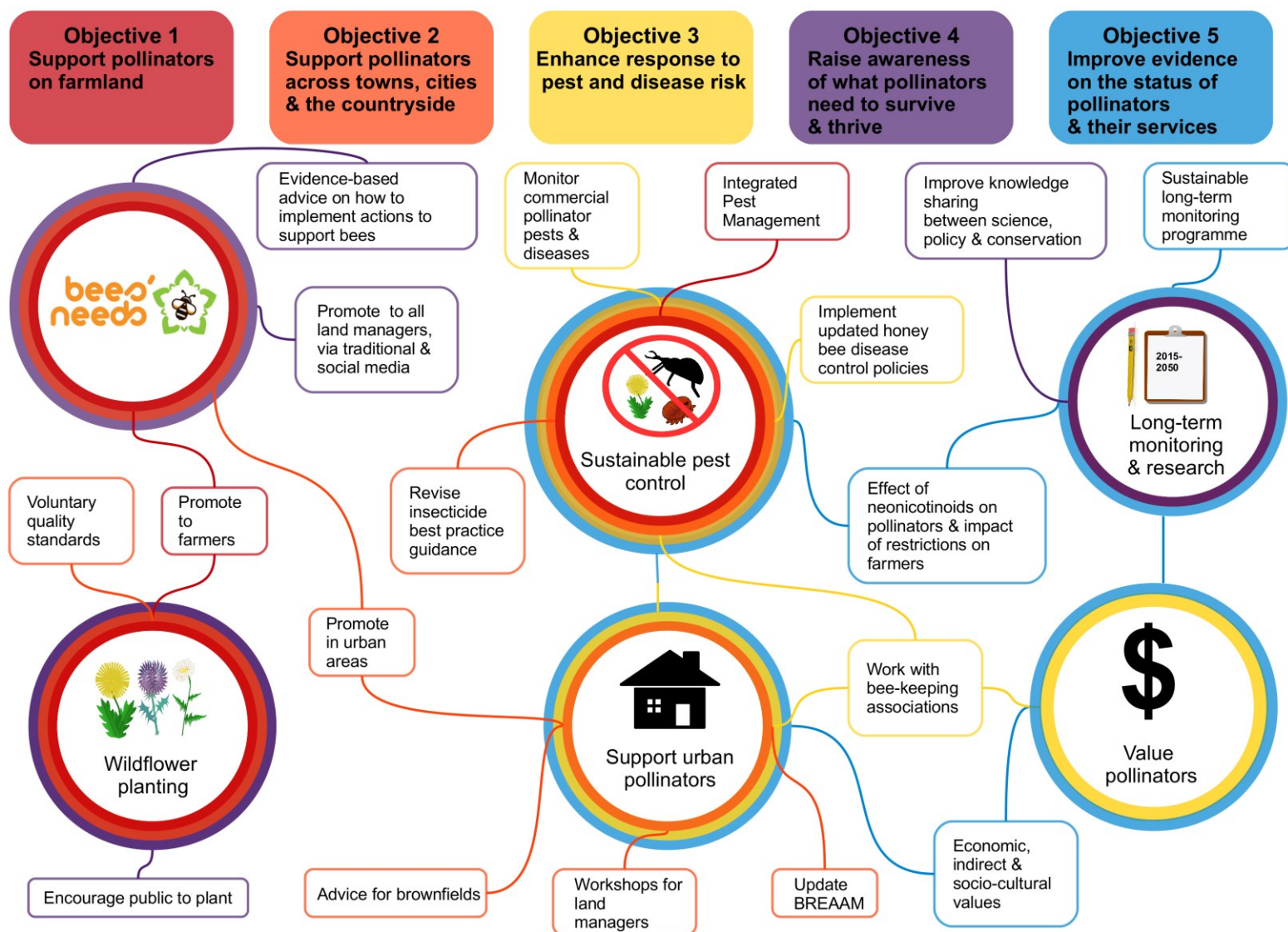
### **3. Steps in the right direction to protect insect pollinator services: policy actions**

Mitigating threats to insect pollinator services has become an important issue for policy and the public. A range of conservation initiatives have been developed to improve understanding of the risks posed, and how to deliver a sustainable pollination service at global, regional and national scales (Table 2). Advancing ecological research into insect pollinators requires an understanding of where current policy stands and how research 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).

The recently launched National Pollinator Strategy for England (Defra, 2014) provides an exemplary case study, in which an independent review of the “status and value of pollinators and pollination services” was commissioned to provide a framework for future 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; iii) raise awareness of what pollinators need to survive and thrive; and, iv) improve the evidence on the status of pollinators and the service they provide. These objectives were accompanied by statements of approach for how they should be achieved, by: a) developing and field testing a new monitoring framework to provide abundance data for insect pollinators and to integrate citizen science; b) assessing economic, social and cultural values of pollinators; and, c) to better understand how agricultural practices, in particular crop protection, affect insect pollinator populations (see Section 4 and Figure 5). The strategy also encourages the research community to carry out longer-term studies that policy-makers need, and policy makers to maintain a continuity of policy approach across different parliaments, negating the traditional short-term government view that can often hinder conservation actions (Pullin et al., 2009).





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

To support wild insect pollinators, agricultural land can be managed to deliver a broad array of public goods, by combining food production alongside other ecosystem services such as maintaining culturally valuable insect pollinator habitats. Within the EU, for instance, the Common Agricultural Policy (CAP) can compensate agricultural land managers (i.e. farmers) for direct losses to income when altering the intensity of farming practices to better support biodiversity and public goods. Through agri-environment schemes (AES) financial compensation is provided to help offset loss of income from setting-aside land that could 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; Batary et al., 2011; Garibaldi et al., 2014; Rundlöf et al., 2013). AES can be used to target ecosystem services that generate yield benefits in agriculture, such as insect pollination, although this objective should be clearly separated from their use to conserve biodiversity, because the necessary actions are likely to be different (Ekroos et al., 2014, Kleijn et al., 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 additional resources for insect pollinators.

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

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

#### **4. Understanding and mitigating specific threats to wild insect pollinators to protect pollinator services**

Understanding the responses of insect pollinators to environmental stressors is important in understanding how we can manage a sustained pollinator service for the future, making it a major priority for both research and policy (Vanbergen et al., 2014a). Given the

complexity of these biological systems, we must avoid approaching pollinator management in 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 pollinators cannot be assumed to be effective if landscape context and land-use type have not been considered. Whilst the objective is to increase biodiversity, many actions will only support increased numbers of common pollinator species rather than re-establishing endangered species (Scheper et al., 2013). It would be unfortunate if advisory actions to support pollinators were communicated to end users based on poorly informed decisions resulting in little practical and conservation impact, as the ramifications are likely to result in a loss of confidence in policy advice along with unwarranted financial costs (Pe'er et al., 2014).

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

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

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

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

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

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 analysing field collections to enable measures of taxonomic diversity and a high-throughput quantification of species abundance (Bohmann et al., 2014; Keller et al., 2015; Richardson et al., 2015), to re-construct with high precision and accuracy the structure of different plant-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 al., 2013; Lebuhn et al., 2013), and quantify pollinator community structure under different environmental stresses or contexts.

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

Obtaining data to study insect pollinator population sizes and pollinator network ecology are reliant on taxonomic identification of species and counts of individuals. For monitoring purposes, quantitative surveys (recording richness and abundances of organisms) are preferable to qualitative surveys (establishing only presence of species per locality: Kerr et al., 2015), but both suffer from time consuming sorting, identifying and counting plant and pollinator diversity, making it slow and financially costly for active management (Lebuhn et al., 2013). Moreover, taxonomic experts are needed regularly but this may not be possible if experts are few and in high demand. Researchers are therefore exploring the developments of novel molecular tools to aid the efforts in both identification and quantification (Kuhlmann, 2015), with the aim of providing greater taxonomic precision, a robust method of monitoring aspects of pollinator populations and to quantify pollinator community structure under 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



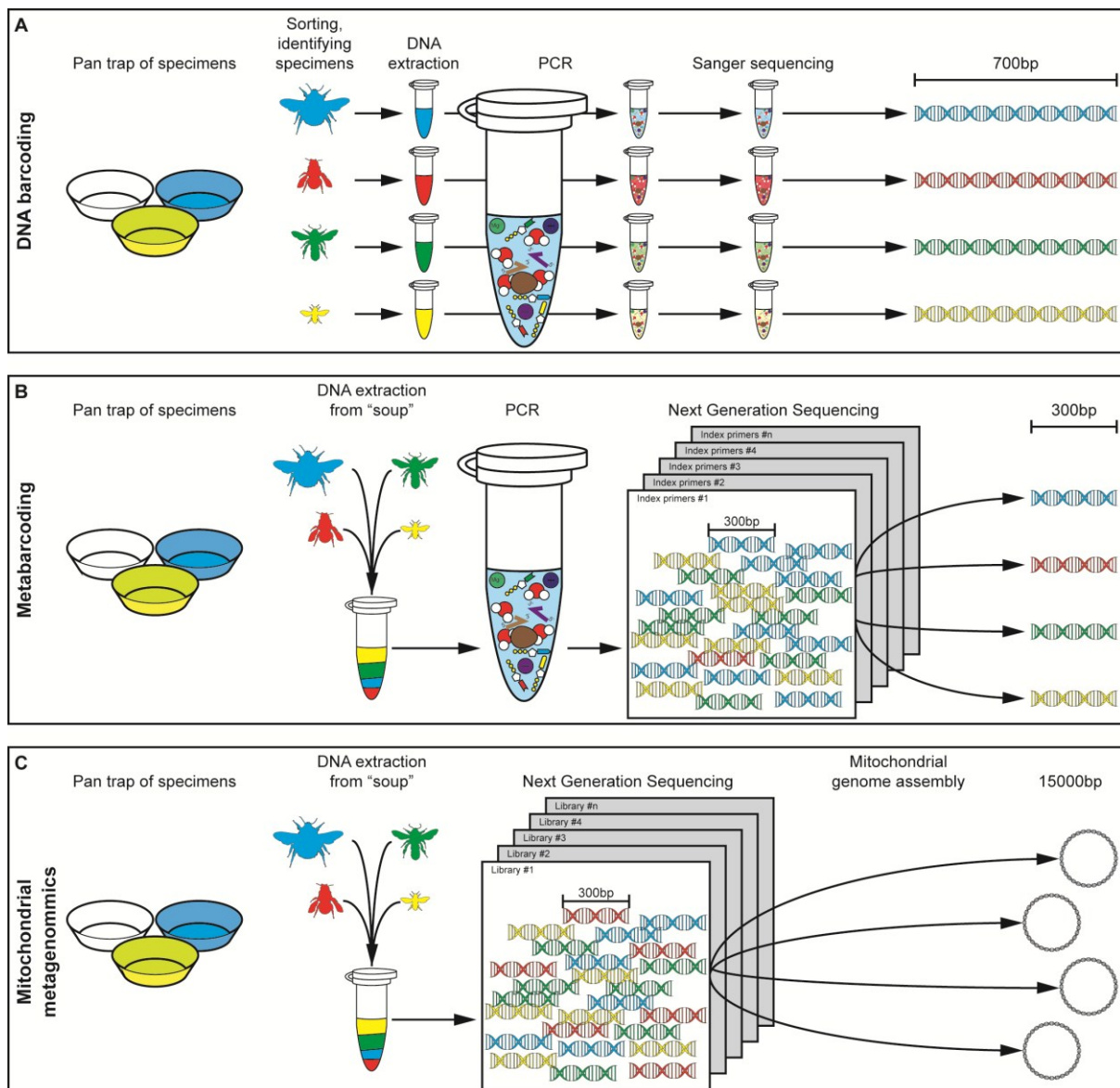
repeatedly over time to assess trends and react adaptively to protecting insect pollinator services.

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

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

possibility to generate sequence data from preserved specimens, as those in museum collections, which can establish the link to known vouchers of taxonomic relevance or to monitor change over time against historical specimens (Hebert et al., 2013; Timmermans et al., 2015). The resulting database of reference sequences then becomes part of a growing framework of genotypes from wider surveys that extend the biogeographic, ecological and taxonomic scope of pollinator studies.

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

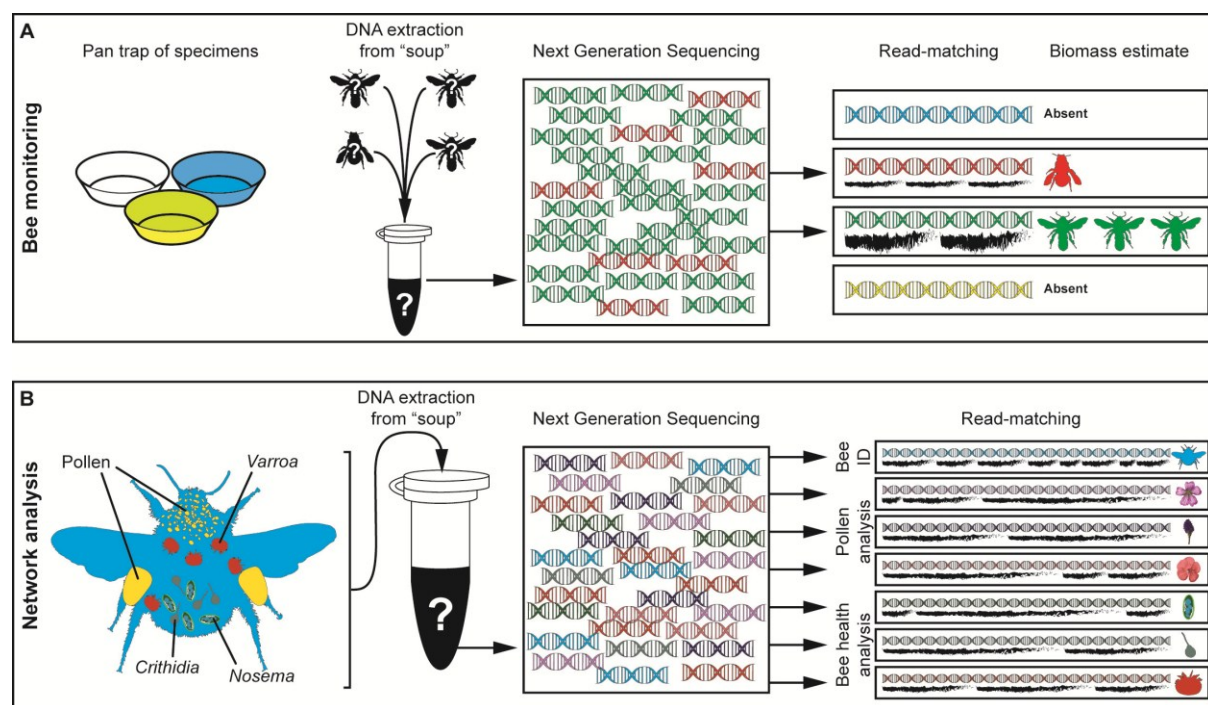


**Figure 6** DNA barcoding, metabarcoding and mitochondrial metagenomics pipelines. **A** Specimens collected (e.g. pan trap) must first be identified by expert taxonomists. For DNA barcoding, specimens and all downstream processes must be kept separate. The DNA from each representative specimen is extracted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

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

Given these drawbacks, the use of PCR-free methods is desirable. Current approaches 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 other markers. Total DNA is extracted from a bulk sample of specimens and subjected to shotgun sequencing to produce millions of short reads. Genome assembly from these reads produce full or partial mitochondrial genomes for each of the species present in the mixed sample. This approach, known as mitochondrial metagenomics (Crampton-Platt et al., 2015), was recently applied to bee communities and provides powerful ‘super-barcodes’ used as a 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 traps that attract and collect flying insect pollinators). Shotgun sequences from the bulk sample are matched against the reference library thus revealing the presence and absence of species from the read-matches. Crucially, this analysis requires many fewer reads than the initial assembly of generating the mitochondrial genome references. Profiling success using this approach has been high (>95%, taking into account false presences and absences combined: Gómez-Rodríguez et al., 2015), and much higher than using metabarcoding (Tang et al., 2015). In addition, studies have established the correlation of read number with abundance and biomass (Gómez-Rodríguez et al., 2015; Tang et al., 2015; Zhou et al., 2013),

and thus read matching can potentially be used for assessment of species abundance (we 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 mapping approach which is approximately 50% less labour intensive than the conventional survey work based on morphological identifications. Alternative approaches for abundance 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 thousands of specimens whose identification is based on sequence data on which to base the specimen count (Meier et al., 2015; Tang et al., 2015; Wong et al., 2014).



**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.

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

would be possible to detect all of the diseases simultaneously.

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

Wild pollinators exist in complex and diverse assemblages. In unperturbed assemblages, endemic parasites may control populations of individual species when showing host specialisation, or, if they are multi-host parasites act through apparent competition to modulate the relative abundance of different species (Dobson, 2004; Holt and Pickering, 1985). In perturbed assemblages, where the abundance of subsets of species is depressed through human impacts, effects of reservoirs (where one host acts as the major carrier of the parasite) and spill-overs (where the parasite is transmitted from reservoir to non-reservoir hosts) may drive host species with anthropogenically reduced populations to extinction (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 extinction if they spread rapidly and have high impacts on individual fitness (de Castro and Bolker, 2005). Hence, understanding the top-down pressure placed on insect pollinator populations by endemic and emerging parasites, alongside infectious diseases (EIDs), is important given that maintaining healthy populations is a prerequisite for a healthy pollination service (Brown, 2015). For example, concerns have been raised over the effect that parasites and infectious diseases are having on the overall pollination service provided by honeybees, as individual infection can impair individual foraging performance (Wolf et al., 2014), and high prevalence in colonies can lead to significant problems (Dainat et al., 2012; Higes et al., 2008; Martin, 2001; Nazzi et al., 2012).

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

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

If we are to understand the impact of endemic parasites and EIDs on wild pollinator populations and its subsequent effect on pollinator services, a number of key questions need to be addressed. First, we need to map the drivers of population dynamics and identify the relative importance of endemic parasites and EIDs within this larger picture. This requires studies of population dynamics within and across years at the same site (see next section 4.4), and the quantification of potential limiting resources, predators, and parasites. Second, the directionality of EIDs needs to be confirmed – who is giving what to whom across the season? And the degree of impact of EIDs on wild pollinators needs to be determined in laboratory studies (Graystock et al., 2013). Third, we need to understand the drivers of 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.

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

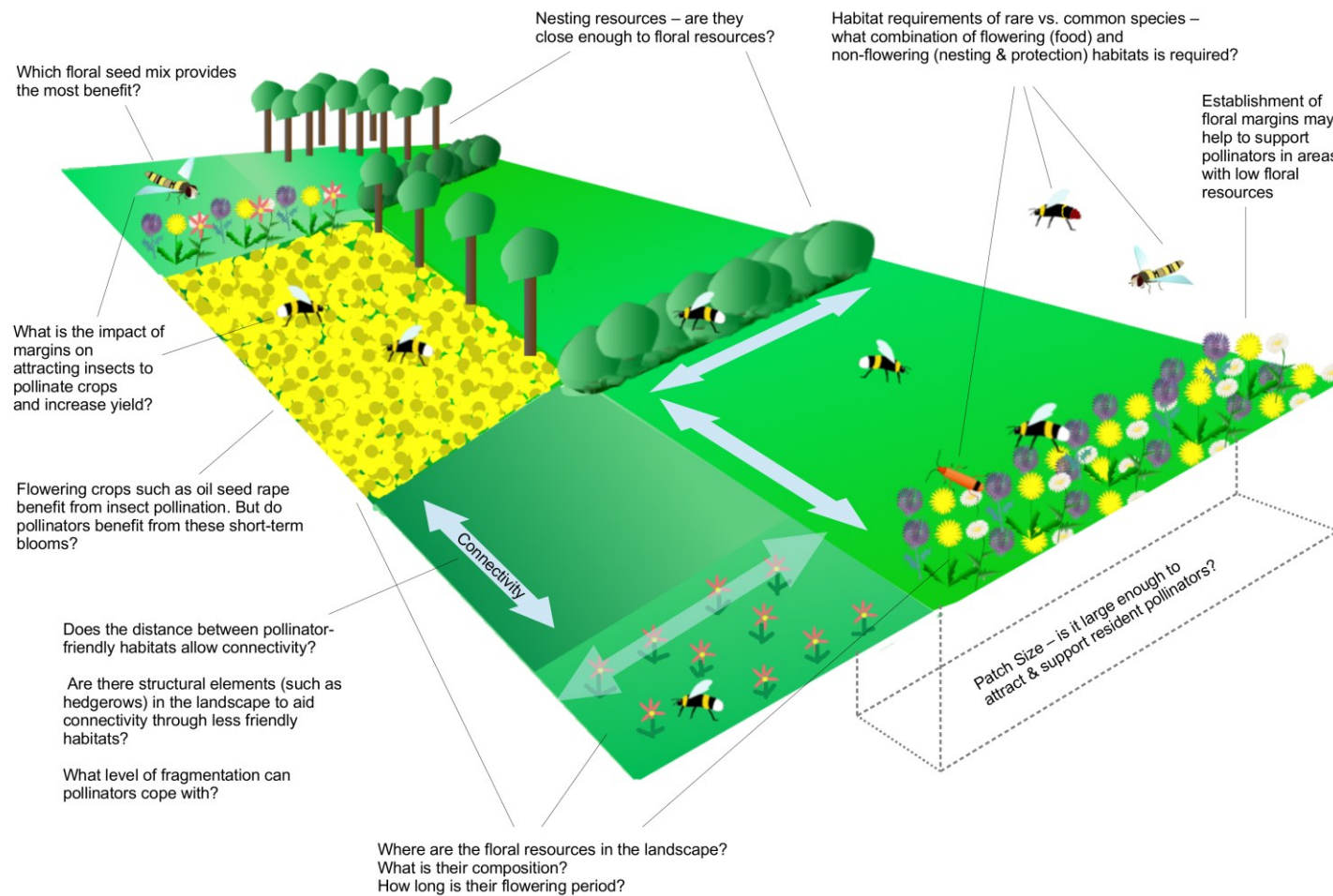
Meeting local pollination demands reliably and throughout the year requires large insect pollinator populations to provide numerical and functional responses to temporal changes (Lautenbach et al., 2012; Polce et al., 2014), and to be stable with long-standing residency in local areas (Klein et al.,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

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

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

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

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

927

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 Tschamtker, 2002; Greenleaf et al., 2007;  
951 Knight et al., 2005; Osborne et al., 1999; Pasquet et al., 2008), and this will be further

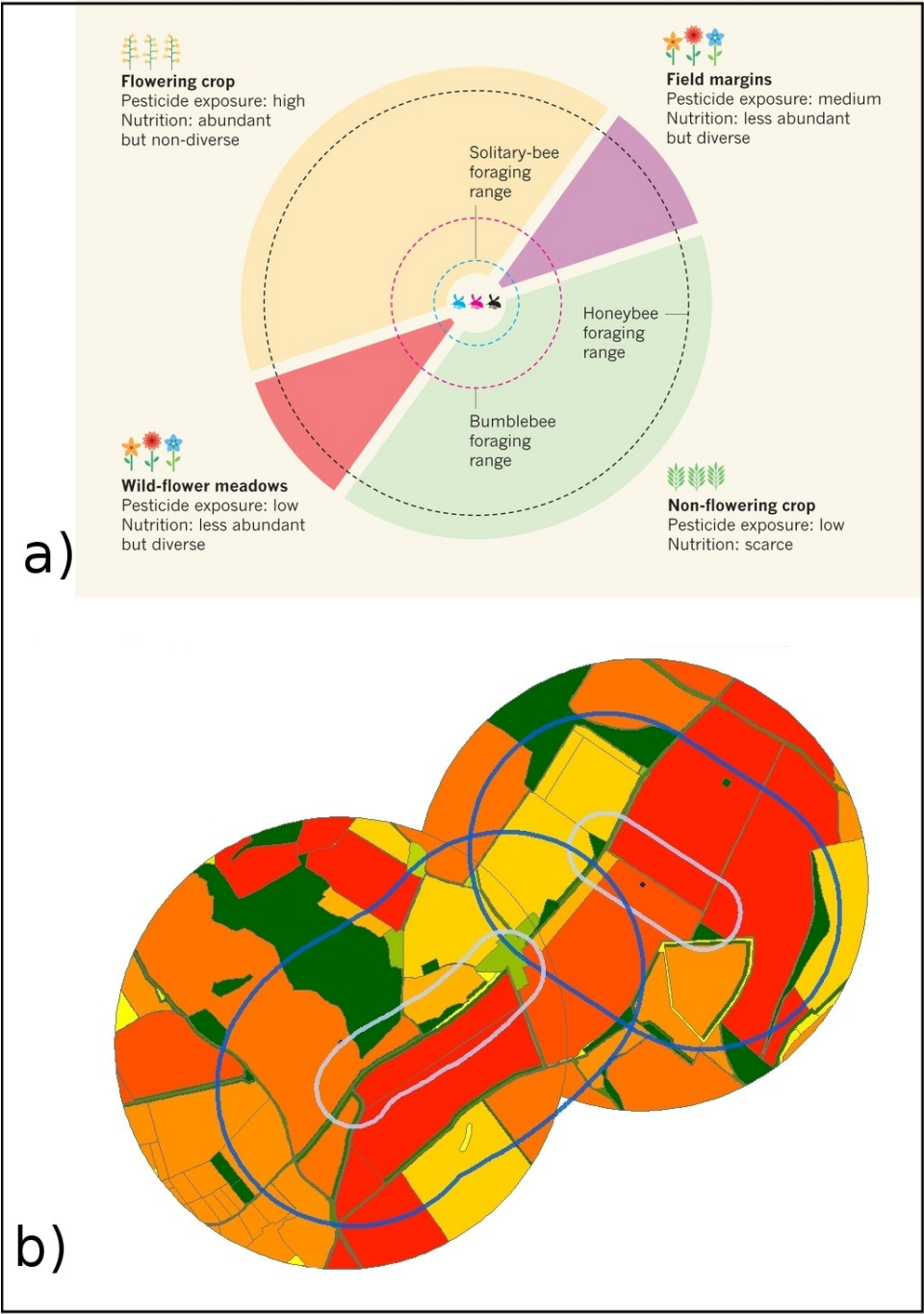
influenced by climatic variables, such as temperature and wind-speed. To inform habitat management practices, efforts should be focused on advancing our understanding on the foraging / dispersal abilities in different landscape complexities for a diverse set of pollinators (Figure 9), taking into consideration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

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

Engineering of certain habitats can increase the delivery of floral resources, nesting areas and protection to support a greater insect pollinator abundance and richness of insect pollinators which can in turn provide a pollination service to improve crop yields, including its reliability and quality (Klatt et al., 2014; Kleijn et al., 2006). Unfortunately, understanding how to engineer the ‘optimal’ agricultural field margin has not proved to be simple to achieve. Crops differ in the level of pollination and the community of insect pollinators required (Albrecht et al., 2012; Fruend et al., 2013), and pollinator species may also differ in their resource requirements throughout the year (Olesen et al., 2008). Wild insect pollinators also differ in their mobility and foraging strategies (Greenleaf et al., 2007) and consequently

the amount and spatial configuration of engineered habitats should determine their effectiveness (Brosi et al., 2008). Furthermore, engineered margins are not necessarily always needed or desirable; a farmer growing predominantly non-flowering crops does not necessarily need a pollination service, so if they were to invest in engineering a pollinator supportive margin the purpose would be for ecological (rather than economic) reasons. The requirement of engineered margins, therefore, needs to be determined with guidance on regional or landscape specific pollinator community abundance or on-farm monitoring schemes. Moreover, relying on engineered margins alone is risky because establishment of the sown species can fail and this requires removing land from production. Therefore, a better option may be to supplement existing habitats that also support insect pollinator communities (Franzen and Nilsson, 2008; Ricketts et al., 2008; Wood et al., 2015a). Thus when managing floral rich habitats we should consider whether it will compliment, rather than conflict, with other blooming periods from other floral sources nearby (Williams et al., 2010), and acknowledge that this will differ in areas where crops are non-flowering versus flowering (Figure 9; Raine and Gill, 2015). The value of such natural or semi-natural habitats in agricultural areas remains largely undefined although national and international projects ([www.queessa.eu](http://www.queessa.eu)) are underway to address this gap.

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



1004 **Figure 9|** Foraging options to central place foragers (such as bees) is dependent on their  
1005 foraging range. **A)** Taken from Raine & Gill (2015) this is a conceptual diagram showing  
1006 some general types, and typical proportions, of habitats that are available to foraging  
1007 pollinators in rural landscapes. Pollinator species show a wide range in dispersal abilities  
1008 which can limit the total amount of suitable habitats that can be viably visited. Evidence  
1009 shows that individual honeybees have a much larger foraging range than either bumblebees



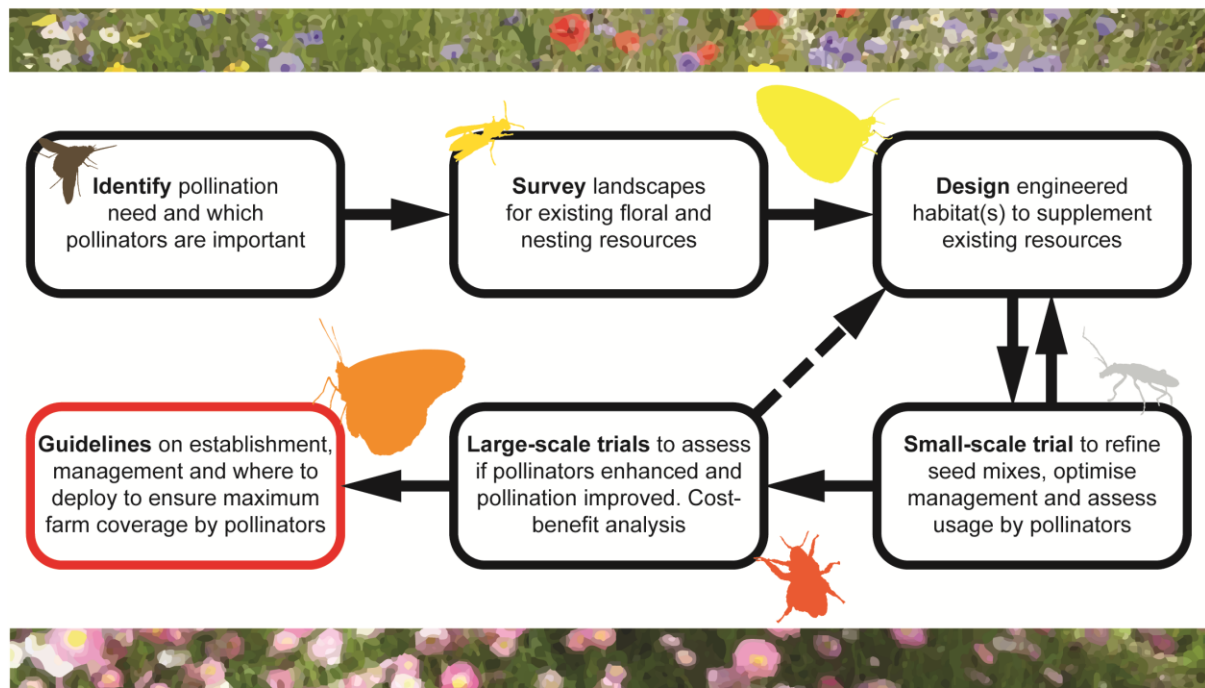
or solitary bees (see section 4.4). **B)** Foraging ranges of solitary bees drawn around the location of an engineered floral field margin strip (black line). Map depicts the real cropping and semi-natural habitats found on a farm in Dorset, UK, with 160m representing the minimum (grey line) foraging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

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

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

pollinators and whether they can realistically subsidise nearby crop pollination. The value of 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 composition and complexity of the landscape (Scheper et al., 2013; Shackelford et al., 2013). Surprisingly, it is still poorly understood whether the attraction of pollinators to flowering crops is enhanced with nearby engineered habitats, although the positive influence of semi-natural habitats has to some extent been demonstrated (Chacoff and Aizen, 2006; Kleijn and Sutherland, 2003; Klein et al., 2003; Kremen et al., 2004; Morandin and Winston, 2006). Even where the level of crop pollination has been quantified it is usually measured by proxies such as pollinator abundance in the field or resulting crop yield, rather than pollen transfer, visitation rates or plant fitness (King et al., 2013; Liss et al., 2013).

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



**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.

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

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

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

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

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

Whilst the wider pollinator community can respond positively to local habitat floral management (Heard et al., 2012; Knop et al., 2006), there have been few studies of diversity and abundance responses at the farm scale or above. This is important since agricultural intensification influences biodiversity and ecosystem processes by reducing the heterogeneity, composition and configuration of habitats at difference spatial scales (Tscharntke et al., 2012). This is expected to have distinct effects on different pollinator guilds and pollination services but remains largely unexplored (Carvell et al., 2011; Holzschuh et al., 2007). There is still debate as to whether currently available AES are enhancing farmland biodiversity efficiently (Kleijn et al., 2011), especially pollinators

(Scheper et al., 2013). In addition, there is concern that AES may suppress yields (e.g. through land-use costs), thereby increasing pressure on non-cropped habitats, with unintended negative environmental consequences. There is thus a clear need to understand and predict how wild pollinator community structure and functional attributes are altered by AES delivery and landscape configuration, especially if a balance must be struck between reducing the effects of multiple pressures and the wider need for more sustainable agriculture. The pollinator communities associated with different habitat types, landscapes and regions are being documented in various research projects and monitoring programmes (e.g. EU project QuESSA, UK project Agriland) are now under development (Baldock et al., 2015; Carvell et al., 2014). The relative importance of different specific resources or their spatial layout to pollinator communities could be estimated using existing ecological knowledge of many pollinators. These approaches could be combined in either highly parameterised process-based models or more generic conceptual models to explore to what extent different actions deployed in different scenarios at landscape scales meet biodiversity protection goals or alter the delivery of more sustainable agriculture (Kremen et al., 2007; Lonsdorf et al., 2009; see: [www.naturalcapitalproject.org/InVEST.html](http://www.naturalcapitalproject.org/InVEST.html)).

#### **4.7 Insect pollinators in urban areas**

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

and fruits) and pollination of native plant species that grow in urban areas, as well as providing aesthetic value to people desiring interaction with nature on their doorstep. Urban habitats can harbour important insect pollinator diversity, with the pollinator fauna of our towns and cities being at least as diverse as those of the surrounding countryside (Baldock et al., 2015; Sirohi et al., 2015). Considering that urbanised land cover in many countries has greatly expanded in the past few decades (for example, across UK (National Ecosystem Assessment 2011) and Europe (Gerard et al., 2010)), and that globally the proportion of people living in urban areas now exceeds 50% (UNFPA 2007), it is perhaps surprising that we know relatively little about the impact of towns and cities on insect pollinator populations, communities and networks (Geslin et al., 2013). Moreover, how should we manage urban areas most effectively to benefit pollinators? Given the recent policy interest in pollinator conservation (see section 3), practitioners require information and advice on how to manage public and private urban land to benefit pollinators. This is challenging, because perhaps more than any other habitat type, urban areas represent a matrix of different land use types (Wray and Elle, 2015), from car parks to allotments. Larger areas with more pollinator friendly habitat, such as nature reserves, parks, allotments and gardens, are connected by strips of potentially pollinator friendly habitat including roadside verges, hedgerows, river banks and canal towpaths, railway cuttings and embankments (Figure 11). Understanding how pollinator populations develop within such a ‘grainy’ landscape requires understanding of how habitat diversity, patch size and connectivity influences their meta-population dynamics (Cane et al., 2006; Perovic et al., 2015).

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

pollinator taxa (bees) but not others (hoverflies) relative to farmland and nature reserves (Baldock et al., 2015), yet we know very little of the connectivity of pollinator populations across habitat types. Quantifying the scale and extent of pollinator movement into and out of cities is crucial to understanding the role of urban pollinator populations in regional ecosystem service provision. This issue is also linked to the roles of landscape features that allow population dispersal – particularly linear features such as hedgerows, roadside verges and waterways. It is important to know how habitat connectivity is influenced by pollinator traits, such as levels of generality in plant associations, population structure (e.g. social vs solitary bees) and observed relationships between body size and dispersal ability (Greenleaf et al., 2007; Hagen et al., 2012). Questions associated with population structure can be addressed using genetic analyses across urban-rural gradients, and across contrasting urban habitat types, replicated in a range of towns and cities of different sizes. In addition, more mark-release-recapture studies are required for direct estimation of dispersal and foraging distances over single generation, ecological timescales (Chapman et al., 2003).

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



genetic assimilation (Wilcock and Neiland, 2002).



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

1236 healthy pollinator community in urban areas in a similar way to agriculture practices in rural  
1237 areas.

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.

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

## **5. Considerations when developing future research and mitigation strategies**

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

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

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

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

## **Contribution**

The order of author appearance broadly depicts the level of contribution to the paper: 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.

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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 ecosystems...and 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 (ICPPR)	Global	ICPPR 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 Pollinator Protection Campaign (NAPPC)	Regional (N. America)	NAPPC's mission is to encourage the health of resident and migratory 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
12	African Pollinator Initiative (API)	Regional (Africa)	API has two main purposes to: (i) facilitate African country participation in 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.