

STATUS AND VALUE OF POLLINATORS AND POLLINATION SERVICES



A REPORT TO THE DEPARTMENT FOR ENVIRONMENT, FOOD AND RURAL AFFAIRS (Defra)

March 2014 ver. 2

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EXECUTIVE SUMMARY

- Wild and managed pollinators are threatened by the individual and combined effects of multiple environmental pressures, although some of the pressures may be beneficial or provide opportunities for pollinators. Evidence for this is drawn from the many individual studies of these impacts at different locations in Britain and elsewhere along with global analyses of available data. The precise impact of these pressures, either individually or in combination, differs between pollinator groups due to variability in ecological and evolutionary traits that predispose a species to be resistant or vulnerable to environmental changes.
- Since the 1950s, the distributions and diversity of some wild pollinator groups (e.g. bumble bees, solitary bees, butterflies and moths) have changed in Britain, with generally more areas showing a loss than an increase in species occurrence (the number of places a species is found) and diversity (number of species in a location). Hoverfly species losses have also occurred in specific locations, but there have been increases in diversity elsewhere. A recent analysis suggests, however, that the losses of wild pollinator and wild insect-pollinated plant diversity might be slowing.
- However, a lack of regular and standardised monitoring of wild bee and hoverflies means that it is not possible to know whether their population sizes (abundance) are changing along with their diversity and occurrence. The number of managed honey bee colonies has generally fallen in recent decades, although there appears to have been a recent increase in England since 2007, such patterns are probably due to environmental pressures but also socio-economic factors affecting the level of bee keeping.
- There remains much uncertainty (and research to be done) around the ecological and biological mechanisms connecting changes in pollinator biodiversity (abundance, composition, diversity, timing of life-cycle) with pollination processes and ultimately the quality and quantity of UK crop yields
- Economic benefits are derived from both commercial and wild pollinators. These benefits are associated with market and non-market values. Market-valued impacts relate to the contribution of pollinators to crop production, whilst non-market values include the pollination of wild plants and the pleasure people derive from seeing bumblebees. In terms of informing policy, the most important concept is the marginal value of pollination services. Marginal values, which relate to the effect changes in the abundance of a pollinator species have on crop economic value, are likely to vary across crops, between pollinator species, over time and among locations. However, no robust empirical estimates of such marginal values exist for UK crops.
- Wild pollinators also have an economic value in terms of the insurance service which they provide to farmers and growers, given the likelihood of sudden declines in commercial or managed pollinators due to outbreaks of pests and diseases.
- Non-market economic values relate to the direct and indirect contributions which wild pollinators make to people's well-being, as measured through the willingness-to-pay of citizens to prevent losses or to achieve gains in wild pollinator populations. That such values exist is demonstrated by public support for organisations such as the Bumblebee Conservation Trust. However, no robust empirical estimates of such values can be found to date.
- Currently there is no all encompassing pollinator monitoring toolkit or single measure of status. Butterfly and moth species, for which there are good data on abundance, cannot be used as a reliable proxy or indicator of decline in other pollinator species due to large ecological differences between them. Species richness and functional diversity (the species traits important to pollination contained in a community) of wild pollinators have a role in insuring pollination service delivery and can be derived from existing records of species occurrence. However, these data lack detail at small geographical and time scales, which makes them only a crude approximation of the distribution of potential ecosystem service providers in the British landscape. The abundance data needed to understand fully the delivery of pollination services to crops are totally lacking.

- From the UK National Ecosystem Assessment three scenarios (Go with the Flow, National Security and Local Stewardship) were adapted to construct narratives up to 2025 outlining potential futures for pollinators and pollination benchmarked against the present day situation.
- Regular and standardised monitoring of pollinator populations is needed to unequivocally establish whether wild insect pollinators are in decline or not, and what the predominant drivers are likely to be.
- Currently the direction and magnitude of changes in pollinator biodiversity, the value and functional relationship of pollinators to agriculture from farm to national scales and how this biodiversity and linked ecosystem service will change in the future remain only partly understood.

INTRODUCTION

At the Friends of the Earth conference on 28 June 2013, Lord de Mauley, Parliamentary Under Secretary at Defra, announced Defra's intention to bring together all interested parties to work together to develop an ambitious and integrated approach to address the threats faced by pollinators. The aim is to develop a National Pollinator Strategy to be published in 2013/14 following public consultation. The process by which this strategy will be developed will be through a review of published literature followed by a workshop involving a wide variety of scientific experts and stakeholders. The workshop activities will critically review the interpretation of the available evidence; confirm key evidence gaps; consider current policies being undertaken by government and other stakeholders, such as NGOs; and aim to identify and agree actions that will support the projections to achieve desired outcomes/scenarios for pollinators over the next decades.

This report is not a systematic or exhaustive literature review but it summarises the key evidence on how environmental pressures alter pollinator populations and communities (e.g. abundance, diversity, complementarity, redundancy, range shifts, phenology) and where possible the effects on pollination services to crop and wild plant species. The ecological and economic impacts are both considered with a focus on the managed (honey bees & bumblebees) and wild pollinators (bumblebees, solitary bees and hoverflies) as the principal taxonomic groups in the UK involved in delivery of pollination services to crops and wild plants. Wherever possible this report sets-out the effects of environmental changes on pollinators and pollination services in different local contexts (e.g. geographic region, landscape type). We identify gaps in scientific knowledge pertaining to basic pollinator ecology, pressures and responses, whether pollinator biodiversity is changing, the role of insects in UK crop pollination and the economic valuation of that ecosystem service. The focus of this review is aimed at England (due to the statutory remit of Defra), but where there is a dearth of evidence from the English context then studies are referred to from other countries in the UK, the EU and other temperate regions. Studies from around the world are also cited to set the wider global context.

AIM AND OBJECTIVES

The overall aim of this report is to distil a clear understanding of the current evidence base on the status of pollinators and pollination services in England. This report will then be used to inform a workshop in late 2013 where scientists and decision makers will assemble to contribute to the development of a national (English) strategy for pollinators.

The objectives of this report are to:

1. Describe the current status of insect pollinators (wild and managed) and the pollination services they provide to insect-pollinated crops and wild plant species
2. Identify the main drivers and pressures on pollinators and pollination in England/UK and how these vary among pollinator groups and geographic locations
3. Define where in the English/UK landscape pollination services are required for crops and if possible wild plants
4. Explain how the economic value of pollinators and changes in pollinator populations could be calculated, and set out the limited evidence to date for the UK.
5. Assess potential indicators of pollinator biodiversity and ecosystem service
6. Develop scenarios (including business as usual) of how the status of pollinators or pollination services may change towards 2025

The overall approach combines an assessment of the scientific literature with some new analyses to frame our current ecological and economic understanding of the effect of pollinator population/community changes on pollination of farmed crops and wild plants. The report clearly identifies gaps in knowledge (e.g. due to a lack of data) and suggests approaches or methods to address them. Any caveats or assumptions pertaining to conclusions drawn from the literature or new analyses performed in this report are clearly stated.

ECOLOGICAL AND ECONOMIC BENEFITS OF POLLINATORS

Pollination as an ecosystem service to global agriculture

Historically, crop yields have been increased through improved agronomy, new breeding techniques and management intensification [1]. There is evidence that such increases in agricultural productivity are levelling off, and while new agricultural technologies must have a role, maintaining and improving ecosystem services will be crucial to future food security [1]. In a global economy, changes in pollination services are likely to have ramifications for geographically distant markets and human responses, such as developing new suppliers. Worldwide a variety of insects including social and solitary bees, flies, wasps, beetles, butterflies and moths provide an ecosystem service to humans by pollinating many crops. Insect pollination has been shown to increase or stabilize yields and quality of fruit, vegetable, oil, seed and nut crops [2-4]. Global cultivation of insect-pollinated crops has expanded since the 1960s, leading to about a 300% increase in demand for pollination services [5]. The global economic value of this pollination service was estimated (in 2005 US\$) to be \$215 billion or 9.5% of global food production value [6]. Similarly, the U.K. National Ecosystem Assessment estimated the production value of insect pollination (in 2007 GB£) to be at £430 million or about 8% of the total market value of crop production [7], although this estimate was based on a very small evidence base with several uncertainties and did not account for behavioural responses by farmers to changes in pollinator populations.

While honey bees are managed for both crop pollination services and honey production [5], honey bee pollination by itself is often unable to deliver sufficient pollen to crops where they are most needed [8, 9], and is a comparatively minor component in the delivery of crop pollination services to UK agriculture, with 2007 honeybee stocks estimated to be capable of supplying at most 34% of total pollination service demands [10]. Paid pollination contracts to bee farmers for pollination services to field and orchard crops are rare in the UK compared with the situation in the USA and Canada where it is a large industry. Furthermore, the spread of the *Varroa* mite and the pathogens it transmits may have led to almost the entire loss of the UK feral honeybee population, although this evidence is largely anecdotal. However, a diversity of pollinators can contribute to sustainable crop pollination, and provide an insurance service to reduce the expected costs of crop failure. Natural habitats support a range of wild pollinators that can increase crop yield through provision of a resilient and complementary pollination service [8, 9, 11]. Given the multiple threats facing pollinators [12-14], any dependence on individual species for agricultural crop pollination is risky [15, 16]. Regional losses of pollinators that alter delivery of crop pollination services to valued commodities (e.g. fruits, coffee, nuts etc) may decrease their availability or increase economic costs of production. If demand for insect-pollinated crops continues to rise and pollinator densities and/or diversity falls then, without agronomic, technological or economic responses, shortages of insect-pollinated crops or price increases might follow [5, 6, 17].

Pollination and human nutrition

Aside from the monetary impacts, and the possible consequences for the socio-economics of human societies, loss of pollination may also affect human nutrition. Although wind-pollinated or largely self-pollinated crops (e.g. grains) provide the largest volume of staple human (and livestock) foods worldwide, insect-pollinated crops are crucial to good human nutrition [18]. Insect-pollinated crops provide dietary variety and nutrients (e.g. lipids, vitamins, folic acid, and

minerals) important for human health [2, 18]. For example, vitamin A deficiency is a major human health concern worldwide. Insect-pollinated crops provide about 70% of this vitamin and pollination increases yields of these crops by about 43% [18]. Loss of pollinators and the service they provide could thus produce problems for human nutrition, although the magnitude of the problem will often depend on geographical location and degree of societal development. For instance, the human health consequences will be greater in developing countries where poorer people are often more locally reliant on insect-pollinated crops, such as beans, for essential subsistence calories and nutrients [18]. In the richer developed countries, the impact of pollinator losses on human health may be less profound but has the potential to erode the quality of human diets, or increase the reliance on synthetic micronutrients (e.g., vitamin supplements).

Potential ecosystem impacts

Whilst acknowledging the importance of other factors (e.g. niche space) changes in pollination of insect-dependent wild plants and their reproductive success (seed set and recruitment to the adult population) are likely to have serious consequences for the wider ecological community. Based on botanical studies, animal (mostly insect) pollination enhances reproductive success in an estimated 78% of temperate flowering plant species [19]. Pollination processes are relatively resilient to loss of individual species because certain ecological characteristics (e.g. behavioural flexibility, species redundancy) confer robustness to networks of plant-pollinator interactions [20, 21]. However, some simulation models indicate that if pollinator extinctions continue unabated then sudden crashes in plant diversity may arise when those species that interact frequently with many others in a network are eliminated [22], though the most highly linked pollinators may be the least sensitive to extinction [23] and shifts in the remaining species may compensate for any losses [24]. Plants underpin terrestrial ecosystems by forming the base of many food webs. Consequently, reduced abundance and loss of pollinators could have serious ecological implications not only for individual plant species but also the wider community of organisms associated with plant and pollinator, and ultimately ecosystem function [19]. These ecological consequences might be particularly felt in temperate regions as recent work has showed that plant-pollinator networks are more specialised in temperate regions and thus are potentially more vulnerable to pollinator extinctions [25]. This is consistent with many of the observations reported in the UK and across the temperate northern hemisphere (see below).

STATUS OF POLLINATORS IN BRITAIN

Are insect pollinators declining?

In practice whether wild pollinators are declining or not is hard to prove for most wild pollinator taxa because there is a lack of systematic and standardised monitoring of pollinator abundances (but see exception for butterflies and moths below). This means that for the pollinator groups thought to be most important to the supply of pollination services to UK crops (mostly bees and flies) we are reliant on inference from studies of specific environmental impacts on particular pollinator populations/communities or on changes in species occurrence as recorded by voluntary organisations (e.g. Bees Wasps and Ants Recording Society, Hoverfly Recording Scheme) and held at the Biological Records Centre (hosted by CEH) where they are accessible via the National Biodiversity Network (www.nbn.org.uk). Such long-term databases of confirmed species records collected at different times by many different recorders provide an important, but limited, source of information on past and present patterns of change in diversity of wild pollinator species.

It should be stressed that whilst of excellent taxonomic quality, these species records were generally not collected in a standardised and systematic way. Thus these data are subject to several potential biases which arise from unequal sampling intensity, varying activity density of the volunteers and shifts in focus from museum collections to comprehensive site lists. This can make the occurrence data relatively sparse and/or geographically patchy; [for example see Fig 1. in 26]. These properties of occurrence data pose analytical challenges, such as how to estimate recorder effort (although a method now exists [27]) and limitations, such as being only able to

compare species occurrence records between tranches of years because of a lack of a time series of abundance data. These issues make it difficult to detect trends in wild bee and hoverfly communities. Nonetheless, these occurrence data are the best currently available for these pollinator groups in the absence of a quantitative (abundance) monitoring scheme.

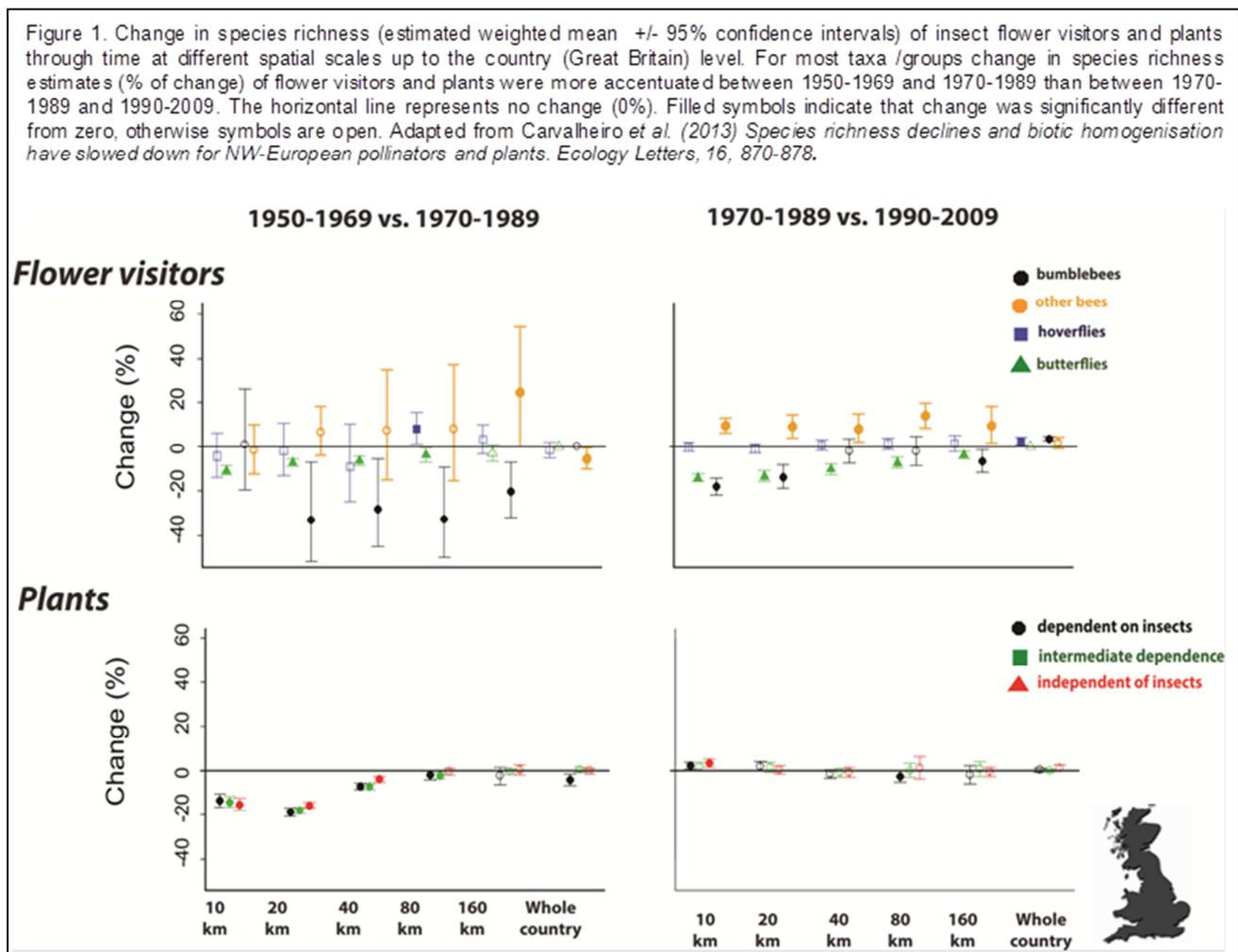
Long-term standardised monitoring data are available for butterflies and moths (Lepidoptera). These wild insects are less important to crop pollination compared with bees and flies, but probably contribute to the pollination of various wild plant species and as part of wider food webs where they interact with other non-pollinator taxa. Through a combination of voluntary and professional scientific efforts (e.g. the Rothamsted Insect Survey and UK Butterfly Monitoring Schemes) these data are collected following regular standardised protocols to produce time series data on both abundance and distributions of these insects [28, 29].

Further description of these datasets is found in the section on indicators at the end of this report.

Wild bees

Species occurrence data has to date been the main tool allowing detection of changes in wild bee distributions or diversity in England/GB. Since the 1950s, thirteen species of wild bumblebees (*Bombus spp.*) have suffered extinction in at least one European country and of the 25 UK bumblebee species present in recent historical times, two are considered extinct, a further eight have undergone major range contractions, there has been one colonisation (*Bombus hypnorum*) and one reintroduction (*B. sylvarum*) [30-33]. Evidence published in 1982 indicated that range contractions of several species of wild bumblebees were occurring as measured by records of species incidence across Great Britain before and after 1960 [34]. This pattern of declining bumblebee diversity is also seen in the Netherlands [26], Ireland [35], Sweden [36], the USA [37] and across many other developed temperate regions of the northern hemisphere [38].

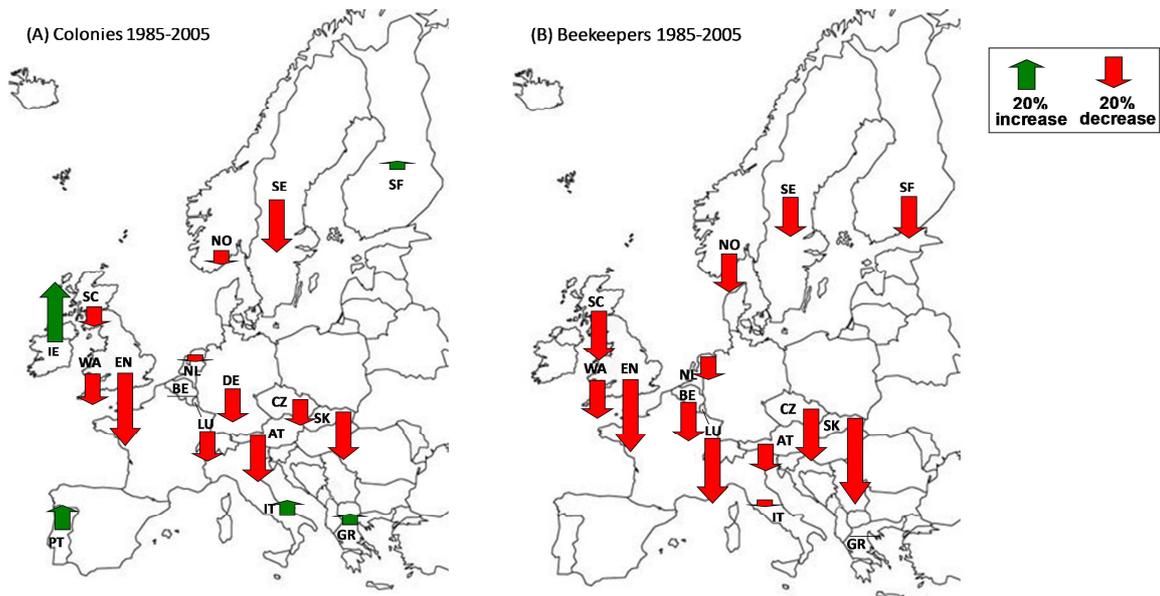
An analysis of British records of wild bee (bumblebees and solitary bees) species occurrence before and after 1980 revealed that the numbers of bee species had declined, at least in the areas (parts of England) where there was sufficient data for analysis at a 10 x 10 km scale [26]. Much of these changes in species richness were thought to reflect shifts in the distributions of many wild bee species leading to the dominance of the bee community by a smaller number of species: 29% fewer bee species accounted for half of the records post-1980 compared to pre-1980 [26]. Moreover, these dominant species tended to be those that were already common before 1980 [26]. Another more recent analysis [39] examined patterns of change in these wild bee distributions in Britain between four 20-year periods (1930-1949 (where data quality allowed), 1950-1969, 1970-1989, and 1990-2009) and at several spatial scales (10km grid up to whole country). This analysis confirmed that in Great Britain between 1950-1969 and 1970-1989, butterfly and bumblebee species richness generally decreased (**Fig.1**) [39]. Furthermore, this analysis also showed an increase in spatial similarity in the species composition of these communities during this period up to 1990, indicating the range expansion and community dominance of common bee species in Great Britain [39]. However, this study [39] also revealed in comparison of species richness between the time periods 1970-1989 and 1990-2009 that the rate of decline and homogenisation of wild bumblebee communities in Great Britain might be slowing down in recent decades (**Fig.1**). For wild solitary bee species, prior to the 1950's there was a decline in species richness, but this has been followed in recent times by a tendency toward increased species richness [39].



Honey bees

As UK honey bee populations are almost entirely domesticated, so their abundance is governed directly by socio-economic factors governing beekeeping (**Figs 2 & 3**) and the effects of environmental factors on abundance may be ameliorated by management. In the UK most beekeepers are hobbyist and the vast majority of the honey bee population are maintained by a very small number of commercial beekeepers, few of whom provide commercial pollination services. Despite a global increase in the uptake of managed honey bee (*Apis mellifera*) colonies, especially in the South Americas [5], there have been extensive long term declines in wild, feral and managed honey bees in Europe (**Fig. 2**) and North America over several decades driven by a combination of biological and socio-economic factors [5, 40-42]. In England, there was a 54% fall in overall honeybee hive numbers between 1985 and 2005 (**Fig. 2**) [40] and recent years have seen up to 30% annual colony losses [43]. However, since 2007 there seems to have been an upsurge in beekeeping, apiary and colony numbers (**Fig. 3**). Annually beekeepers may merge weakened colonies and replace lost hives by splitting existing stocks, collecting swarms or buying a new colony from a supplier, this contributes to high levels of uncertainty in estimates of honey bee populations and the subsequent conclusions that can be reliably drawn [40]. Direct census data for wild or feral honeybee populations are absent. However, indirect methods (i.e. estimated genetic diversity and colony densities from microsatellites [42]), along with anecdotal evidence from beekeepers, suggest that wild or feral honeybee populations in England, like most other European countries, have been wiped out by *Varroa* and diseases. While small feral honey bee populations may frequently occur due to beekeepers losing swarms without human management they may be unlikely to survive in the long-term, although there is little published data on this.

Figure 2. Graphical summary of the net proportional changes (%) in total numbers of honey bee colonies (A) and total numbers of beekeepers (B) between 1985 and 2005. Red arrows indicate decreases, green arrows indicate increases, and the height of the arrow is proportional to the percentage change with reference arrows provided in the legend.



Reproduced from Potts, S.G. *et al.* (2010) *Declines of managed honey bees and beekeepers in Europe. Journal of Apicultural Research*, **49**, 15-22.

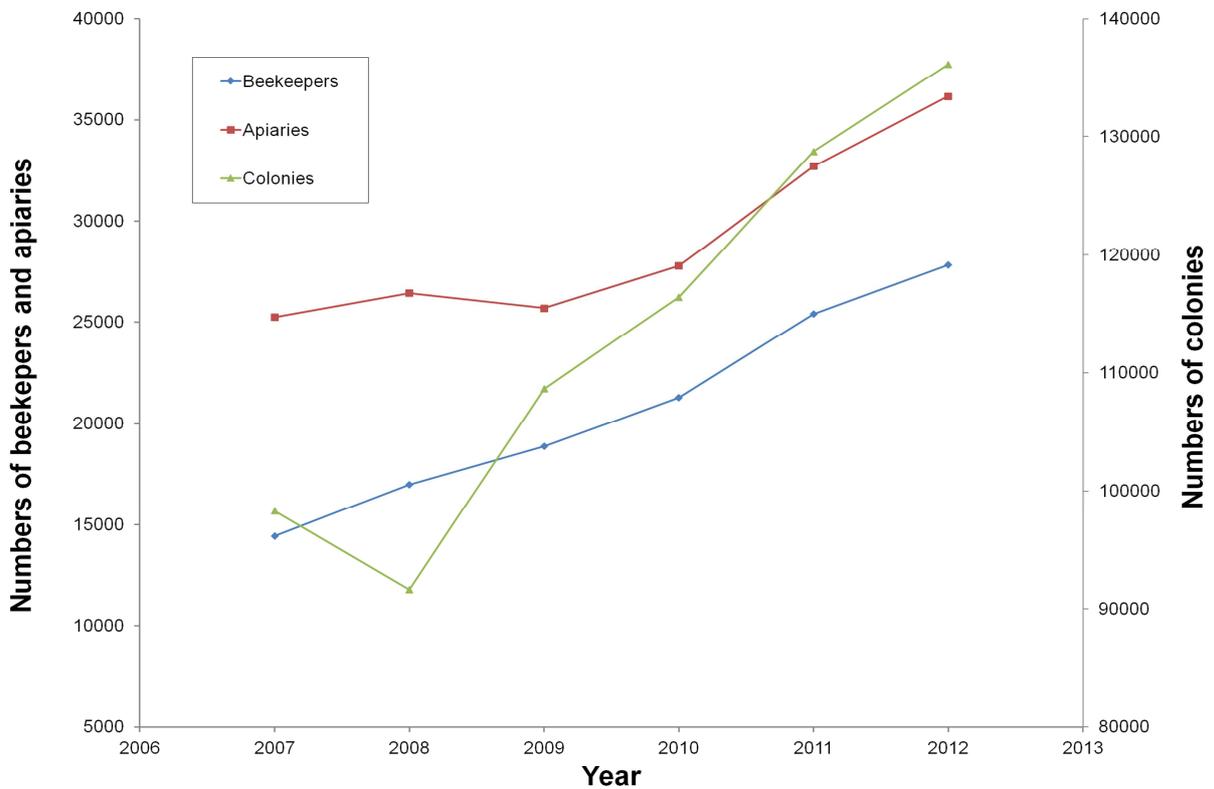


Figure 3. The numbers of honey bee keepers, apiaries and colonies in England & Wales 2007-2012. Data are voluntary records deposited in Beebase, National Bee Unit, FERA.

Hoverflies

Changes in hoverfly species richness were slightly more complicated than that of wild bees, one analysis showed that the numbers of hoverfly species (pre- and post-1980) had increased (25% of the 10 x 10 km grid cells with sufficient data) and decreased (33%) in different parts of Britain [26]. Shifts in the structure of hoverfly communities were also recorded pre- and post-1980 with a smaller number (29% fewer) of species dominating, and as with wild bees these tended to be those species that were already common [26]. These hoverfly distribution data were subsequently re-analysed with an explicit consideration of the effects of sampling intensity and spatial and time scales when assessing the percentage change in hoverfly species richness pre- and post-1980 [44]. This approach confirmed the complex picture of changes to hoverfly species richness but detected losses in hoverfly richness at fine spatial scales (e.g. 10 x 10 km) which shifted to gains in species richness at much larger (e.g. >80 x 80 km) spatial scales [44]. The authors' interpretation was that these observed gains in the number of species at larger spatial scales were probably due to increased turnover in species composition with increasing spatial scale (beta diversity). This potentially indicates that the species losses observed at fine scales may not yet have translated into declines in the wider landscape. The latest study [39] in Great Britain showed that hoverfly species richness did not vary significantly at most spatial scales examined or over time (1950-1969 versus 1970-1989 or 1970-1989 versus 1990-2009) (**Fig. 1**). However this study did also show that up to 1990, but weakening thereafter, there was a significant increase in spatial similarity in the species composition of hoverfly communities indicating that there was a process of range expansion and community dominance by common hoverfly species in Great Britain [39]. Hoverflies are highly mobile and have contrasting nutritional requirements at adult (e.g. nectar) and larval (e.g. aphid predator) stages, these ecological traits may partly explain the heterogeneity in patterns of diversity for this group, for example they are able to utilise agricultural cereal crops which provide high densities of aphid prey.

Butterflies and moths

In Britain, there is little to no evidence (e.g. observed visitation to flowers) to support the presumption that butterflies and moths deliver pollination services to insect-pollinated crops, as they do in other geographic regions (i.e. tropics). It is very likely they have a functional role as pollinators of wild plant species and as part of the wider food web, consequently they do represent one tool to monitor ecosystem health [28]. Furthermore, trends in the abundance of butterflies and moths may provide a potential indicator of the level of threat to insect pollinators generally. However, it must be stressed that life history differences between butterflies and moths and other insect pollinators (e.g. in the larval stage they are herbivorous and have specific host-plant requirements) which may make them more or less vulnerable to a particular environmental threat compared with nest or colony forming bee species. Moreover, the non-random sampling distribution of survey sites (transects) on which observations are recorded over time may inject a certain level of bias or at least doubts about the representativeness of the data¹.

With those caveats in mind, these data do reveal some prominent trends in both the distribution and abundance of these insect species. Overall in Britain, 62 moth species (macro and micro-moths) became extinct during the twentieth century and there was a significant decline (28%) between 1968 and 2007 in the total abundance of larger macro-moths (**Fig. 4A**). Of the 337 previously common and widespread macro-moth species 66% declined in abundance, with 37% of species decreasing in population size by at least 50% [28]. Regional differences were evident with large reductions in macro-moth abundance (40%) in southern regions of Britain (**Fig. 4C**), whilst in regions north of York/Lancaster there was no significant change in abundance (**Fig. 4B**) [28]. Set against this pattern of declining moth abundance, a third of these 337 macro-moth species became more abundant with 53 species (16%) showing at least a doubling in population size over the 40 years [28]. The lack of decline in northern areas of Britain appears to be due to losses of local species being countered by immigration of species previously limited to southern areas [28]. As with other insect pollinators, migration plays a role in these biodiversity changes

¹ Although this is now countered by the Wider Countryside Butterfly Survey (WCBS) –see indicators section

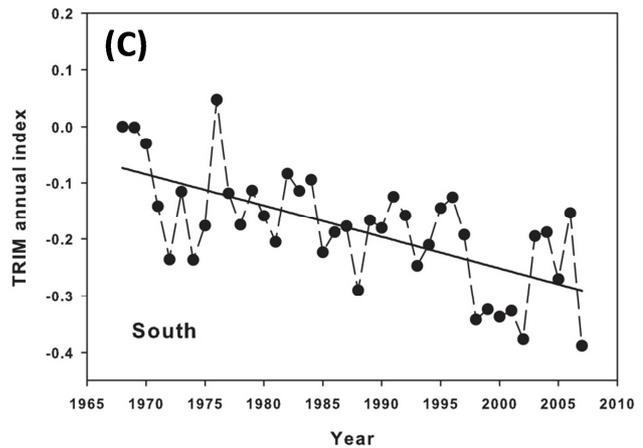
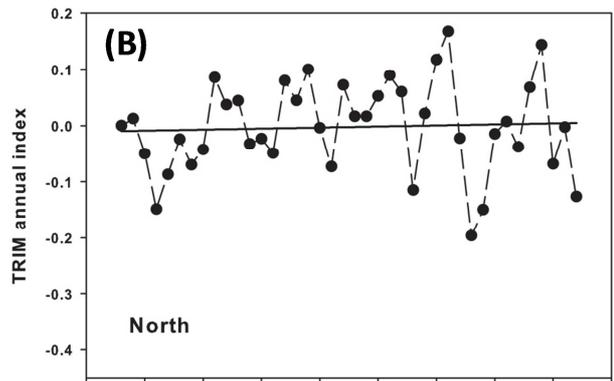
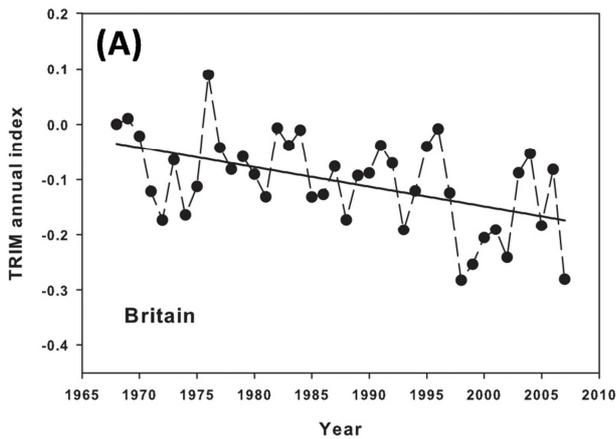


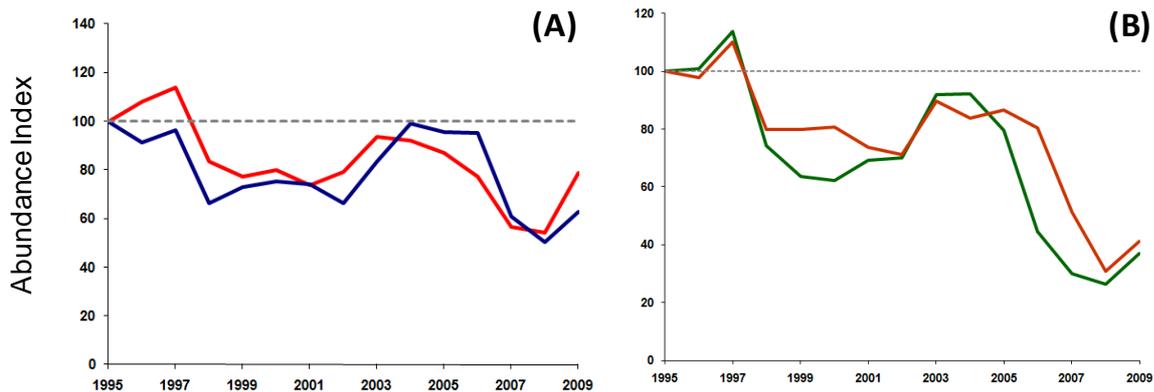
Figure 4. Change in the total abundance of large moths caught in the Rothamsted light-trap network 1968-2007

Reproduced with permission from Fox, R., et al. (2013) *The State of Britain's Larger Moths. Butterfly Conservation and Rothamsted Research Wareham, Dorset, UK*

with more than 100 moth species (macros and micros) recorded for the first time in Britain this century, with 27 moth species as established since the year 2000 [28].

Butterflies have also generally declined in abundance and species distributions [45, 46]. In Great Britain between 1950-1969 and 1970-1989, butterfly species richness generally decreased and in contrast to bees this was maintained in the period since 1990 (Fig.5) [39]. This decline was accompanied by an increase in the heterogeneity of butterfly community composition, implying that range contractions of some species might be occurring [39]. Ten-year trends in abundance show that 72% (38 species) of the monitored butterfly species with sufficient data for trend calculation (53 species) declined in abundance, while only 26% of species exhibited an increase [29]. The UK distributions of 54% (32 of the 59 species assessed) of butterflies also decreased during the decade, while the distribution of 41% (24) of assessed species increased and the remaining 5% of assessed species showed no change in distribution [29]. The long term decline of species specialist in their habitat requirements has continued and, for the first time, a significant decrease in the abundance of butterflies more generalist in their habitat requirements has also been detected (Fig. 5A) [29]. Regionally, larger population decreases in farmland and woodland habitats were observed in England (Fig. 5B) compared with Scotland [29].

Figure 5. Trends in butterfly abundance for (A) habitat specialists (blue line) and wider countryside species (red line) in the UK and (B) woodland (green line) and farmland (brown line) species in England



Reproduced with permission from Fox, R., *et al.* *The State of the UK's Butterflies 2011. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, Dorset.*

Insect-pollinated wild plants

In Britain, patterns in the native and naturalised wild plant species richness in Britain broadly mirrored that of pollinators. Studies have found that losses of wild plant species tend to be greater in species with a dependence on pollinators for their reproduction [26, 47]. One study found that on average outcrossing plants totally reliant on insect pollinators for reproduction were declining, wind-pollinated species were increasing and plant species reliant on insect pollinators for outcrossing, but able to self-pollinate, showed an intermediate response [26]. An investigation into changes in the forage plants of bumblebees in Britain revealed a decline in the distributions of these insect-pollinated plants between 1930–1969 and 1987–1999, relative to other native or long-established species (**Table 1**) [47]. This same study also showed that 76% of bumblebee-pollinated plants in Countryside Survey plots declined in frequency between 1978 and 1998 and this pattern of decline was significantly greater than losses of plant species that were not reliant on insect pollination (**Table 1**) [47]. The most recent analysis [39] also revealed a decline in plant species richness at fine (10 km - 40 km grid) scales comparing data from 1950-1969 with 1970-1989. This study, however, revealed that this rate of decline in wild plant species richness had substantially reduced in more recent decades with no significant change between 1970-1989 and 1990-2009 [39]. Furthermore, these plant decline patterns reported in [39] were similar for all recorded plants irrespective of whether they depended on insect pollinators for pollen exchange and reproductive success. This highlights the fact that declines in insect-pollinated plants may be due to concomitant losses in pollinators, but they may also or instead reflect other ecological processes (e.g. N deposition) governing the distribution of plants.

Table 1. Trends in the distribution and frequency of key bumblebee forage plant species². Each species was tested independently using the Z test for two proportions which looked at change in number of occupied plots between 1978 and 1998 as a proportion of the total number of plots sampled. Statistically significant changes indicated in bold. Negative values indicate decline.

Plant species	Distribution Change index (1930–1969 to 1987–1999)	CS frequency % change 1978–1998	Z-test significance
<i>Ajuga reptans</i>	-0.56	-43.75	<0.05
<i>Arctium agg.</i>	0.05	-6.25	n.s.
<i>Ballota nigra</i>	-0.37	180.00	<0.05
<i>Bryonia dioica</i>	-0.50	-54.55	n.s.
<i>Centaurea nigra</i>	-0.25	-45.93	<0.001
<i>Chamerion angustifolium</i>	-0.01	-29.23	n.s.
<i>Cirsium arvense</i>	0.47	-2.51	n.s.
<i>Cirsium palustre</i>	0.15	-10.69	n.s.
<i>Cirsium vulgare</i>	0.80	-28.51	<0.001
<i>Convolvulus arvensis</i>	-0.70	11.54	n.s.
<i>Epilobium hirsutum</i>	0.12	-21.95	n.s.
<i>Filipendula ulmaria</i>	-0.10	-23.64	<0.05
<i>Glechoma hederacea</i>	-0.56	-12.31	n.s.
<i>Iris pseudacorus</i>	0.16	8.33	n.s.
<i>Lamium galeobdolon</i>	1.07	-16.67	n.s.
<i>Lathyrus pratensis</i>	-0.17	-44.55	<0.001
<i>Leucanthemum vulgare</i>	-1.14	-65.00	<0.01
<i>Lotus corniculatus</i>	1.09	-26.87	<0.01
<i>Lychnis flos-cuculi</i>	-0.79	-15.38	n.s.
<i>Mentha aquatica</i>	-0.11	-39.47	<0.05
<i>Odontites vernus</i>	-0.46	166.67	<0.05
<i>Prunella vulgaris</i>	0.60	-18.54	<0.05
<i>Ranunculus acris</i>	0.30	-6.83	n.s.
<i>Rhinanthus minor</i>	-0.49	-79.31	<0.001
<i>Rubus fruticosus agg.</i>	-0.29	-1.43	n.s.
<i>Senecio jacobaea</i>	0.11	5.50	n.s.
<i>Stachys sylvatica</i>	-0.49	2.00	n.s.
<i>Trifolium dubium</i>	-0.11	-18.60	n.s.
<i>Trifolium pratense</i>	-0.18	-39.22	<0.001
<i>Trifolium repens</i>	1.31	-11.98	<0.01
<i>Vicia cracca</i>	-0.37	16.67	n.s.

Case study: national scale wild plant distributions and links to pollinators

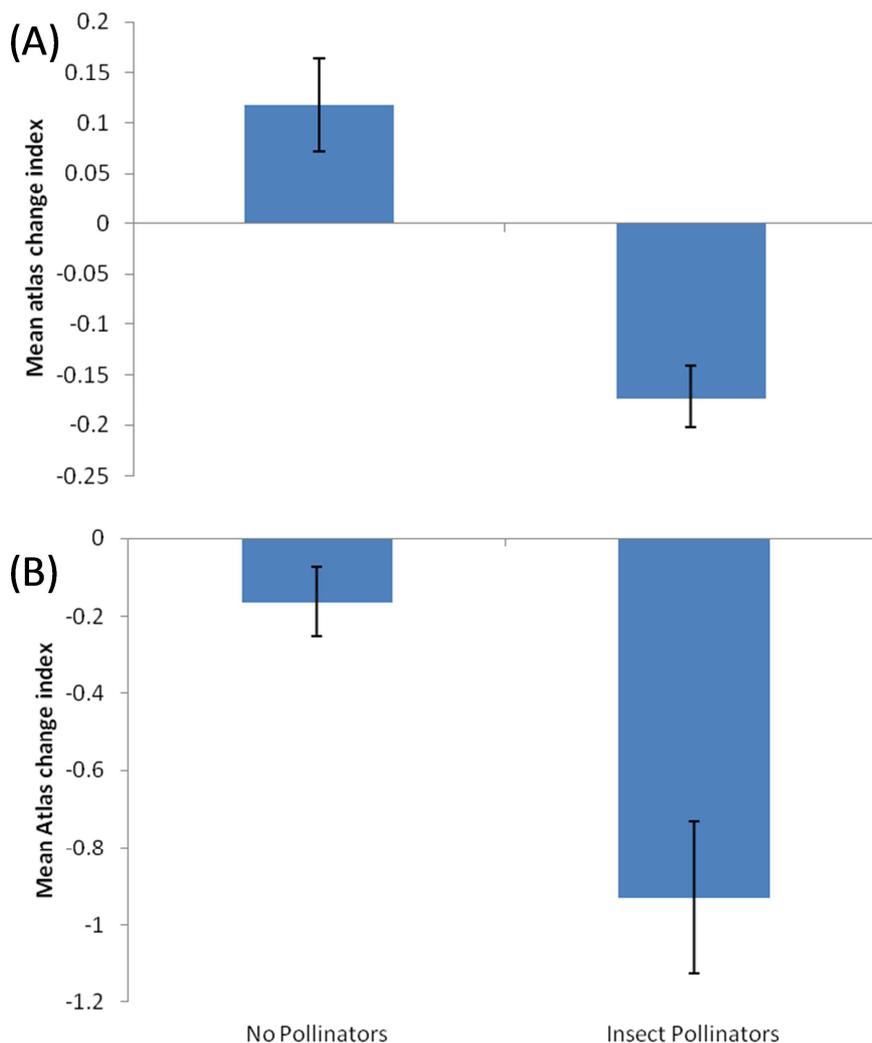
Reductions in the reproductive connectivity between plants can lead to population isolation which, along with lowered population densities, can cause declines in seed production and quality that, if substantial enough, can cause local extinction [48]. However, our understanding of the importance of different factors (e.g. habitat fragmentation, land-use and disturbance) affecting insect mediated pollen transfer in wild plants in Britain [49-52] and other countries remains incomplete [53-56] with the breadth and flexibility of plant mating systems adding much complexity to plant species responses [52, 57-59]. Very few studies have simultaneously evaluated the influence of pollinators on the interaction between ecological effects that may directly affect population persistence (e.g. reduced pollen transfer leading to lowered seed

² Adapted from Carvell et al. (2006) Declines in forage availability for bumblebees at a national scale *Biological Conservation*, 132, 481-489.

production) and genetic effects that maintain genetic diversity and fitness and drive longer term population processes (e.g. reductions in pollen flow and outcrossing rates) [60].

In the absence of detailed demographic data for this report we assessed the links between national scale distributions of plants in Britain and their links to pollinator communities³, as has

Figure 6. Changes in range size of plant species with associated with differing pollination requirements (A) species with no special conservation status ($t = 5.23$, d.f.= 465.72, $P < 0.001$) or (B) species with conservation status (after Cheffings 2004; $t = 3.53$, d.f.= 48.63 $P < 0.001$). Range changes from 1930-69 to 1987-99 were measured by the Atlas change index for 10-km squares.



been done elsewhere [26, 39]. We analysed large-scale changes in plant range between two survey periods (1930-69 to 1987-99), using data from the New Atlas of the British and Irish Flora [61] and changes in local-scale frequency between 1978-1998 and 1998-2007 using the Countryside Survey of Britain (<http://www.countryside.gov.uk/home>) [62]. Only species treated as natives, probable natives or archaeophytes (plants believed to have become naturalised before AD 1500) by were included in the analyses.

Changes in the distributional range of plants from the atlas were quantified at the 10-km square scale using a 'change index' [63]. This index does not represent species range increases or decreases in absolute terms but instead gives the relative magnitude of change in relation to the 'average' species. Changes in forage plant species frequency were based on data recorded as part of CS which

compares a large stratified sample of 1-km squares from 32 land classes Britain. Within each square, a number of fixed plots were established in a range of different habitats. Within each plot (n=2500-17000 depending on sampling year) the presence (frequency) of all vascular plant species was recorded. Changes in plot frequency of individual plant species between 1978-1998 and 1998-2007 for which CS data were available were assessed by calculating the percentage change in number of occupied plots between the survey periods (referred to as relative % change) with the minimum sample size for analysis set at six occurrences in either year. These change data were then combined with data on conservation status (all threat categories

³ Note – this specific analysis was carried out for this report and while following earlier published analyses, it has not undergone peer –review. Also note that because the data had unequal variance between the two groups the Welch-Satterthwaite approximation was used to account for this and provide an estimate of the degrees of freedom.

combined) [64] and trait data on insect visitation and flower morphologies derived from a combination of survey and literature based data.

Plants visited by insect pollinator species declined in both large-scale range (**Fig. 6**) and local-scale frequency (**Fig. 7**) between the survey periods. These changes were of greater magnitude than changes in other native plant species, reflecting serious reductions in both the quality of foraging resources for pollinators and plant populations. At the large scale it is clear that plant species currently classified as threatened declined disproportionately when they were associated with insect pollinators (**Fig. 6b**). The rate of change in these species was over four times greater than for threatened plants not associated with pollinators (**Fig. 6b**) and five times higher than that observed for more common species associated with insect pollinators (**Fig. 5a**). This is in broad agreement with an earlier study [26]. While the long term trend in change rates has been negative there is a suggestion that in the last decade the relative rate of decline of plants associated with insect pollinators has slowed (**Fig. 6**) in agreement with [39]. However in contrast to this study the decline rates were not similar for non-pollinator and pollinator associated plants suggesting that different processes may be affecting the overall patterns of change (**Fig. 6 & 7**). What is clear from the analysis of the larger scale atlas data is that floral traits of plants are correlated with decline rates with species exhibiting more 'specialised' floral structures (e.g. longer corollas, hidden nectaries) more vulnerable to decline (**Fig. 8**). Many of these species were associated with rarely disturbed habitats composed of semi-natural vegetation. Specifically, of the species included in the long-tongued flower morph category 29% were associated with permanent boundary and linear features (hedges, roadsides etc), 23% with calcareous grassland and 21% with broadleaved/mixed woodlands. Such habitats have suffered degradation throughout the latter half of the 20th century as a result of the intensification of agriculture and landscape use [65].

Figure 7. Changes in frequency of British plants with different pollination requirements surveyed across two time periods. Non-insect pollinated species= blue and insect pollinated species =red . Frequency changes were measured as relative % change in frequency of occupied Countryside Survey (CS) plots within 1-km squares between each period. $F_{1,432}=11.91$, $P<0.001$

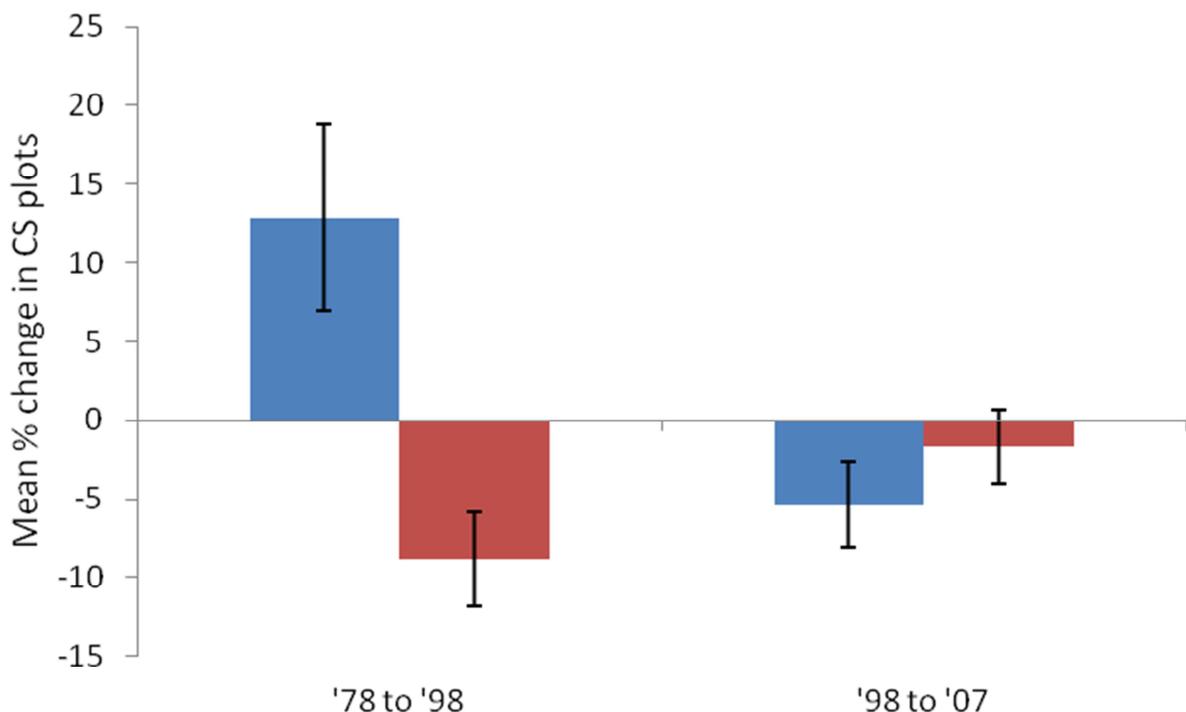
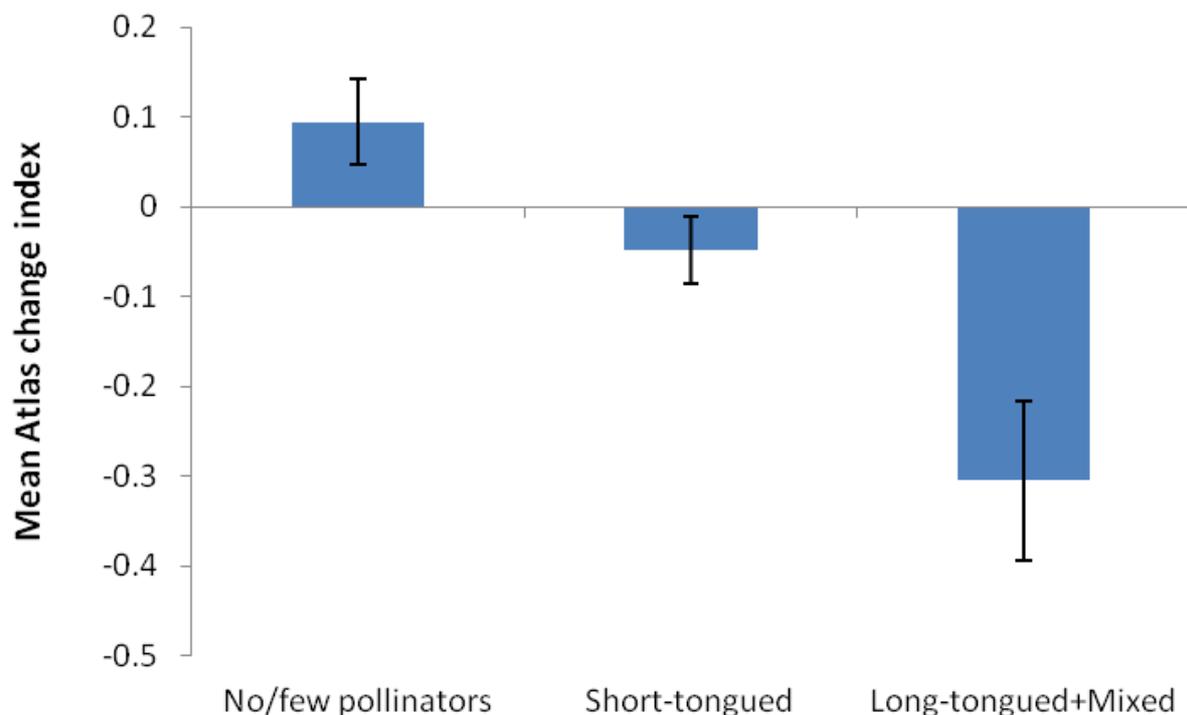


Figure 8. Changes in range size of plant species with differing flower morphologies that influence type of visiting pollinator ($F_{2, 1128}=8.58$, $P<0.001$). Short tongued = flower morphs that select for insects with $<7\text{mm}$ tongues (e.g. beetles, small bees, wasps, syrphids and other flies). Long tongued = flower morphs that select for insects $>7\text{mm}$ tongues including Lepidoptera and longer tongued bumblebees. Mixed = wide range of flower morphs and visitors. Range changes from 1930-69 to 1987-99 were measured by the Atlas change index for 10-km squares.



Summary of evidence and uncertainty

- In Great Britain, there appears to have been an overall decline in the diversity of wild bees in recent decades with some areas showing an increase in diversity, but a significantly greater area showing a decline. Observed declines are driven, at least in part, by significant range contractions for specialist species that are associated with natural or semi-natural habitat or have narrow forage requirements
- Changes in hoverfly diversity over recent decades have been less clear with no clear trends at the national scale because losses in some locations are balanced by gains elsewhere. Declines in hoverfly species occurrence have only been detected at local scales to date. There is some indication that hoverfly communities may be becoming dominated by generalist species.
- In Great Britain, there has been a change in the abundance of butterflies and moths over the last 35-40 years, with a greater number of species showing significant declines compared to the those showing significant increases (but noting non-random sampling framework).
- The long term trend of losses of wild plant diversity may indicate patterns of loss in pollinators. Some studies show plant species dependent on insect pollination exhibited greater range contractions and decreases in frequency (in field surveys) than plants dependent on other modes of pollination (e.g. wind). This was most pronounced in plant species dependent on more specialised species of pollinator (e.g. long-tongued bumblebees). However, plant species with specialist pollinators often have alternative modes of pollination (e.g. partial wind- or self-pollination) and reproduction, (vegetative reproduction). There is, however, a suggestion that in the last decades the relative rate of

decline of plants associated with insect pollinators has slowed [123]. Other evidence has found changes in plant species distributions were unaffected by dependence on insect pollination. There is therefore the possibility that trends in wild plants are responding to drivers (e.g. nitrification) other than pollination.

- We do not know how the abundance of wild bees and flies has changed with observed changes in diversity. There are no existing long term⁴ data sets to detect changes in population densities of wild bees and hoverflies, so we have no ability currently to understand the population dynamics of these pollinators. Moreover, such abundance data are what is required if we are to detect and predict changes in pollination service delivery over space and time.
- Evidence on changes to UK wild bee and hoverfly populations and communities is drawn from haphazardly collected species distribution records. These are long-term (since 1950s) datasets with high taxonomic resolution (i.e. species identification by experts) and relatively wide geographic spread, advantageous features for the detection of changes in pollinator species richness across the UK landscape. However, the lack of standardised and systematic sampling in collecting these data means that there is some bias (e.g. unknown sampling effort) and spatial patchiness (e.g. more records in areas of greater human population density) in the data. This means particular statistical approaches [27] are required to detect reliable trends in species richness.
- Data on honey bee populations are based on surveys of beekeepers compiled by the National Bee Unit at FERA (and its predecessors). These data also have limitations due to the way in which they are collected. For instance, the data underpinning the analysis in Fig. 2 [40] and in Fig. 3 are based upon the number of hives on government registers, as registration is optional, these numbers may be under-estimated to an unknown extent. Similarly, annual colony losses are self-reported and as such may be biased to an unknown extent [43].
- Focus of plant analyses on native and long-established wild plant species associated with semi-natural habitats means the potentially positive effect that introduced plant species could have on bumblebee and other pollinator populations may be overlooked.
- 100% of the papers/reports cited in this section drew on correlative field data.

Knowledge gaps and priorities for future research

- The extent of changes in wild pollinator (bumble bee, solitary bee, hoverfly) populations due to a lack of long-term and large-scale monitoring of their abundances
- Whether changes in butterfly/moth abundances can be a reliable proxy for changes in other wild pollinator groups
- Whether greater dominance of pollinator communities by generalist species inferred from distribution data signifies an actual shift in the numerical dominance of these species
- The identity of insect species which pollinate different wild plant species and whether parallel changes in insect/plant population densities are happening
- Quantitative links between different pressures and changes in wild bee and hoverfly population densities
- The extent to which changes in pollinator distributions or abundance leads to deficits in wild plant pollination and lower mating and reproductive success

⁴ The Bumble Bee Conservation Trust has established a UK wide network of bumble bee transects where the abundance of this taxon is recorded in a standardised way. However, this is a recent endeavour (~3 years) so data are not yet sufficient, moreover the financial/human resources to run this may not be secure in the long-term.

DRIVERS AND PRESSURES ON POLLINATORS AND POLLINATION

As elsewhere in the world, insect pollinators are under threat in England and across the UK from multiple environmental pressures, which singly and in combination may jeopardize the delivery of pollination services to crops and wild plants. These environmental pressures include three aspects of land-use intensification (landscape alteration, cultivation in monocultures and agrochemical use), as well as urbanization, invasive alien species, the spread of diseases and parasites and climate change [12-14].

Landscape alteration

A major driver of wild pollinator losses is thought to be the degradation, destruction and fragmentation (and their interactions) of the many semi-natural habitats in the landscape on which pollinators rely for food sources and breeding sites [31, 32, 45, 66-69]. The primary cause of this change to the habitat resources for pollinators in the British landscape is that of agricultural intensification [65, 70-72]. Overall the more specialised a pollinator is, the greater the chance that they will be vulnerable to such habitat changes [26, 31, 73]. Those bumblebees having undergone declines in the UK tend to be long-tongued species that emerge late in the season, as opposed to short-tongued species with early phenology and broader diets [31, 73]. The former group of bumblebees tend to forage on plants typical of unimproved flower-rich grasslands (e.g. Fabaceae) or legume crops (e.g. red clover), both habitats that declined in extent in Britain during the late twentieth century [31, 47]. Across other temperate regions of the world, wild bee and hoverfly species that are more specialised, nest above ground or have limited dispersal abilities are also more vulnerable to habitat loss and degradation [74-76]. The impacts on pollinators of changes in habitat quantity or quality (e.g. fragmentation, destruction or creation through agri-environment interventions) tend to be pronounced in spatially homogeneous landscapes, such as those dominated by agricultural monocultures [77-80]. This suggests that the presence of locally diverse and well-connected pollinator habitats in landscapes is important for wild pollinator diversity.

Habitat fragmentation can isolate species, raising the risk of extinction. Populations of certain bumblebee species (*Bombus sylvarum*, *B. distinguendus*, *B. muscorum*) threatened in Britain have become isolated through habitat fragmentation and consequently exhibit relatively low gene diversity and have very low effective population sizes [81-83]. Such barriers to gene flow and potential loss of genetic diversity in isolated populations of pollinators can lead to still greater vulnerability to other pressures (e.g. parasites) [84]. Common species (e.g. *B. pascuorum*, *B. lapidarius*), however, may be less affected by habitat fragmentation due to their ability to disperse over greater distances [85, 86]. There are also >200 solitary bee species in the UK that are little studied but they have highly specialised life cycles requiring particular nesting sites (e.g. a sandy bank) close to foraging habitats, these narrow habitat requirements may make these solitary bees particularly vulnerable to the effects of habitat fragmentation.

Monocultures

Many farms in arable crop growing areas have simplified crop rotations that often result in large areas of monoculture. At a regional scale there has also been a general shift away from mixed farming towards arable farming in the east of England and grazing in the west. This can have a negative impact on pollinators due to the loss of forage and nesting resources (see above) and the extensive use of pesticides (see below). Although the mass flowering crops (e.g. oilseed rape, orchard or soft fruits) typically grown in monoculture can provide abundant sources of nectar or pollen for insect pollinators in England [87] and in W. Europe [88-90] they do so in a short, synchronous pulse which is unlikely to provide sufficient nutrition for pollinator species active throughout the growing season [91, 92]. Furthermore, there is some evidence that large resource pulses have the potential to negatively impact on pollination of nearby wild plants [93, 94] or increase parasitism rates of bumblebee nests [95]. An emerging and rapidly moving area of study is the extent to which neonicotinoids or other pesticides used on mass flowering crops may affect

bee health and performance (see below) but the effects are little understood outside highly controlled experimental settings.

Pesticides

Another feature of agricultural intensification is the direct and indirect impact on pollinators of pesticides. In English field sites lower bumblebee species richness has been associated with intensive agriculture and higher pesticide loads at regional scales, while at farm scales bumblebees (in arable situations) and butterflies responded positively to organic management [96]. Landscape-scale surveys of wild bees and butterflies in Italy also showed that species richness tends to be lower where pesticide loads and cumulative exposure risk are high [97]. Such correlative patterns may indicate field impacts of pesticides and herbicides on pollinators and their forage plants. However, these pollinator populations (and other components of biodiversity) are governed by a complex of ecological processes that operate at multiple spatial scales. Recently, there have been concerns raised about the direct effects on pollinators of one class of pesticide, the neonicotinoid insecticides [98]. Used widely in the developed world, these systemic pesticides spread throughout plant tissues and can occur in plant nectar and pollen [99, 100]. Neonicotinoid exposure can produce sub-lethal negative effects on honey bee performance and behaviour [98], impair honey bee brain function in laboratory experiments [101] and there are some indications that it affects learned abilities of foraging honey bee workers to discriminate floral rewards [102] and locate the hive in a French field experiment [103]. There are some indications that sensitivity to doses of neonicotinoid may be greater in bumble bees than honey bees [104]. In British semi-field conditions, experimental neonicotinoid exposure at doses approaching field realistic levels reduced the foraging performance, growth rate and queen production of bumblebee (*Bombus terrestris*) colonies [105, 106]. However while the experimental results are mounting they remain questioned in some quarters on the grounds of lacking field realism. The research challenge therefore is to determine the dose, exposure and impact of neonicotinoid and other pesticides on different kinds of pollinators at scales ranging from experiments with greater field realism to large-scale field manipulations. This is needed to address the question of ecological realism, but remains a challenging and relatively costly undertaking. Furthermore the consequences of pesticide impacts on pollinators for agricultural production (e.g. yield quantity and quality, market value, etc.) are not at all clear.

Urbanization

The destruction of semi-natural habitat by urban or sub-urban sprawl is likely to have similar negative impacts to agricultural intensification by reducing the availability of pollinator habitat and food resources. High levels of industrial, commercial and transport related impervious materials (e.g. concrete) offer few resources to pollinators. This has been shown in the USA to be a significant barrier to gene flow between bumble bee populations and may ultimately jeopardise their population viability [107]. French urban landscapes support less numerous and less diverse plant-pollinator interactions compared with agricultural and semi-natural habitats, with hoverflies and solitary bees in particular suffering, while bumble bees were not affected [108]. Urban landscapes, however, may also comprise a mosaic of different habitats such as parks and playing fields, gardens, allotments, derelict industrial sites, cemeteries, road and rail sides, which all have the potential to provide numerous nesting and floral food resources for pollinators. In England, sub-urban areas have been shown to be comparatively better for bumblebee colony growth than agricultural land [109]. Across Britain, gardens may offer high quality pollinator habitat often superior to many other agricultural and woodland habitats as indicated by greater density and survival of bumblebee nests [110, 111]. This has also allowed managed honeybee populations to exist in many major cities, including London and Sheffield, where beehives are maintained on rooftops. Gardens also benefit the process of pollination as evidenced by greater wild plant reproduction in gardens compared with arable/mass flowering crop situations [51]. Similar beneficial effects of gardens on bee abundance and diversity patterns have been reported from Sweden [112]. The generalist bumble bee *Bombus terrestris* is able to produce another generation per year in UK cities. This is because the warmer urban microclimate combined with a variety and sequence of horticultural, ornamental and weed flowering over time enhances the

bee's capacity to forage on floral foods [113]. However, the overall impacts of urbanisation are unknown as there is insufficient evidence to support a general conclusion.

Alien species

Pollinators adapted to forage on a broad range of plant species (e.g. bumblebees, honey bees) are more likely than more specialist species to incorporate invasive alien plants into their diet [31, 114]. Alien plants that provide copious floral rewards can come to dominate pollinator-plant assemblages [31, 114-116] potentially modifying the pollination success of native wild plant species and pollinator community structure [114, 116]. Himalayan balsam (*Impatiens glandulifera*) provides a rewarding nectar source and is an established alien plant across the UK and Europe, in England it has a documented positive effect on pollinator community diversity but potentially negative impacts on native plant pollination [114]. A similar pattern has been found in Ireland [117]. However, in certain situations invasive alien plants may underpin the pollination of native plants by supporting an abundant community of shared pollinators, as seen in England with the rare insect-dependent *Trinia glauca* (Apiaceae) [118]. Many ornamental garden plant species are aliens planted for aesthetic reasons, because of their origins they often have a range of flowering times which provide a longer foraging window for those generalist pollinators (e.g. certain bumble bees) pre-adapted to exploit them [113].

The global human trade in managed pollinators for agricultural pollination services represents a threat to indigenous pollinators. Introduced insect pollinator species may outcompete native pollinators or disrupt plant-pollinator interactions. For example, the importation of the southern European bumblebee sub-species *Bombus terrestris dalmatinus* for glasshouse pollination services may threaten the sub-species (*B. t. audax*) endemic to the British Isles through hybridisation or competition [119, 120]. However it is possible that introduced or invading generalist insect pollinators may fulfil or enhance pollination services in particular contexts, e.g. as with the honey bee in Latin America [121]. The global trade in honey bees has caused the spread of pests and helped emerging pathogens to become established (see below). A clear example is that of the *Varroa* mite, originally a parasite of Asian honey bees, it was accidentally spread across the globe through trade and movement of managed honey bees, is now widespread and common (only certain offshore locations in UK are *Varroa* free) and changed the global viral landscape that both honeybees and other pollinators exist in [122, 123]. There are probably future threats as predatory or parasitic organisms migrate into the UK either under climate change or after accidental introduction (e.g. Asian hornet *Vespa velutina nigrithorax* - a significant predator of bees and other pollinators accidentally introduced to France is likely to spread to parts of the UK).

While there are a number of specific pressures on pollinators (as documented above), it is not possible to say whether the overall impact of alien species is negative, positive or neutral.

Pathogens and parasites

Most of the evidence on threats to pollinators from pests and diseases in England and around the globe comes from managed honey bees [12, 14, 124]. Long term gradual decline in managed honeybee colonies in the UK is also linked with various social and economic factors [40], although recent media interest has seen a short term spike in the number of beekeepers in the UK. Bacterial infections such as European (*Melissococcus plutonius*; EFB) and American (*Paenibacillus larvae*; AFB) foul broods can lead to colony death without management interventions (e.g. husbandry, antibiotics) [125]. EFB is the most prevalent bacterial disease in England but there are regional differences with greater incidence in the south of the country [125]. Large and widespread honey bee colony losses since the 1950's were associated with the global spread of the parasitic mite *Varroa destructor*, which feeds on the haemolymph (blood) of the host bee and their larvae, reproducing in the sealed brood cells that contain the developing bee pupae [122, 126]. The tracheal mite *Acarapis woodi* was another invertebrate pest in the British Isles associated with over-winter losses of apparently strong honey bee colonies [127], but its impact has diminished following increased surveillance and the use by beekeepers of pesticides in hives

to control *Varroa*⁵. By feeding on honeybees, *Varroa* transmits pathogens, particularly Deformed Wing Virus (DWV), into the bee host and exacerbates viral impact [123, 124, 128] possibly by reducing the function of the bee immune system [129].

An array of pathogens has been implicated in colony losses but with different organisms implicated in mortality in England [128], Spain [130] and America [131, 132]. This geographical variability in pathogen identity and impact may partly explain why no single agent or group of causative disease agents has yet been conclusively identified [122, 124]. For example, the microsporidian fungal pathogen *Nosema ceranae* has been implicated in colony losses in Spain [130, 133] but in no other country in the EU or USA. Furthermore, colony collapse disorder (CCD) the syndrome allegedly responsible for the death of millions of managed honey bee colonies in the USA, has never been reported in the adjoining countries of Mexico and Canada. So there is the possibility that some of these geographic differences may reflect research interests of local groups, rather than real biological differences. However, recent evidence is pointing to Deformed Wing Virus (DWV) vectored by the *Varroa* mite being the most prevalent viral pathogen in honeybee populations and having the principal role in colony losses [123, 128, 129, 134]. In England, deformed wing virus has been correlated with greater honey bee mortality [128] and this is an active area of enquiry in the UK Insect Pollinators Initiative. However, co-infection by other multiple viruses, microsporidian fungi and bacteria in honey bee hosts over time and space is common [131, 135] and how these interact remains poorly understood but is being investigated [136].

Pathogens and parasitoids are also known to be important mortality factors for wild bumble bees [137-139] There is abundant emerging evidence from around the world (especially N. America) that many of these pathogens (especially DWV) and other parasitic organisms (e.g. microsporidian fungi, parasitoids) can be shared between managed honey and bumble bee populations and the wider community of wild bees and flies [140-146]. Such pathogens have been implicated in losses in species diversity of wild bumblebees in North America [37, 144]. The extent to which disease or parasite transmission occurs between managed honey bees/bumble bees and wild pollinators is unknown in the UK but is likely based on global evidence [140-147]. Furthermore, the consequences of this community epidemiology [143] for the population dynamics of different pollinator species are not understood.

Climate change

Insect and plant distributions have already been altered by recent climate change and differential rates of migration of plants and pollinators may lead to spatial or temporal disruption of pollination. There is a relationship between climatic niche and *Bombus* declines in Britain [30] and general declines in European bee richness are predicted under climate changes, although this did not include British data [148]. Phenological mismatch may be a key biodiversity change under climate change and there is evidence that pollinator phenological responses may become decoupled from their forage plants [149]. This negatively affects specialist pollinators more than generalists due to narrow diet breadth, although reductions in generalist diet breadth were also predicted [45, 149]. Thus, climate change has the potential to decrease abundance, shift ranges, and ultimately increase extinction risk, with these effects exacerbated for specialist species. Simulations of bumblebee species' responses to climate change found that gaps in floral food sources and curtailment of foraging season were less and more likely, respectively [92]. Given the importance of early and late season foraging by queens for colony establishment and survival, curtailment by climate shifts is likely to be a significant problem for bumblebee populations [92]. A recent study in the USA of pollinator activity on watermelon crops under different climate change scenarios predicts that while overall pollinator activity may not change the species involved in the service provision may; in this case the contribution to pollination from honey bees decreased and wild pollinators increased, respectively [150]. However, pollinators currently limited by their climatic niche may, as the climate warms and where suitable habitat is available, colonize new regions and increase diversity of recipient communities [28, 45]. Furthermore, where evolutionary

⁵ Also referred to as veterinary medicines – see <https://secure.fera.defra.gov.uk/beebase/index.cfm?pageid=93>

history has produced species that are robust or flexible to environmental changes then those plant-pollinator interactions may persist or flourish [113]. Unlike all other pollinators the managed honey bee populations may be generally more protected from the effects of climate change because of their managed status and near global distribution from northern regions of Scandinavia and Canada down to tropical areas of America, Asia and Africa.

Multiple, interacting threats to pollinators

In the real world, it is likely that many of these different global changes (e.g. climate change and habitat fragmentation, nutrition and pesticides/pathogens, pesticides and existing and emerging pathogens, climate change and alien species) will combine or interact leading to an overall increase in the pressure on pollinators [12, 13]. However, this inherent complexity means that, to date, this phenomenon has only been demonstrated to occur in comparatively few studies that are limited in the scope of species (e.g. honey bees and bumblebees) or combinations of pressures (e.g. pairs of global change pressures) considered [12, 13 and citations therein]. Consequently, the current empirical evidence base is relatively poor due to a relative lack of study to date. Nonetheless, this variety and multiplicity of threats to insect pollinators and pollination has the potential to seriously affect future food security, human health and ecosystem function [12, 14]. Of the few studies of multifactorial impacts on pollinators that have been performed, most have been carried out elsewhere in the world [excepting recently: 45, 151, 152]. However, as the pressures on pollinators are generally common worldwide it is likely there is a multifactorial pressure on pollinators and pollination in Britain.

Summary of evidence and uncertainty

- The individual pressures identified in this report can have negative impacts on pollinator health, diversity and abundance. Some pressures (i.e. alien plant species, urbanisation) may also exert positive influences on pollinators in certain circumstances.
- Interactions between two or more drivers can be synergistic in their negative effect. However, very few combinations have been studied to date and then only for a restricted number of pollinator taxa.
- We currently lack the knowledge and data to reveal, with a high degree of certainty, the relative contribution of different global change pressures to changes in pollinator biodiversity.
- Considerable uncertainty exists because impacts are likely to vary greatly between different pollinator taxa (social bees versus solitary bees versus flies etc) due to different evolutionary (e.g. climate tolerance) and ecological (e.g. diet breadth) life-histories.
- Particular impacts or combinations of impacts are extremely likely to be context dependent, making generalisation difficult, e.g. by varying simultaneously over space and time.
- Ecological dynamics, such as competitive interactions between social bee species [153], are likely to introduce further complexity and hence increase uncertainty when predicting impacts of a particular pressure on pollinators. For example, it is probable that a pressure or disturbance may favour certain species over others, altering species interactions with concomitant impacts on overall structure of the ecological community, although empirical examples are few [154, 155].

Pressures on pollinator groups:

The pressures on different pollinator groups are summarised below. Numbers indicate a suggested ranking for the pressures (1 to 5, where 1=most important. Repeated numbers =equal ranking). These ranks are only indicative and cannot be viewed as a simple unequivocal scheme. This is due to the uncertainty around the incomplete evidence, including publication biases toward significant findings, and the fact that the ranking of the impacts will vary within taxa, depend on local temporal and geographic factors, and also on specific driver characteristics within each category of pressure.

Honey bees

1. Pests and Pathogens: Aside from socio-economic factors affecting beekeeping, *Varroa* and disease are the primary constraint on honey bee populations, certain in-hive pesticides used to control *Varroa* may also affect behaviour or abundance or colony function. **2. Landscape alteration:** Loss of food sources in intensively managed landscapes as habitats are converted/lost/fragmented may contribute to malnutrition in honey bee populations probably threatening colony survival and potentially increasing vulnerability to other stressors. **2. Monocultures:** Increased monocultures/simplified rotations have adverse effects on food resources, mass flowering crops may contribute to bee nutrition but do not substitute for wild floral resources available over longer time periods. **2. Pesticides:** Use of herbicides will reduce amount of floral resources for pollinators; lethal and sub-lethal effects of insecticides may directly, and possibly indirectly via interaction with other stressors, contribute to reduced colony performance and survival. **3. Climate Change:** overall the impact of climate change for the species will be low due to near global distribution of this semi-domesticated species, but increasing climate variability at local to regional scales (e.g. false spring events, adverse weather) will be important to honey bee survival by affecting the ability of workers to forage and maintain hive temperatures and possibly increasing disease incidence. **4. Urbanization:** Socioeconomic effects may mean urban environments are areas of high honey bee density; however, nutritional resources for colonies may depend on the amount and quality of urban habitats and this is little studied. **5. Alien species:** honey bees are generalist in their food requirements and can thus integrate alien plants that offer copious and rewarding floral resources into their diet but future invasions by insect predators may have an impact.

Bumble bees, solitary bees and hoverflies:

1. Landscape alteration: Loss of feeding and nesting habitat in intensively managed landscapes as habitats are converted/lost/fragmented are likely to contribute to malnutrition and reduced breeding in wild pollinator populations threatening their survival and probably making them more susceptible to further stressors. **2. Monocultures:** Increased monocultures/simplified rotations have adverse effects on food resources, mass flowering crops may contribute to pollinator nutrition but also have adverse effects and do not substitute for wild floral resources for long lived species e.g. bumble bees. **3. Pesticides:** Use of herbicides will reduce amount of floral resources for pollinators; lethal and sub-lethal effects of pesticides may directly, and possibly via interaction with other stressors, contribute to reduced bumble bee colony and population performance. Effects on solitary bees and hoverflies are less predictable. **3. Pests and pathogens** many viruses, fungi and parasitoids infect all pollinators and probably transmit between wild and managed pollinator species. They are likely to have a role in population dynamics but the population and community epidemiology is poorly understood in wild insects and data is very sparse in the UK at this time. **4. Urbanization** may have negative impacts associated with the destruction or degradation of semi-natural habitat but positive effects where suitable urban habitats provide alternative resources for generalist species with requisite adaptive flexibility. Hoverflies are known to do well in urban habitats. **4. Alien species** will have positive impacts for generalist species where the plants offer copious floral rewards but potentially negative effects where invasive insect species outcompete, prey on/parasitize or interbreed with native pollinators **4. Climate change** will affect species according to their specific ecology (e.g. specialists at risk from phenological decoupling but generalists may persist). Increasing climate variability at local to regional scales (e.g. false spring

events, adverse weather) will affect the ability of workers to forage and possibly increase disease incidence. Much of the current evidence is largely based on insights from simulation modelling of effects on wild bees and not empirical observations

Butterflies & moths:

1. Landscape alteration: Loss of feeding and larval habitat in intensively managed landscapes as habitats are converted/lost/fragmented. These effects are highly likely to be the predominant influence on population dynamics of these insects, especially those species with narrow habitat or dietary requirements. **2. Monocultures:** Increased monocultures/simplified rotations reduce food resources for adults and larvae, mass flowering crops may contribute to pollinator nutrition but do not substitute for the diversity of wild floral resources **2. Climate change** is altering the distributions of these insects leading to range expansions and contractions, species currently limited by their climatic niche may, as the climate warms and where suitable habitat is available, colonize new regions **3. Pesticides:** Use of herbicides will reduce adult feeding and larval host-plant resources for different species leading to reductions in diversity; lethal and sub-lethal effects of pesticides may directly, and possibly via interaction with other stressors, contribute to reduced population sizes/diversity.**3. Pests and pathogens** many viruses and fungi infect all pollinators, probably transmit between wild and managed species and have a role in population dynamics, but the population and community epidemiology is poorly understood in wild insects and data is very sparse in the UK at this time. **4. Urbanization** effects on butterflies are not well understood, but in all probability rare specialists do not persist in these environments without direct management interventions to support their particular ecology. **5. Alien species** little is understood about the effects of alien plant species on butterflies and moths as pollinators, whereas much more is known about the ability of caterpillars of polyphagous species to assimilate new plants into their herbivorous diet.

Knowledge gaps and priorities for future research on the pressures on pollinators

- The causal link between floral resource availability and pollinator abundance/diversity at landscape scales
- Effects of pathogens, pesticides and malnutrition on different pollinator species at a range of biological scales (e.g. genetic, cellular, individual, population)
- The pathology and epidemiology of shared pathogens within a community of pollinators
- Evolution of new emerging pathogens
- Pollinator (meta)population and (meta)community dynamics across fragmented landscapes
- The landscape-scale impacts on pollinator densities, diversity and behaviour of multiple pressures (e.g. ecosystem fragmentation, climate change, disease, alien species)
- Pollinator species endurance across different gradients of habitat degradation

CROP POLLINATION SERVICES IN BRITAIN

Across the world it has been shown that while pollinator abundance (e.g. honey bee densities) is important for delivery of pollination services to insect-pollinated crops [8, 9, 156, 157], wild pollinator species richness is also critical for crop productivity (e.g. seed set, yield), through processes such as complementarity, redundancy or facilitation [8, 9, 11, 21, 158-160]. These diversity effects may be especially important to UK producers as current honeybee stocks are thought to be at ~34% of levels required to supply pollination services [10]. Functional diversity has also been shown to increase plant reproductive success and crop yield [11, 53]. Functional diversity is the morphological and behavioural species traits (dietary specialisation, activity period, foraging range, nesting behaviour, sociality etc) assembled in the pollinator community that support their functional role in delivering the pollination service [161].

Although pollination services from wild insects and managed bees (honeybees and bumblebees) provide substantial economic benefits in the UK [7, 10] to growers of soft and orchard fruits and oilseed rape there is a dearth of studies on the ecological processes that underpin pollination service delivery to such crops⁶. In the UK, oilseed rape is economically the most important crop with some dependence on insect pollination (**Table 2** below) [162-164]. Insect pollinators are not essential for pollen transfer in oilseed rape and much can be attributed to wind dispersal of pollen [3, 162]. Yet there is evidence that social bees (honey bees and bumble bees) are more efficient than wind at pollen transfer [163] and insect pollination has been shown to increase the yield and quality of oilseed rape crops in experimental settings [164]. Honey bees are individually less efficient than bumble bees or solitary bees at pollinating oilseed rape, but their abundance may compensate [157], flies may also provide a service at times of day when bee activity drops [165]. Massive commercial contracts are awarded in Canada and the USA for honeybee pollination of crops, so allowing the full economic benefits of honeybee pollination to be exploited. This highly commercial industry does not occur in the UK or EU. Widespread payments to beekeepers for pollination contracts could represent a way to increase long term numbers of honeybees in the UK and increase people's awareness of the value of pollinators. An attendant risk, if not properly managed and regulated, could be competition with wild pollinators and the spread of diseases through long distance movement of honey bees for crop pollination, which is likely to have occurred in the USA.

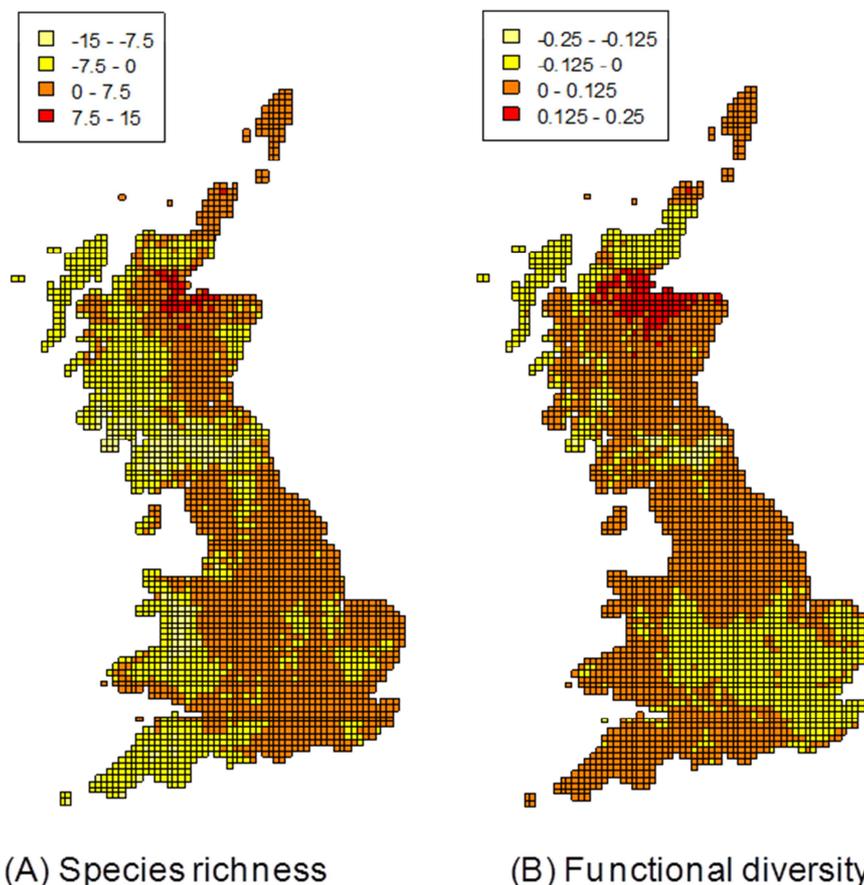
Case study: oil seed rape pollination by wild bees

A recent study in the UK [161] used wild bee distribution data (45 bumble bee and solitary bee species) known to pollinate oilseed rape to map the species richness and functional diversity [166] of these pollinators, as a proxy for pollination services to this mass-flowering crop at the national scale (**Fig. 9**).

These national distributions of bee species richness and functional diversity were corrected for unknown recorder effort [167] and latitudinal gradients in bee distributions (fewer bees in northern Britain) [161]. Adjustment for latitudinal gradients in species richness was necessary otherwise there could be a risk that management interventions intended to support pollination service providing bees (e.g. agri-environment schemes) might be targeted toward northern areas on the misconception that there was a local ecosystem service deficit. The analysis revealed that intensively managed arable landscapes, such as regions of central and eastern England were not associated with low levels of bee species richness, even after correcting for the greater bee species richness in southern Britain (**Fig. 9a**) [161]. Moreover, species richness was negatively correlated with the extent of semi-natural habitat [161]. This might seem contrary to findings showing strong positive relationships between those semi-natural habitats that provide high quality resources to pollinators cover and pollinator diversity [9, 168, 169] In this instance, however, the lack of such a relationship was probably due to the analysis being restricted to wild bees known to visit crop flowers, and thus a particular subset of the pollinator community that

⁶ This knowledge gap is being currently addressed by the Insect Pollinators Initiative (IPI) project 'Sustainable pollination services to UK crops'.

Figure 9. National scale patterns (10 km² resolution) in (A) species richness and (B) functional diversity of wild bee species known to visit the flowers of oil seed rape (*Brassica napus*). Yellow cells indicate areas of low taxonomic or functional bee diversity and thus the potential delivery of pollination service to this crop. Values are corrected for unknown recorder effort and a negative cline in bee richness with increasing latitude.



Source: Woodcock et al. (2013) *National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops* Journal of Applied Ecology, DOI: 10.1111/1365-2664.12171

possessed the requisite adaptations for survival in the intensively managed arable landscape. If the analysis had included habitat specialist species, which rarely visit flowering crops, we would have expected those species to show a positive relationship with semi-natural habitat cover in the landscape [40, 75].

Nonetheless, whilst the occurrence of these crop-visiting bee species was unaffected, it is conceivable that they may persist at lower population densities in the arable situation compared with less intensively managed habitats. However, there is a total lack of data at the national scale with which to make such an assessment. Species richness is an intuitive and useful indicator of biodiversity. Yet it may have limitations as an indicator of changes in ecosystem service delivery because it makes no allowance for the rarity of individual species and their correspondingly reduced functional role in pollination. There are, however, indications from different studies around the world that show the value of wild pollinator species richness providing some insurance or complementarity in pollination service delivery [8, 9, 160, 170].

Functional diversity is potentially a better indicator of pollination service potential than species richness because, while it is still based on species composition, it also incorporates information about the assemblage of traits in the pollinator community that govern ecosystem service delivery [166]. Functional diversity has another advantage over species richness because it is weighted for the probability of species occurrence, hence as species become rarer their contribution to functional diversity and ecosystem service provision is reduced accordingly [161, 166]. However, it must be noted that functional diversity without corresponding abundance data still only gives a compositional picture of the community characteristics required for pollination service delivery; hence much uncertainty remains around this the relationship of functional diversity to service provision. While there are no studies testing directly how functional diversity [sensu 166] directly relates to pollination service delivery and crop yields, another metric, functional group richness, has been shown to enhance pumpkin crop yields in Indonesia [11]. This analysis of functional diversity at the national scale showed that in the intensively managed arable landscapes in central and eastern England there are low levels of bee functional diversity, which may indicate that there is potential for a deficit in oil seed rape pollination (**Fig. 9b**) [161]. The greatest potential for pollination service delivery, as indicated by greater functional diversity, was in north and south-west England, Scotland and Wales (**Fig. 9b**). In contrast to species richness, bee functional diversity was positively correlated with the cover of semi-natural habitat in the landscape [161]. This may show how agri-environment interventions or habitat restoration and conservation of bee habitats, by increasing the probability of species occurrence, may have a role in enhancing the functional diversity of ecosystem service providers to crops [161].

Sources of evidence and uncertainty

- In field-scale to farm-scale studies, honey bee and wild pollinator abundance/visitation rate and wild pollinator diversity are known to be factors which can influence the delivery and stability of pollination services to crops [8, 9, 160, 170]. The shape (i.e. gradient of linear relationship and point where asymptote is reached) of the functional relationship between pollinator densities and crop yields and quality is not well understood, and gradients in pollinator diversity or abundance sometimes only weakly translate into differences in yields [164, 168]. There remains much uncertainty (and research to be done) around the ecological and biological mechanisms connecting changes in pollinator biodiversity (abundance, composition, diversity, phenology) with pollination processes and ultimately the quality and quantity of crop yields. This is particularly so in the case of UK flowering crops.
- Maps of potential pollination service delivery (e.g. Fig. 8) based on species distribution records must be treated with appropriate caution because of the spatial resolution and lack of process information therein. For instance, in this case study the resolution of the map was at a 10km x 10km scale. The ecological process of insect pollination operates at the individual flower scale with insect movement typically scaling-up the process from metres to kilometres, depending on the species of pollinator. Consequently, these maps represent a coarse level of understanding that only crudely indicates the distribution of potential ecosystem service providers to flowering crops.
- Crucially, there is a total lack of systematically collected data on wild pollinator abundance with which to model the effects of pollinator population sizes on crop pollination services at the scales relevant (regional, national, international) to policy development. Furthermore, the available 'abundance' data on honey bee populations in the UK are based on the number of hives on government registers, and as registration is optional the quality of these data are geographically patchy and potentially biased.
- These data limitations mean that currently it is very difficult to establish if the apparent changes in pollinator diversity (indicated by changes in species distributions) are reflected in changed wild pollinator population sizes (except perhaps for butterflies and moths thought to play little role in crop pollination in the UK).
- Furthermore, while new experimental results are emerging from the UK IPI which suggest that sub-optimal pollination in two cultivars of apple affect the crop quantity and quality [171, 172], we simply cannot say with any confidence whether deficits in crop pollination

are generally occurring in UK crops. The maps produced in this report and [161] at best suggest where, with respect to pollinator diversity only, there is potential for such pollination deficits to occur in the British landscape.

Knowledge gaps and priorities for future research

- The contribution to the yield and/or quality of multiple crops from (1) individual pollinator species and (2) pollinator communities
- The relative importance to crop pollination in UK settings of pollinator abundance, taxonomic or functional diversity or pollinator guilds
- Direct evidence of how changes in managed and wild pollinator densities and composition impact crop pollination
- Establish whether regions with apparently low pollination service potential suffer from crop pollination deficits
- How regional changes in crop and pollinator distributions as a result of climate change may produce pollination deficits
- The extent to which socioeconomic (i.e. pollination contracts) and environmental influences on beekeeping decisions affect crop pollination services
- The efficacy of mitigation measures (e.g. agri-environment schemes) aimed at pollinators on adjacent crop productivity

ECONOMIC VALUATION OF POLLINATOR POPULATIONS

Conceptual models of pollinator economic values

In this section, the way in which pollinator populations generate economic values is explained for (i) commercial, market-valued outputs (ii) non-market values. Economic value is best thought of in terms of marginal values. That is, as a pollinator population rises or falls by one “unit” (e.g. one bee, one percentage point), what is the change in the value of objective function? We give more detail below. What is more we can distinguish between the economic benefits which are obtained annually from pollinators; and the value of this flow of benefits over time, which is attributable to a stock of pollinators.

1. Annual economic benefits arising from pollinators

Commercial values

For commercial, market-valued outputs such as agricultural crops, we know that pollination services (*PS*) are an input to production [2]. For any crop dependent on insect pollination, we could write down the general form of a production function which relates the physical yield of a given crop, X_1 , to variations in the supply of pollination services *PS*:

$$Q(x_1) = f(Y, PS, \epsilon) \quad (1)$$

where $Q(x_1)$ is tonnes of output per hectare is shown to be a function (f) of Y , a vector of inputs such as labour hours, machinery time, fertiliser and pesticides, and stochastic factors ϵ such as rainfall and temperature. Pollination Services are thus thought of as an input to production, and in many ways are treated in conceptually the same way as other inputs such as fertiliser. There will be a separate production function for each crop ($x_1, x_2, x_3...$) relevant to a farmer’s choices of what to grow.

However, the supply of pollination services is different from other agricultural inputs in three important ways. First, the effects on output of a given population of pollinators are stochastic: there is some probability that each flower in the crop will be pollinated. Call this v . But that means there is also a non-zero probability $(1-v)$ that the crop will not be pollinated. Farmers can only partially control this probability. The lower is the chance of a flower being pollinated, the higher the marginal

value of additional pollinators [173]. Second, once a flower has been pollinated, it does not benefit from any further inputs of *PS*, whilst providing other inputs in the “no pollination” scenario can generate zero output for some crops. This is quite unlike other inputs such as fertiliser [173]. It is generally wrong, therefore, to think of pollination services and other inputs as perfect substitutes for each other in production. This contrasts with most other inputs farmers use. Third, whilst farmers have to pay for many other inputs they use (seed, fertiliser), some pollination services are provided at no cost to the farmer.

The potential supply of pollination services *PS* depends on the diversity and abundance of different insect species (honey bees, bumble bees, hoverflies etc), labelled *S1*, *S2* and *S3*. As the abundance of any of these species falls or rises, then we wish to know the marginal effects of this on the output (yield) of *X1*, holding all other factors constant. This quantity – the change in $Q(x1)$ for a marginal (one-unit) change in *S1* - is known as the marginal physical product of *X1*. Or, we can ask how the quantity of output of *X1* changes as the supply of pollination services, *PS*, changes by one unit. This is the marginal physical product of pollination services. These marginal product values will vary across crops and possibly also across the country, due for example to variations in soil fertility or climate. They will also vary for any farmer according to how much of each input they utilise, so that the marginal products are not constants, but vary as a function of the quantity of other inputs and the quantity of output. One important example relates to the farmer’s use of pesticides in crop production, which can reduce the supply of pollination services to his or his neighbour’s farmland. Finally, as noted above, the marginal products are not defined with certainty, since pollination is a stochastic event.

The relationship between the overall supply of pollination services in a landscape, *PS*, and the abundance of individual pollinator species, will depend on their effectiveness as pollinators and the extent to which they either act as substitutes for each other (that is, to what extent can a 5% decline in visitation by species *S1* be compensated for by a *z*% increase in visitation by species *S2*?); or as complements for each other (both *S1* and *S2* are required to produce the crop; or more of *S2* enhances the yield given a fixed level of *S1*). This information on effectiveness and substitution/complementarity is contained within the empirical (functional) form of the pollination services production function, which will be crop-specific:

$$PS(x1) = f(S1, S2, S3, \dots) \quad (2)$$

Species abundance at any site for any point in time will depend on a range of factors, including food availability.

So far we have discussed the value of pollination services in terms of yields. However, farmers’ production decisions depend on expected profit, not yields. For any crop, we could define a profit function which showed how profits per hectare from growing *X1* vary according to the price the farmer receives for *X1* and the costs of the inputs *Y* (fertiliser, pesticides..) including any costs of purchasing pollination services *PS* (e.g. by buying-in commercial bees). Profits will also depend on the marginal physical products of each input, including pollinators. Such a profit function could be defined at the level of the farm. In this case, the prices of all outputs (crops) the farmer could grow, along with the costs and marginal physical products of each input, would be relevant to determining the maximum profit he can make, and determining the combination of crops and management regime which result in this maximum.

To understand the commercial value of any pollinator species⁷, consider an experiment where we can quantify the effect of a 10% change in the abundance of species *S1* on the supply of pollination services, holding all other factors constant. Suppose this leads to a 5% loss in pollination services, we then ask what change in the maximum profit each farmer can make results from this 5% decline in *PS*. If such an experiment could be repeated for a range of changes in *S1* and thus in *PS* for a given crop or across a range of crops, this would trace out a function which would tell us the marginal value of pollinator species *S1* in terms of market or commercial values –

⁷ To which might be added their value in honey production for honey bees.

its value in agricultural production. Since such an experiment would be hard to conduct, such a function could be estimated econometrically, observing levels of S_1 and PS , and levels of profit, and the controlling for other factors in (1) and (2) statistically. However, data to do this well do not currently exist for the UK. The partial derivative of this profit function with respect to S_1 gives the marginal value of the species, which might well vary with the abundance of the species (and, as should be clear from the above, with the abundance of other pollinators – other determinants of PS in (2)). This marginal value could exhibit great discontinuities if there are threshold effects present in the system (e.g. sudden collapses in wild bee populations under a particular pressure).

Therefore, in estimating the value of a particular pollinator species in agriculture, it is important for the researcher to know the form of the pollination services supply function (2), as well as the profit and production functions facing each farmer. As a species such as S_1 increases or decreases in abundance, the economic benefit or cost of this change will thus depend on:

- The extent to which other species can replace the functioning of S_1 in the supply of PS , as in (2);
- The extent to which farmers can and do change their production methods in producing a given pollinated crop, for example by changing their use of other inputs;
- The costs to farmers of such changes, and the costs of switching to alternative crops with different pollination demands.
- Since the price of outputs (crops) and the price of inputs are part of the profit function, then the costs of a decline in pollinators will also depend on crop prices and other input costs. For example, as crop prices rise, the costs of losing pollination inputs also rise. As input prices rise, the cost of losing pollination inputs might fall, since higher input prices could imply the farmer choosing to target lower yields through less intensive cultivation systems.

An empirical estimation of the commercial value of pollination is thus quite complicated, but absolutely vital if policy-makers need a robust figure for the market-valued economic benefits of protecting pollinator populations, and thus the economic costs of declines in pollinators.

An alternative view of this approach to conceptualising the economic value of an ecosystem service such as pollination as an input to the production of a marketed crop is provided in [174 - see chapter 6]. Here, the focus is on the effects of a change in ecosystem service supply (here, the supply of PS) on production costs rather than profits, and the resultant impacts on consumers if production cost changes are big enough to produce price changes for the marketed crop, via an adverse output shock. The price and output change happens as the fall in pollination services shifts the supply curve for the crop in question. This means measuring the costs of a fall in the supply of pollination services as the change in producers' and consumers' surplus. See [174] for a more formal explanation and for examples.

Finally, wild pollinators act as an insurance for farmers in terms of the supply of pollination services [175]. If there is an unexpected decline in commercial bee populations (due, for example, to a disease outbreak), then the presence of wild pollinators can act as (partial) substitutes for this input. Wild pollinators thus reduce the variability of farm profits over time (reduce its variance), and farmers might opt to invest in a range of such wild pollinators – for instance, by planting wild flower margins – in a similar way in which they can opt to pay insurance premia. However, an important consideration in this case is whether the risks of commercial pollinator decline are positively or negatively correlated with the risks of wild pollinator decline.

Amenity or non-market values

Insect pollinators provide benefits to society in many ways which are additional to their role in commercial farming. From an economic value viewpoint, this happens in at least two ways:

- First, individuals derive pleasure from seeing pollinators, especially the larger, showy and distinctive species, and knowing they exist. Such use and non-use values are direct benefits to individuals from the presence, diversity and abundance of pollinators such as

bumblebees. Informal evidence on the existence of such values can be seen from members of the public paying to become members of the Bumblebee Conservation Trust. As presence, abundance and/or diversity increases, then utility may also increase. The monetary value of such increases in utility is given by an individual's willingness to pay for such an improvement in pollinators. For an individual a , we could write:

$$U_a = f(S_1, S_2, S_3, Y, N, E) \quad (3)$$

where Y is income, E is other environmental attributes and N is all other goods and services in the individual's choice set. The marginal, direct non-market value of a change in population S_1 is thus the partial derivative of (3) with respect to S_1 . For honeybees, the direct utility value can occur through the pleasure that bee-keepers obtain from their hobby.

- Second, individuals may care about the consequences of pollinators' actions. For example, this could be through the effects of wild pollinators on the diversity and abundance of wild flowers and trees. If people enjoy flower meadows, then they get an indirect benefit from the actions of pollinators. People who enjoy growing flowers and vegetables in their own gardens or allotments also get an indirect benefit from the actions on pollinators. If we assume that the variable E in equation (3) captures the importance of wild flowers and trees and of gardens and allotments to people, then the indirect, non-market economic value of pollinators is given by the effects of changes in a population or several populations on E . Ideally, we would want to empirically measure the partial derivative of E with respect to S multiplied by the partial derivative of U with respect to E .

2. *Pollinators as a natural capital stock: values over time.*

Increasing attention is being paid to the idea of ecosystems as natural capital, or assets. Ecosystems are biotic and abiotic stocks which generate a series of benefits over time [176]. The present value of the sum of discounted benefits provided by ecosystem service flows over time is equal to the economic value of such assets. Ecosystem assets can depreciate over time if the value of service flows over time decline, but society can also choose to invest in such assets (e.g. by restoring habitats). The stock of wild pollinators in the UK can be considered a natural capital asset, which is both renewable but can be depleted. Honeybees are semi-domesticated, managed in hives which can persist continuously for years, but are affected by some of the same environmental pressures as wild pollinators, including changes in climate, pesticide use and the threats of pests and diseases. Commercialised bumblebees in contrast are supplied as disposable nests from laboratory grown stock, and provide pollination for about 2 months before they are discarded or die off. Honeybees and commercial bumblebees can be owned and the placement of hives can be controlled, whereas wild populations of pollinators cannot be owned and can only be managed to a limited and relatively poorly understood extent. Therefore we are considering an asset that is made up of a mix of a conventional asset comprising managed honey and bumble bees which can be measured and are privately controlled and owned, and non-conventional assets made up of wild populations which are not. The services from wild populations are provided for 'free', and may be under-valued by land users and un-priced by markets, although habitat maintenance and restoration for pollination services may incur a cost.

The value of the stock of pollinators at any point in time depends on their contribution to (i) market-valued outputs (ii) direct contributions to utility (iii) indirect contributions to utility via effects on landscape quality and gardens, that is, on the benefits society receives from the stock of pollinators over time. It also depends on the extent to which effective pollination is dependent on substitutive or additive effects between different commercial and wild pollinator species, since that determines how changes in individual populations translate into changes in the delivery of pollination services. The ability of the stock to provide the current service flow is likely endangered by reductions in species diversity or by declines in abundance or performance (e.g. effects of insecticides on navigation). Reductions in species diversity would result in a decline in the value of pollination services if there is imperfect substitutability between species in terms of which flowers they can pollinate (so that an increase in honeybees would not necessarily maintain all the service value if

there is a decline in wild pollinators). Threshold effects in the supply of pollination services due to a decline in the condition of the pollinator asset would result in large changes in the shadow price of this asset.

As with any form of wealth, year-on-year changes in the value of the stock of pollinators could be included in an assessment of the extent to which natural capital or total capital is being maintained in a country [177]. This measure of net investment or dis-investment in capital can be linked to likely changes in future well-being, according to economic theory [178, 179]. However, it would be hard in practice to measure this net investment/dis-investment term in a comprehensive and correct manner, as is the case for many types of ecosystem assets, particular as limited data are available (particularly for wild insects) on the overall populations of pollinating insect species, and their response to management.

To date there has only been a limited assessment of the pollination service capital (natural and managed) in the UK. Honeybee numbers are officially reported as 270,000 across the country in 2010, a fall of 5% from 2005 [180] but to date there is no estimate of the number of other managed pollinators purchased annually. Wild pollinator stocks are not actively monitored, however, models for estimating the local availability of wild pollinator populations have been applied to the UK which suggested that between 5 and 10% of most UK agricultural land consists of habitat suitable for pollinators [181].

Methods for estimating values

Market values

There are two approaches to estimating the value of pollination services to markets; either through their contribution to profit through increasing production or through reduced costs. Presently, most studies have focused upon the former, estimating the value of pollination as an input into crop production, often using a simplified production function known as a dependence ratio (DR). DR studies estimate the proportion yields (drawn from national statistics) that would be lost without pollination service using published studies into the yield responses of different crops to pollination. Although some extremes cases exist where crops will not set without pollination, yield declines typically vary from moderate (e.g. field beans; 25%) to high (e.g. apples; 85%) between crops. This approach was taken in the UK NEA [7] for all UK crops in 2007 (**Table 2**, updated for 2010) and has been similarly applied in a number of other countries [e.g. USA 182] as well as globally [6]. The approach serves to highlight those crops (and thus farmers) which are especially vulnerable to pollinator declines. While these figures are based on generalised estimates of pollinator dependence from the full range of available literature, they are subject to a range of uncertainties, discussed below, and should be interpreted with caution.

Table 2. Crop dependencies on pollinators and annual value of pollination in 2010

Crop	Dependence on Pollinators (%)	Production Value (£ millions) 2010	Pollination Value (£ millions) 2010
Oilseed Rape	25	674	169
Strawberries	45	261	118
Dessert Apples	85	63	54
Raspberries	45	103	46
Cucumbers	65	53	35
Culinary Apples	85	40	34
Tomatoes	25	115	29
Runner Beans	85	17	14
Pears	65	16	10
Plums	65	13	8
Other	5-85	285	88
Total			Approx. 603

Although this approach is simple, as the dependence ratios themselves can be drawn from review papers [2], the insect pollinator dependence ratios used are often based upon studies from different countries or even continents, are not collected in a standardised manner and usually only consider changes in crop quantity, neglecting effects on quality parameters which may affect prices paid. Furthermore, they may not be fully reflective of local cultivars and growing conditions in the UK which are likely to vary in their dependence upon pollination and inherently assume that pollination services are already at their maximum level. Recent field studies have attempted to correct these faults by evaluating the benefits of pollination services to yields and quality of crops in the field and extrapolate this to a national scale. For example, a recent study estimated that insect pollination in the two main varieties of English dessert apple orchards (Gala and Cox) added ~65% to per hectare market output by increasing the number and weight of apples produced and the proportion of class 1 apples; adding £36.7M nationally [171]. The same study noted that pollination limitation in Gala apples was costing producers around £7M, although no such limitation was observed in Cox [159]. Nonetheless, these studies still overestimate the role of pollination by not accounting for the effects of other inputs on yield. Moreover, by focussing on average (per tonne) values, they do not tell us what the marginal cost of a decline in pollinator services would be, still less about how these marginal values change over time or space. Finally, this method assumes that farmers do not respond to changes in the supply of pollination services by switching production to less-dependent (although probably less profitable) crops.

Presently, most DR studies assume that crop prices, and therefore consumer demand, would not change. Some studies however expand upon this by using models to estimate losses to consumer welfare resulting from increasing prices, for instance it has been estimated that without pollination services prices rises would cost consumers €153Bn-€222Bn/year [6]. Estimating price responses to changing quantity is complex because of market heterogeneity for different crops and requires long term production and trade data, making it difficult to undertake accurately for all crops nationally. If world supply of a particular crop is unaffected by a fall in pollinators in one country, then world prices may not rise due to consumers switching demand from home production to imports. This would reduce any loss in consumers' surplus in the home country where pollinators have declined. Again, these estimates reflect average rather than marginal values, and so are of limited use from a management standpoint. An international trade model would be required to simulate the effects of a decline in domestic production of a given crop due to a pollinator collapse in that country on prices paid by consumers, and thus the extent of any change in consumers' surplus.

Alternatively, the value of pollination services can be equated to the costs of replacing these services artificially, reflecting the costs to producers avoided by the presence of pollinators. For example, it has been estimated that it would cost an additional ~£370-£1,400/ha produce tree fruit such as apples and plums by hand pollination [183]. Unlike DR studies, replacement cost studies do not over-attribute benefits to pollination services and can transfer work hour and materials costs between countries. However, it is unlikely that this method would be applicable for all crops as artificial pollination methods have proven ineffective on a number of crops [e.g. raspberry 184], may result in over-pollination [e.g. apple 159], and are likely to be too costly for producers in developed nations where labour costs are greater, increasing the likelihood of switching production unless crop prices were to rise sufficiently. More importantly, the approach tries to measure the value of a benefit by using the avoided cost approach; we know that this is very unlikely to produce a figure which is close to the real value of a beneficial ecosystem service, due to issues of substitutability and joint products.

Finally, a recent study [185] has attempted to combine dependency and avoided-cost methods into a single assessment of the value for watermelon production in Pennsylvania. By extrapolating observed benefits of pollination services to a county scale and the estimated effects on prices at a state wide level should insect pollination collapse within that county only, the authors provide an estimate of both producer and consumer losses. Using field data on the relative contribution of wild pollinators and honeybees to watermelon yields, estimates are made of the costs involved in replacing wild pollinators with managed honeybees by estimating the number of additional honeybee colonies that would have to be hired to replace the observed pollination from wild

insects. This study remains the most comprehensive assessment of the economic value of pollination to a single crop and the methods can be readily applied elsewhere, subject to the availability of sufficient market data.

Non-market values

In the previous section, we set out two ways in which pollinators could provide non-market benefits to individuals. These were (i) direct benefits, whereby people care about the population of certain pollinators in and of themselves – eg for bumblebees; (ii) indirect values, whereby pollinators contribute to the production of things which people care about – wild flower meadows, garden plants. In both cases, markets fail to register the full value of these benefits, since they have the characteristics of non-rivalness (the number of people who benefit from an increase in wild pollinators does not affect the value to any individual of this change) and non-excludability (if pollinator populations are increasing, then no-one can be excluded from benefitting from this increase even though they did not pay for it).

Economists have developed a range of methods for measuring such non-market values, which are described in numerous texts [174, 186]. For both direct and indirect values, it seems likely that only *stated preference* approaches would be a feasible choice of method for pollinators in the UK. Stated preferences work by asking a sample of individuals to either state whether they would be willing to pay a particular sum of money for an increase in an environmental good, or their willingness to accept compensation for a decline in this good (contingent valuation); or by asking people to make choices between different “bundles” of environmental attributes and a price (choice experiments). These responses are obtained in the context of a carefully-constructed hypothetical market for the good in question. Features of such markets which have been shown to be important are (i) that respondents feel that their responses are consequential (ii) that a non-voluntary payment mechanism be used (iii) that the environmental change in question be clearly described, and (iv) that the hypothetical market is realistic and does not encourage ethical rejection.

For direct benefits, where people care about the populations of pollinators, either contingent valuation or choice experiments could be used to estimate willingness to pay for a change in such populations (e.g. a 10% increase in bumblebee abundance over a 5 year period in Surrey). Choice experiments would enable the researcher to measure the impacts of different attributes of such a policy change on people’s preferences – such as whether they prefer an increase in species diversity rather abundance, or whether they prefer policy to be targeted at endangered or common species. Either method could be used to show how the non-market direct benefits of pollinators vary across the country and across income groups.

For indirect benefits, choice experiments and contingent valuation could be used to value changes in the environmental goods which pollinators help to produce, such as wild flower meadows. However, it would be difficult to design a study in such a way that one could isolate the contribution of (wild) pollinators to the production of the environmental good which people are valuing (e.g. a 25% rise in the number of wild flower meadows in Devon). Thus, identifying this indirect, non-market value of pollinators would be a challenging exercise.

Whilst there are many studies in the literature which apply stated preference methods to estimate the value of conserving individual species [187] and aspects of biodiversity [188, 189], at present only one (un-published) study has undertaken stated preference estimates of either direct or indirect non-market pollinator benefits. The existence value of protecting honeybees in the UK has been valued at £1.77bn/year [190]. However, this study is based on a small and non-random sample of the UK public, whilst the question used⁸ to elicit willingness to pay means that this figure confuses the market- and non-market values of pollinators. Moreover, since the survey did not

⁸ The precise wording was: “*The results of several surveys suggest the number of honey bees in the UK has reduced in recent years, perhaps due to building on green spaces and climate change. We aim to evaluate how much public interest there would be in preventing further declines and maintaining the number of honeybees in the UK indefinitely. Would you be willing to pay to support a policy to maintain bee populations at the current level? If yes, how much would you be willing to pay?*”

contain any statement regarding the consequentiality of responses (and since the payment mechanism was un-specified), there was no incentive for participants to reveal their true values. The information content of this value estimate is thus rather low.

Knowledge gaps and priorities for future research

As the last section makes clear, there are very large gaps in the knowledge base on the economic value of pollination services. This means that we are unable to provide robust answers to important questions such as:

- What are the economic costs of declines in pollinator populations and pollination services in the UK?
- Are pollination services at optimal or marginally sub-optimal levels?
- What are the economic costs and benefits of restricting neonicotinoid use in the UK, and how do these relate to the relationships between neonicotinoid use, yields and the effects of these chemicals on pollinators?

In the latter case, there is no robust evidence base on the value of marketed output lost or gained due to changes in pollinator populations for a range of relevant crops – even if we knew what changes in pollinator populations would result from implementing or maintaining a ban. We also have no clue about the non-market economic benefits of increases in pollinator populations that might result. Additionally, there is a lack of knowledge of the ecosystem production functions that relate changes in ecosystems to changes in pollinators; or the agricultural production functions that relate changes in inputs of pollinator services to changes in yields. Given the extent to which the marginal value of pollinators is likely to be highly variable across crops and across the country, it is hard to state with confidence whether the widely-cited figure of the value of pollination services to crop production in the UK [7] is an over- or an under-estimate. It is also not clear how policy-makers could use this value to inform decisions.

From an economics viewpoint, therefore, the three key priorities to filling knowledge gaps are:

1. Derive estimates of how changes in the supply of pollination services produce changes in expected profits for a range of agricultural crops and farm types in the UK, though an econometric or simulation modelling approach; and consider what general equilibrium effects this would have on consumer prices, given current trade patterns for relevant crops
2. Derive estimates of the direct and indirect non-market values associated with changes in the abundance and diversity of wild pollinator populations in the UK, though a national random sampling stated preference experiment.
3. Undertake combined ecological-economic modelling to better understand threshold effects on the marginal value of wild and commercial pollinators.

POTENTIAL INDICATORS OF POLLINATOR BIODIVERSITY AND ECOSYSTEM SERVICE

Main monitoring activities in the UK that could underpin development wild pollinator indicators are:

- Data on bumble and solitary bee species and hoverfly species occurrence. These provide the ability to monitor distributions of species richness over time and space. An important limitation is that the data are haphazardly collected by the voluntary recording societies (e.g. Hoverfly Recording Scheme, Bees Wasps and Ants Recording Society, Bumble Bee Conservation Trust) so sampling effort is unknown. However, there is now a statistical method which can estimate recorder effort by determining the probability of individual species occurrence in 10km x 10 km grid cells (the lowest spatial resolution of these data) [27]. These data do not constitute a systematic time series so comparisons of species richness can only be made by aggregating the data into decadal tranches [see 26, 39].
- The UK Butterfly Monitoring Scheme (UKBMS) is jointly run by CEH/JNCC/Butterfly Conservation. The UKBMS provides a time series (since 1976) of butterfly occurrence and abundance collected in >1000 transects across the UK. These transects tend to be a non-random sample of the landscape, but give good coverage of lowland semi-natural habitat and habitat specialist species.
- Since 2007/8 (pilot years) the Wider Countryside Butterfly Survey (WCBS) has been operated jointly by CEH, British Trust for Ornithology and Butterfly Conservation to advance this monitoring effort with a survey of 723 randomly selected 1-km squares to assess the changing abundance of widespread summer-flying butterfly species across the general countryside.
- Rothamsted light trap survey has run since 1968 with the help of volunteers across a network of 80 sites to monitor at daily intervals the abundance and distribution of larger (macro) moth species
- There is an incipient time series (~3 years) for bumble bee abundance at the genus (*Bombus*) level. Organised by the Bumble Bee Conservation Trust covering ~100 transects across the UK, which are surveyed monthly by volunteers.

Potential for indicators of pollinators and pollination services:

- Currently there is no all encompassing pollinator monitoring toolkit or single indicator.
- Data on butterfly and moth distributions collected as part of the Rothamsted and UKBMS/WCBS have much merit as indicators of changes in some other components of biodiversity (e.g. herbivorous diet of larvae mean that butterflies/moths may indicate plant community change) and climate or other habitat changes (these insects are very temperature sensitive and can have strict microhabitat requirements).
- However, although there is some evidence of correlation between butterfly and solitary bee diversity [e.g. 191], possibly due to similar habitat specialism, other evidence suggests a low level of congruence between the diversity of different pollinator taxa (wild bumble bees, hoverflies and butterflies) or indeed other ecosystem service providers (e.g. insect predators) [e.g. 192, 193]. This is likely due to substantial ecological and life history differences among taxa.
- There is little evidence that butterflies and moths pollinate flowering crops in the UK, hence the data on butterfly/moth species occurrence or abundance may have little utility as a pollination service indicator.
- Wild insect-pollinated plants may provide an indicator of changes to pollinator populations, but variable dependence on pollinators and the complexity of plant mating systems (e.g. self-fertilisation versus outcrossing) within insect-pollinated plant species introduces noise. Furthermore other correlated drivers may drive the observed patterns in plant populations.
- Wild bees, honey bees and flies provide the bulk of pollination service provision to UK crops, although the identity and dominance of different species/higher taxa will depend on crop (and potentially cultivar) and geographic location.

- Currently, species richness and functional diversity data obtained via voluntary recording societies offer a possible proxy measure of pollination service potential. The diversity of wild pollinators has been shown to contribute to the amount and stability of crop yields by providing some insurance or complementarity in pollination service delivery.
- Functional diversity may present an opportunity to refine the diversity-function relationship by including information on species traits relating to their functional role as pollinators (e.g. tongue length, body size, foraging range (mobility) and phenology). Thus it may better represent the pollination service than species richness alone.
- Functional diversity and species richness may provide an indication of the species pool and redundancy of pollination service providers over time. The former may represent a more refined option for an ecosystem service indicator at this time.
- For pollination service indication the main strength of the compositional datasets available in the UK is that they have a large temporal and spatial coverage; the major drawback is that they have low temporal resolution, some potential biases and sensitivity making them only a coarse indicator.
- Data on the abundance of pollination service providers is essential to derive and test a reliable indicator of pollination service delivery. There is, however, a total lack of abundance data with broad geographic coverage for wild bees and hoverflies resolved at the species level. The nascent monitoring programme for bumble bees established by the Bumble Bee Conservation Trust has good geographic coverage but only ~3 years data at this moment and is mainly resolved to the *Bombus* genus level. Available data on honey bee abundance derived from government registration suffer from some bias or uncertainty (e.g. associated with human density, voluntary registration) which makes them unlikely to be tightly coupled with service provision to crops.
- To accurately indicate changes in pollination service delivery to flowering crops would require data on community composition (species richness and/or functional diversity) weighted by data on relative abundance of the different taxa involved. In turn, this composite measure of pollination service would have to be shown to indicate changes in crop productivity, preferably tied to an economic valuation.
- At present we only have a partial and coarse tool for pollination service indication in the form of spatial patterns in the species richness and functional diversity of pollination service providers.

UK POLLINATION SCENARIOS UP TO 2025

Overall approach

In this report we use the already developed UK National Ecosystem Assessment (NEA, <http://uknea.unep-wcmc.org>) scenarios as a basis which can be adapted to include pollinator and pollination service specific elements for 2025. We develop a series of “what if?” narrative storylines to forecast how pollinators/pollination services might change with respect to scenarios of anthropogenic environmental changes (e.g. increased biofuel cropping or green infrastructure). In addition to the basic scenarios we will provide a description of a limited number of “additional events”, such as emergence and rapid spread of a severe honeybee pathogen, which can be included in the scenarios if required.

Uncertainty is likely to be very high in this forward look due to the combined uncertainties in:

- The base scenarios (which is recognised by NEA);
- The current status and trends of pollinator populations and service delivery;
- Future impacts of multiple drivers on pollinator population;
- Major upcoming agricultural policies (e.g. CAP reform, biofuels, pesticides);
- Policies specific to pollinators under the National Pollinator Strategy;
- National and global food market demands for insects pollinated commodities.

NEA Scenarios

The six NEA scenarios were developed to gather insight into how ecosystem services and human well-being might change under a range of plausible futures. They explore how emerging driving forces might combine to create different socio-political and economic conditions in the future and describe different ways the world might look up to 2060. The NEA scenarios are:

1. **Green and Pleasant Land (GPL):** a scenario in which the conservation of biodiversity and landscape are dominant driving forces.
2. **Nature@Work (N@W)** a scenario where population growth and the adoption of new technologies are dominant driving forces.
3. **World Markets (WM):** a scenario driven by the push for economic growth through the complete liberalisation of trade.
4. **National Security (NS):** a scenario driven primarily by increasing global energy prices that force most countries to seek greater self-sufficiency and efficiency in many of their core industries.
5. **Local Stewardship (LS):** a scenario driven by similar external pressures to National Security, but society has made a more conscious effort to reduce the intensity of economic activity and the high levels of consumption that were a characteristic of the early years of the century.
6. **Go with the Flow (GF):** a scenario in which the dominant socio-political and economic drivers acting on the UK at the end of 2010 continue.

The storylines take different approaches in their focus on different aspects of biodiversity and ecosystem character. In **Green and Pleasant Land** a more static 'preservationist' attitude seeks to conserve native flora and fauna as well as cultural landscapes. In contrast, in **Local Stewardship**, and particularly in **Nature@Work**, a more dynamic view of ecosystems is taken, and adaptability is considered more important than the degree of 'nativeness'.

Full descriptions of the storylines, drivers, biodiversity and ecosystem service and land cover responses, as well as an analysis across scenarios can be found in Chapter 25 of the NEA Technical report.

Choice of NEA scenarios

The NEA scenarios are longer-term projections (up to 2060) and the aim of this section is to explore shorter-term projections (up to 2025). Some of the NEA scenarios are unlikely to be strongly differentiated by 2025; therefore we use a sub-set of scenarios likely to represent the range of likely alternative futures for the UK by 2025. The NEA recognises that in general differences between high and low climate change versions of each scenarios are smaller than the difference observed between different scenarios. Consequently, we ignore climate change differences in our scenarios.

A non-exhaustive set of key pollinator relevant attributes of the scenarios are summarised in **Table 3**. These describe the main storylines for land use (agriculture, environment and ecosystems) and also the state and trends of wild biodiversity (wider biodiversity including pollinators) and pollination services.

Table: 3. Selected attributes (for 2060) of the six NEA scenarios relevant to pollinators and pollination services.

Attribute ⁹	GPL	N@W	WM	NS	LS	GF
Land use & landscape	Highly protected, diverse, local character.	Highly protected; 'optimised' balance of ecosystem services provision.	More homogenous and industrial.	For production. Food and energy come first. Homogenised.	Very diverse, different regional characters.	Token efforts towards biodiversity protection doesn't hide further homogenisation of countryside.
Agriculture	Extensive farming low-input, agri-environment schemes popular.	Reduction in meat – replaced by crop protein. more sustainable, precision techniques.	Industrialised and GM dominate.	Heavily subsidised. Technology advances push yields; GM adopted.	Localised, value added, regional products.	Increasingly industrialised.
State of the environment	Good, protected landscapes	Very good. Provisioning optimised but careful balance with regulation and biodiversity.	Poor in most places	Agriculture and energy decrease biodiversity few areas protected.	'Optimised' landscape but high biodiversity.	Many habitats in favourable condition. Loss of some species to climate change though.
Ecosystems management	Co-benefit of landscape preservation.	Underlying concept. Includes education.	Some trading of ecosystem services (mostly energy) otherwise little regard	Little regard. Other things over-ride it.	Full understanding of how to maintain ecosystem services. Local pride in management.	Some landscape management in flood areas.
Area of enclosed farmland¹⁰	Decrease	Decrease	Increase	Increase	No change	No change
Wild species diversity in semi-natural grasslands¹¹	Very high, improving some	Very high, improving some	Low, some deterioration	Low, some deterioration	Very high, improving some	High, some deterioration
Wild species diversity in enclosed farmland	Very high, improving some	Very high, some improvement	Low, deteriorating	Low, deteriorating	Very high, improving some	Medium, some improvement
Pollination services in semi-natural grasslands	Very high, improving some	Very high, improving some	Medium, deteriorating	Low, deteriorating	Very high, unknown trend	High, some improvement
Pollination services in enclosed farmland	Very high, improving some	Very high, improving some	Medium, deteriorating	Low, deteriorating	Very high, unknown trend	High, some improvement

Based on the main attributes of the six NEA scenarios we have chosen **Go with the Flow** as our business as usual baseline. To capture key elements of Green and Pleasant Land, Nature@Work and Local Stewardship, where there are land use strategies more or less aiming to balance food

⁹ Modified from NEA Ch 25 Table 25.5.

^{10 2} Estimates relative to GF Low scenario taken from Figure 25.3.

¹¹ Taken from figures 25.6, 25.8, 25.10, 25.12, 25.14 and 25.16.

production with wider environmental services, we have adopted the **Local Stewardship** scenario. To contrast this, where focus is primarily on food production, with elements from World Markets and National Security we have adopted the **National Security** scenario. Local Stewardship and National Security represent two strongly contrasting possible futures though the attributes listed in Table 3 will only be partially realised, if at all, by 2025 (12 years ahead), as the original scenarios are focussed on 2060 (47 years ahead). However, these two scenarios allow us to explore differences between them and relative to a business as usual baseline.

Adapting scenarios to include pollinators and pollination services

Using the general elements of the three chosen scenarios, and the current baseline of 2013, we have estimated the range of key parameters relating to pollinators and services and their expected trend; these are summarised in **Table 4 up to 2025**.

Table 4. Pollinator and pollination relevant metrics for the chosen NEA scenarios up to 2025. Italicised text is a first estimate to give a potential range of values, which may be subject to modification once better data is available. ‘Declines’ here refer to range contractions, losses of diversity for wild bees and hoverflies, butterflies and moths. Data on declines in abundance are only known for butterflies, moths and honey bees. There is considerable uncertainty (see above sections) in the present day due to data limitations, which will increase with forward projection.

Metric	Baseline (2013)	Go with the Flow (2025)	National Security (2025)	Local Stewardship (2025)
Honeybee colonies	247,000 colonies in the UK, declining in number ¹²	<i>5-20% loss relative to the baseline condition (i.e. ~200k colonies) over the time period 2013 - 2025, as interventions not fully effective</i>	<i>Stable or increasing (0-30%), as honeybees recognised as agricultural input and technology solutions applied to support honeybee industry</i>	<i>Stable (±10% change), due to improvements in honeybee health but declines not fully reversed</i>
Wild pollinators	Many species declined, up to ~10% loss per decade, in species richness or distribution during 20 th century. Some (generalists) increasing over same time scale. <i>Some early indication that rate of decline may be slowing since 1990s¹³</i>	<i>Declines continue at similar rates to historic 20th century (~0-10%)</i>	<i>Declines more severe (10-30%) as focus is on managed pollinators and farmland becomes increasingly intensified</i>	<i>More species stable (0%) or increasing (0-10%) with farmland better optimised for food production and biodiversity conservation</i>
Insect-pollinated wild flowers	Some species stable, some declining in range or frequency (up to 10% per decade) during the 20 th century. <i>Some early indication that rate of decline may be slowing since 1990s¹</i>	<i>Declines continue at similar rates to historic 20th century (~0-10%)</i>	<i>Declines more severe (10-30%) as focus is on food production and farmland becomes increasingly intensified</i>	<i>More species stable (0%) or increasing (0-10%) with farmland better optimised for food production and biodiversity conservation</i>
Area of insect pollinated crops	~900,000 ha (includes area of oilseed rape – below)	<i>Small loss of food crop area (1-5%) as biofuels more widely grown</i>	<i>Increased by 5-10% as demand for UK food increases meaning some marginal land converted to farming</i>	<i>No change, or small loss (0-5%), as balance between food and fuel crops remains stable</i>
Area of insect pollinated biofuel crops	~705,000 ha of all oilseed rape crop	<i>Increased by 50-100%, driven by EU and UK biofuel targets</i>	<i>Large increases (100-500%) driven by EU/UK targets & fuel security</i>	<i>Small increases (0-30%) as biofuels increasingly grown and used locally</i>

¹² European Commission (2010) Commission Regulation (EU) No 726/2010

¹³ Note - drawn from single study: Carvalheiro et al. (2013) Ecology Letters, 16, 870-878.

Assessment of scenarios for UK pollinators and pollination services

The analysis below uses the NEA scenarios as a general guide, but it recognises that these represent a view of 2060, and so their extent is greatly reduced in applying them to 2025. All three scenarios do not include any new or adapted policies directly or indirectly targeting pollinators or pollination services (e.g. under a National Pollinator Strategy).

Go with the Flow:

- Drivers and policies remain similar to current situation.
- Honeybees continue to decline (5-20%) as no major change in honeybee management practices or environmental conditions.
- Wild pollinators, especially bumblebees and butterflies, generally declining 0-10%, though for solitary bees the pattern is mixed with some declines (0-10%) and some increases (0-10%). Pollinator communities become more homogenised as generalist species tend to dominate.
- Area of insect-pollinated crops decreases (1-5%) as farmers switch to wet biofuel crops which increase in area (50-100%) in response to increased global market prices driven by EU biofuel policy. Overall pollination service demands increase moderately with wild pollinator providing the majority of the services.
- Insect pollinated wild flowers are either stable due to protection or continue to decline at rates similar to those currently documented (0-10%).

National Security:

- Increased food production in the UK becomes a major driver of land use and policies aim at enhancing food security over biodiversity protection.
- Honeybees are seen as a short-term solution to supporting increased demands for crop pollination as crop area rises. Current declines in numbers are halted, or reversed, as honeybee health technology and management practises are improved in order to provide honeybees as an agricultural input.
- All wild pollinators, especially bumblebees and butterflies, declining 10-30%, as farmland becomes increasingly intensified for food production, and pollinator friendly-farming practices become less prevalent. Pollinator communities become much more homogenised as generalist species dominate.
- Area of insect-pollinated crops increases (5-10%) as increased food and biofuel demand drives more marginal land to be cultivated. Areas used for biofuel increase markedly (100-500%) as result of fuel security and EU biofuel policies. Overall a substantial increase in the demand for pollination services which are mostly supplied by honeybees.
- Insect pollinated wild flowers decline (10-30%) as farmland becomes increasingly intensified for food production, and wild flower friendly-farming practices become less prevalent.

Local Stewardship:

- Policy and practice increasingly supports the integration of food production and biodiversity conservation into the landscape.

- Honeybees become more or less stable ($\pm 10\%$) as productive farmland also provides good quality habitat for honeybees to forage on coupled with some improvements in honeybee health management.
- Wild pollinator declines slow down and some species recovering (0-10%) as farming less intensive and the landscape provides more and better quality pollinator habitats.
- Area of insect-pollinated crops remains stable or decreases (0-5%) as biofuels grown more (0-30%) locally and used locally. Overall demand for pollination services increases slightly with the majority of service provision coming from wild pollinators.
- Insect pollinated wild flowers are either stable or increasing as biodiversity protection is improved through less intensive farming and their wild pollinators are recovering.

Additional Events

These events can be included, or not, with the subset of NEA scenarios to provide additional ways of exploring plausible futures for UK pollinators and pollination services.

1. **Honeybee pandemic:** where an existing or emergent disease strongly impact honeybee stocks in the short-term (1-3 years), resulting in a significant decrease in the supply of pollination services from managed pollinators. *Low probability but high impact.*
2. **Fuel crisis:** Availability of cheap non-renewable energy is severely restricted due to geopolitical event(s) (e.g. war in the Middle East) causing a sharp rise in the cost of imported fuel; the UK response is a large increase in the area of wet biofuel crops (e.g. oilseed rape) coupled with large increases in the demand for pollination services. *Moderate probability and high impact.*
3. **Disruption of food imports:** Availability of cheap food is severely restricted due to geopolitical or economic event(s) (e.g. jump in global food prices) causing a sharp rise in the cost of imported food; one UK response is increases in the areas of food crops (cereals, fruits, vegetables) coupled with large increases in the demand for pollination services. *Moderate probability and high impact.*

Table 5. Pollinator and pollination relevant metrics for additional events

Metric	Honeybee pandemic	Fuel crisis	Disruption of food imports
Honeybee colonies	10-50% loss in 1 year	No change	No change
Wild pollinators	No change	No change	No change
Area of insect pollinated food crops	No change	Decrease (1-10%) as food crops converted to biofuel crops	Increases (1-10%) with need for home grown food
Area of insect pollinated biofuel crops	No change	Increases (100-500%) with need for biofuels	Decrease (0-50%) as biofuel crops converted to food crops
Insect-pollinated wild flowers	No change	No change	No change

CONCLUSION

Pollinators and pollination faces multiple threats from global environmental changes. Ecological and evolutionary traits (e.g. degree of specialism, sociality) determine the extent to which a given species is affected by these threats. Altogether there is good evidence that the species diversity and ranges of wild bees, numbers of honey bee colonies and abundance of butterflies and moths are changing in Britain with more areas showing a decline than increase. However, the many limitations of the available data (e.g. spatial or temporal coverage/resolution) mean the results should be treated with appropriate caution. Importantly there is a total lack of abundance data for wild bees and hoverflies species which precludes us from detecting actual changes in population sizes. Data on honey bee colony numbers exist, but the accuracy is questionable due to the source of those data (voluntary registration). Abundance data on butterflies and moths indicate a general decline in abundance of habitat specialist species and those in central and southern of England, yet these patterns are not a reliable proxy for other species and these insects do not indicate changes in pollination service delivery to UK crops. The relationship between pollinator biodiversity, pollination processes, agricultural productivity and crop market value is not well understood, especially in the UK landscape, and the market value used in the UK NEA should be recognised as having high uncertainty. Current indications of crop pollination service potential at national scales require cautious interpretation because of the limitations and assumptions in the underlying data. Without systematic and standardised monitoring of pollinator populations it is impossible to state unequivocally whether wild insect pollinators are in decline or not. This lack of data means the scientific community has great difficulty in accurately answering policy-directed questions such as the direction and extent of changes in pollinator biodiversity, the value and functional relationship of pollinators to agriculture from farm to national scales and how this biodiversity and linked ecosystem service will change in the future.

REFERENCES

1. Godfray, H.C.J., et al., *The future of the global food system*. Philosophical Transactions of the Royal Society B-Biological Sciences, 2010. **365**(1554): p. 2769-2777.
2. Klein, A.M., et al., *Importance of pollinators in changing landscapes for world crops*. Proceedings of the Royal Society B-Biological Sciences, 2007. **274**(1608): p. 303-313.
3. Free, J.B., *Insect Pollination of Crops* 1993: Academic Press, London.
4. Garibaldi, L.A., et al., *Global growth and stability of agricultural yield decrease with pollinator dependence*. Proceedings of the National Academy of Sciences of the United States of America, 2011. **108**(14): p. 5909-5914.
5. Aizen, M.A. and L.D. Harder, *The global stock of domesticated honey bees is growing slower than agricultural demand for pollination*. Current Biology, 2009. **19**(11): p. 915-918.
6. Gallai, N., et al., *Economic valuation of the vulnerability of world agriculture confronted with pollinator decline*. Ecological Economics, 2009. **68**(3): p. 810-821.
7. Smith, P.E., et al., *Regulating Services*, in *The U.K National Ecosystem Assessment Technical Report* 2011: U.K National Ecosystem Assessment UNEP-WCMC Cambridge. p. 535-597.
8. Garibaldi, L.A., et al., *Wild pollinators enhance fruit set of crops regardless of honey bee abundance*. Science, 2013. **339**: p. 1608-1611.
9. Garibaldi, L.A., et al., *Stability of pollination services decreases with isolation from natural areas despite honey bee visits* Ecology Letters, 2011. **14**(10): p. 1062–1072.
10. Breeze, T.D., et al., *Pollination services in the UK: How important are honeybees?* Agriculture, Ecosystems & Environment, 2011. **142**(3–4): p. 137-143.
11. Hoehn, P., et al., *Functional group diversity of bee pollinators increases crop yield*. Proceedings of the Royal Society B-Biological Sciences, 2008. **275**(1648): p. 2283-2291.
12. Vanbergen, A.J. and the Insect Pollinators Initiative, *Threats to an ecosystem service: pressures on pollinators*. Frontiers in Ecology and the Environment, 2013. **11**(5): p. 251-259.
13. González-Varo, J.P., et al., *Combined effects of global change pressures on animal-mediated pollination*. Trends in Ecology & Evolution, 2013. **28**(9): p. 524-534.

14. Potts, S.G., et al., *Global pollinator declines: trends, impacts and drivers*. Trends in Ecology & Evolution, 2010. **25**(6): p. 345-353.
15. Brittain, C., C. Kremen, and A.-M. Klein, *Biodiversity buffers pollination from changes in environmental conditions*. Global Change Biology, 2013. **19**(2): p. 540-547.
16. Klein, A.-M., et al., *Wild pollination services to California almond rely on semi-natural habitat*. Journal of Applied Ecology, 2012. **49**(3): p. 723-732.
17. Aizen, M.A., et al., *Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency*. Current Biology, 2008. **18**(20): p. 1572-1575.
18. Eilers, E.J., et al., *Contribution of pollinator-mediated crops to nutrients in the human food supply*. PLoS ONE, 2011. **6**(6): p. e21363.
19. Ollerton, J., R. Winfree, and S. Tarrant, *How many flowering plants are pollinated by animals?* Oikos, 2011. **120**(3): p. 321-326.
20. Memmott, J., N.M. Waser, and M.V. Price, *Tolerance of pollination networks to species extinctions*. Proceedings of the Royal Society of London Series B-Biological Sciences, 2004. **271**(1557): p. 2605-2611.
21. Bartomeus, I., et al., *Biodiversity ensures plant–pollinator phenological synchrony against climate change*. Ecology Letters, 2013. **16**(11): p. 1331-1338.
22. Kaiser-Bunbury, C.N., et al., *The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour*. Ecology Letters, 2010. **13**(4): p. 442-452.
23. Aizen, M.A., M. Sabatino, and J.M. Tylianakis, *Specialization and rarity predict nonrandom loss of interactions from mutualist networks*. Science, 2012. **335**(6075): p. 1486-1489.
24. Valdovinos, F.S., et al., *Adaptive foraging allows the maintenance of biodiversity of pollination networks*. Oikos, 2013. **122**(6): p. 907-917.
25. Schleuning, M., et al., *Specialization of mutualistic interaction networks decreases toward tropical latitudes*. Current biology, 2012. **22**(20): p. 1925-1931.
26. Biesmeijer, J.C., et al., *Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands*. Science, 2006. **313**(5785): p. 351-354.
27. Hill, M.O., *Local frequency as a key to interpreting species occurrence data when recording effort is not known*. Methods in Ecology and Evolution, 2012. **3**(1): p. 195-205.
28. Fox, R., et al., *The state of Britain's larger moths 2013*, Butterfly Conservation and Rothamsted Research Wareham, Dorset, UK.
29. Fox, R., et al., *The state of the UK's butterflies 2011*, Butterfly Conservation and the Centre for Ecology & Hydrology: Wareham, Dorset.
30. Williams, P.H., M.B. Araujo, and P. Rasmont, *Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth?* Biological Conservation, 2007. **138**(3-4): p. 493-505.
31. Kleijn, D. and I. Raemakers, *A retrospective analysis of pollen host plant use by stable and declining bumble bee species*. Ecology, 2008. **89**(7): p. 1811-1823.
32. Goulson, D., G.C. Lye, and B. Darvill, *Decline and conservation of bumble bees*. Annual Review of Entomology, 2008. **53**: p. 191-208.
33. Goulson, D., et al., *Biotope associations and the decline of bumblebees (*Bombus* spp.)*. Journal of Insect Conservation, 2006. **10**(2): p. 95-103.
34. Williams, P.H., *The distribution and decline of British bumble bees (*Bombus Latr.*)*. Journal of Apicultural Research, 1982. **21**(4): p. 236-245.
35. Fitzpatrick, U., et al., *Rarity and decline in bumblebees - A test of causes and correlates in the Irish fauna*. Biological Conservation, 2007. **136**(2): p. 185-194.
36. Bommarco, R., et al., *Drastic historic shifts in bumble-bee community composition in Sweden*. Proceedings of the Royal Society B: Biological Sciences, 2011. **279**(1727): p. 309-315.
37. Cameron, S.A., et al., *Patterns of widespread decline in North American bumble bees*. Proceedings of the National Academy of Sciences of the United States of America, 2011. **108**(2): p. 662–667.
38. Williams, P.H. and J.L. Osborne, *Bumblebee vulnerability and conservation world-wide*. Apidologie, 2009. **40**(3): p. 367-387.

39. Carvalheiro, L.G., et al., *Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants*. Ecology Letters, 2013. **16**(7): p. 870-878.
40. Potts, S.G., et al., *Declines of managed honey bees and beekeepers in Europe*. Journal of Apicultural Research, 2010. **49**(1): p. 15-22.
41. vanEngelsdorp, D., et al., *A survey of managed honey bee colony losses in the USA, fall 2009 to winter 2010*. Journal of Apicultural Research, 2011. **50**(1): p. 1-10.
42. Jaffe, R., et al., *Estimating the density of honeybee colonies across their natural range to fill the gap in pollinator decline censuses*. Conservation Biology, 2010. **24**(2): p. 583-593.
43. BBKA, *Winter survival survey 2013*:
http://www.bbka.org.uk/files/pressreleases/bbka_release_winter_survival_survey_13_june_2013_1371062171.pdf.
44. Keil, P., et al., *Biodiversity change is scale-dependent: An example from Dutch and UK hoverflies (Diptera, Syrphidae)*. Ecography 2011. **34**(3): p. 392-401.
45. Warren, M.S., et al., *Rapid responses of British butterflies to opposing forces of climate and habitat change*. Nature, 2001. **414**(6859): p. 65-69.
46. Thomas, J.A., et al., *Comparative losses of British butterflies, birds, and plants and the global extinction crisis*. Science, 2004. **303**(5665): p. 1879-1881.
47. Carvell, C., et al., *Declines in forage availability for bumblebees at a national scale*. Biological Conservation, 2006. **132**(4): p. 481-489.
48. Ghazoul, J., *Pollen and seed dispersal among dispersed plants*. Biological Reviews, 2005. **80**(3): p. 413-443.
49. Cranmer, L., D. McCollin, and J. Ollerton, *Landscape structure influences pollinator movements and directly affects plant reproductive success*. Oikos, 2011. **121**(4): p. 562-568.
50. Kunin, W.E., *Population size and density effects in pollination: Pollinator foraging and plant reproductive success in experimental arrays of Brassica kaber*. Journal of Ecology, 1997. **85**(2): p. 225-234.
51. Cussans, J., et al., *Two bee-pollinated plant species show higher seed production when grown in gardens compared to arable farmland*. PLoS ONE, 2010. **5**(7): p. e11753.
52. Vanbergen, A.J., et al., *Grazing alters insect visitation networks and plant mating systems*. Functional Ecology, 2014. **28**(1): p. 178-189.
53. Albrecht, M., et al., *Diverse pollinator communities enhance plant reproductive success*. Proceedings of the Royal Society B: Biological Sciences, 2012. **279**(1748): p. 4845-4852.
54. Klank, C., A.R. Pluess, and J. Ghazoul, *Effects of population size on plant reproduction and pollinator abundance in a specialized pollination system*. Journal of Ecology, 2010. **98**(6): p. 1389-1397.
55. Vazquez, D.P. and D. Simberloff, *Indirect effects of an introduced ungulate on pollination and plant reproduction*. Ecological Monographs, 2004. **74**(2): p. 281-308.
56. Donaldson, J., et al., *Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa*. Conservation Biology, 2002. **16**(5): p. 1267-1276.
57. Bartomeus, I., M. Vila, and I. Steffan-Dewenter, *Combined effects of Impatiens glandulifera invasion and landscape structure on native plant pollination*. Journal of Ecology, 2010. **98**(2): p. 440-450.
58. González-Varo, J.P., J. Arroyo, and A. Aparicio, *Effects of fragmentation on pollinator assemblage, pollen limitation and seed production of Mediterranean myrtle (Myrtus communis)*. Biological Conservation, 2009. **142**(5): p. 1058-1065.
59. Eckert, C.G., et al., *Plant mating systems in a changing world*. Trends in Ecology & Evolution, 2010. **25**(1): p. 35-43.
60. Lennartsson, T., *Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations*. Ecology, 2002. **83**(11): p. 3060-3072.
61. Preston, C.D., D.A. Pearman, and T.D. Dines, *New atlas of the British and Irish flora.2002*, Oxford: Oxford University Press.
62. Smart, S., et al., *An integrated assessment of countryside survey data to investigate ecosystem services in Great Britain. Technical report No. 10/07, NERC Centre for Ecology & Hydrology 230pp., (CEH Project Number: C03259), 2010.*

63. Telfer, M.G., C.D. Preston, and P. Rothery, *A general method for measuring relative change in range size from biological atlas data*. *Biological Conservation*, 2002. **107**(1): p. 99-109.
64. Cheffings, C., *New plant status lists for Great Britain*. BSBI News, 2004. **95**: p. 36-43.
65. Robinson, R.A. and W.J. Sutherland, *Post-war changes in arable farming and biodiversity in Great Britain*. *Journal of Applied Ecology*, 2002. **39**(1): p. 157-176.
66. Kells, A.R. and D. Goulson, *Preferred nesting sites of bumblebee queens (Hymenoptera : Apidae) in agroecosystems in the UK*. *Biological Conservation*, 2003. **109**(2): p. 165-174.
67. Hill, J.K., et al., *Impacts of landscape structure on butterfly range expansion*. *Ecology Letters*, 2001. **4**(4): p. 313-321.
68. Winfree, R., et al., *A meta-analysis of bees' responses to anthropogenic disturbance*. *Ecology*, 2009. **90**(8): p. 2068-2076.
69. Kearns, C.A., D.W. Inouye, and N.M. Waser, *Endangered mutualisms: The conservation of plant-pollinator interactions*. *Annual Review of Ecology and Systematics*, 1998. **29**: p. 83-112.
70. Lawton, J.H., et al., *Making space for nature: a review of England's wildlife sites and ecological network 2010*. i-xii, 1-107.
71. Winn, J., et al., *The drivers of change in UK ecosystems and ecosystem services*, in *The UK National Ecosystem Assessment Technical Report 2012*: U.K National Ecosystem Assessment UNEP-WCMC Cambridge. p. 27-63.
72. Osgathorpe, L.M., et al., *The trade-off between agriculture and biodiversity in marginal areas: Can crofting and bumblebee conservation be reconciled?* *Ecological Economics*, 2011. **70**(6): p. 1162-1169.
73. Goulson, D., et al., *Causes of rarity in bumblebees*. *Biological Conservation*, 2005. **122**(1): p. 1-8.
74. Williams, N.M., et al., *Ecological and life-history traits predict bee species responses to environmental disturbances*. *Biological Conservation*, 2010. **143**(10): p. 2280-2291.
75. Bommarco, R., et al., *Dispersal capacity and diet breadth modify the response of wild bees to habitat loss*. *Proceedings of the Royal Society B-Biological Sciences*, 2010. **277**(1690): p. 2075-2082.
76. Schweiger, O., et al., *Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe*. *Oikos*, 2007. **116**(3): p. 461-472.
77. Scheper, J., et al., *Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis*. *Ecology Letters*, 2013. **16**(7): p. 912-920.
78. Batary, P., et al., *Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis*. *Proceedings of the Royal Society B-Biological Sciences*, 2011. **278**(1713): p. 1894-1902.
79. Heard, M.S., et al., *Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes*. *Biology Letters*, 2007. **3**(6): p. 638-641.
80. Carvell, C., et al., *Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality*. *Ecological Applications*, 2011. **21**(5): p. 1760-1771.
81. Ellis, J.S., et al., *Extremely low effective population sizes, genetic structuring and reduced genetic diversity in a threatened bumblebee species, *Bombus sylvarum* (Hymenoptera : Apidae)*. *Molecular Ecology*, 2006. **15**(14): p. 4375-4386.
82. Darvill, B., et al., *Population structure and inbreeding in a rare and declining bumblebee, *Bombus muscorum* (Hymenoptera : Apidae)*. *Molecular Ecology*, 2006. **15**(3): p. 601-611.
83. Charman, T.G., et al., *Conservation genetics, foraging distance and nest density of the scarce Great Yellow Bumblebee (*Bombus distinguendus*)*. *Molecular Ecology*, 2010. **19**(13): p. 2661-2674.
84. Whitehorn, P.R., et al., *Genetic diversity, parasite prevalence and immunity in wild bumblebees*. *Proceedings of the Royal Society B-Biological Sciences* 2010. **278**: p. 1195-1202.

85. Carvell, C., et al., *Molecular and spatial analyses reveal links between colony-specific foraging distance and landscape-level resource availability in two bumblebee species*. *Oikos*, 2012. **121** p. 734-742.
86. Lepais, O., et al., *Estimation of bumblebee queen dispersal distances using sibship reconstruction method*. *Molecular Ecology*, 2010. **19**(4): p. 819-831.
87. Knight, M.E., et al., *Bumblebee nest density and the scale of available forage in arable landscapes*. *Insect Conservation and Diversity*, 2009. **2**(2): p. 116-124.
88. Westphal, C., I. Steffan-Dewenter, and T. Tscharntke, *Mass flowering crops enhance pollinator densities at a landscape scale*. *Ecology Letters*, 2003. **6**(11): p. 961-965.
89. Stanley, D.A. and J.C. Stout, *Quantifying the impacts of bioenergy crops on pollinating insect abundance and diversity: a field-scale evaluation reveals taxon-specific responses*. *Journal of Applied Ecology*, 2013. **50**(2): p. 335-344.
90. Le Féon, V., et al., *Solitary bee abundance and species richness in dynamic agricultural landscapes*. *Agriculture, Ecosystems & Environment*, 2013. **166**(0): p. 94-101.
91. Carvell, C., et al., *Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins*. *Journal of Applied Ecology*, 2007. **44**(1): p. 29-40.
92. Memmott, J., et al., *The potential impact of global warming on the efficacy of field margins sown for the conservation of bumble-bees*. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 2010. **365**(1549): p. 2071-2079.
93. Holzschuh, A., et al., *Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination*. *Proceedings of the Royal Society B: Biological Sciences*, 2011. **278**(1723): p. 3444-3451.
94. Diekötter, T., et al., *Oilseed rape crops distort plant-pollinator interactions*. *Journal of Applied Ecology*, 2009. **47**(1): p. 209-214.
95. Carvell, C., et al., *Effects of resource availability and social parasite invasion on field colonies of *Bombus terrestris**. *Ecological Entomology*, 2008. **33**(3): p. 321-327.
96. Gabriel, D., et al., *Scale matters: the impact of organic farming on biodiversity at different spatial scales*. *Ecology Letters*, 2010. **13**(7): p. 858-869.
97. Brittain, C.A., et al., *Impacts of a pesticide on pollinator species richness at different spatial scales*. *Basic and Applied Ecology*, 2010. **11**(2): p. 106-115.
98. Cresswell, J.E., *A meta-analysis of experiments testing the effects of a neonicotinoid insecticide (imidacloprid) on honey bees*. *Ecotoxicology*, 2011. **20**(1): p. 149-157.
99. Goulson, D., *An overview of the environmental risks posed by neonicotinoid insecticides*. *Journal of Applied Ecology*, 2013. **50**(4): p. 977-987.
100. Blacquiere, T., et al., *Neonicotinoids in bees: a review on concentrations, side-effects and risk assessment*. *Ecotoxicology*, 2012. **21**(4): p. 973-992.
101. Palmer, M.J., et al., *Cholinergic pesticides cause mushroom body neuronal inactivation in honeybees*. *Nature Communications*, 2013. **4**: p. 1634.
102. Williamson, S.M. and G.A. Wright, *Exposure to multiple cholinergic pesticides impairs olfactory learning and memory in honeybees*. *Journal of Experimental Biology*, 2013. **216**(10): p. 1799-807.
103. Henry, M.I., et al., *A common pesticide decreases foraging success and survival in honey bees*. *Science*, 2012. **336**: p. 348-350.
104. Cresswell, J.E., et al., *Differential sensitivity of honey bees and bumble bees to a dietary insecticide (imidacloprid)*. *Zoology*, 2012. **115**(6): p. 365-371.
105. Whitehorn, P.R., et al., *Neonicotinoid pesticide reduces bumble bee colony growth and queen production*. *Science*, 2012. **336**: p. 351-352.
106. Gill, R.J., O. Ramos-Rodriguez, and N.E. Raine, *Combined pesticide exposure severely affects individual- and colony-level traits in bees*. *Nature*, 2012. **491**: p. 105-108.
107. Jha, S. and C. Kremen, *Urban land use limits regional bumble bee gene flow*. *Molecular Ecology*, 2013. **22**(9): p. 2483-2495.
108. Geslin, B., et al., *Plant pollinator networks along a gradient of urbanisation*. *PLoS ONE*, 2013. **8**(5): p. e63421.
109. Goulson, D., et al., *Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats*. *Oecologia*, 2002. **130**(2): p. 267-273.

110. Goulson, D., et al., *Effects of land use at a landscape scale on bumblebee nest density and survival*. Journal of Applied Ecology, 2010. **47**(6): p. 1207-1215.
111. Osborne, J.L., et al., *Quantifying and comparing bumblebee nest densities in gardens and countryside habitats*. Journal of Applied Ecology, 2008. **45**(3): p. 784-792.
112. Samnegard, U., A.S. Persson, and H.G. Smith, *Gardens benefit bees and enhance pollination in intensively managed farmland*. Biological Conservation, 2011. **144**(11): p. 2602-2606.
113. Stelzer, R.J., et al., *Winter active bumblebees (*Bombus terrestris*) achieve high foraging rates in urban Britain*. PLoS ONE, 2010. **5**(3): p. e9559.
114. Lopezaraiza-Mikel, M.E., et al., *The impact of an alien plant on a native plant-pollinator network: an experimental approach*. Ecology Letters, 2007. **10**: p. 539-550.
115. Stout, J.C., et al., *Pollination ecology and seed production of *Rhododendron ponticum* in native and exotic habitats*. Biodiversity and Conservation, 2006. **15**(2): p. 755-777.
116. Nienhuis, C.M., A.C. Dietzsch, and J.C. Stout, *The impacts of an invasive alien plant and its removal on native bees*. Apidologie, 2009. **40**(4): p. 450-463.
117. Dietzsch, A., D. Stanley, and J. Stout, *Relative abundance of an invasive alien plant affects native pollination processes*. Oecologia, 2011. **167**(2): p. 469-479.
118. Carvalheiro, L.G., E.R.M. Barbosa, and J. Memmott, *Pollinator networks, alien species and the conservation of rare plants: *Trinia glauca* as a case study*. Journal of Applied Ecology, 2008. **45**(5): p. 1419-1427.
119. Ings, T.C., N.L. Ward, and L. Chittka, *Can commercially imported bumble bees out-compete their native conspecifics?* Journal of Applied Ecology, 2006. **43**(5): p. 940-948.
120. Ings, T.C., N.E. Raine, and L. Chittka, *Mating preference in the commercially imported bumblebee species *Bombus terrestris* in Britain (Hymenoptera : Apidae)*. Entomologia Generalis, 2005. **28**(3): p. 233-238.
121. Dick, C.W., *Genetic rescue of remnant tropical trees by an alien pollinator*. Proceedings of the Royal Society of London. Series B: Biological Sciences, 2001. **268**(1483): p. 2391-2396.
122. Le Conte, Y., M. Ellis, and W. Ritter, *Varroa mites and honey bee health: can Varroa explain part of the colony losses?* Apidologie, 2010. **41**(3): p. 353-363.
123. Martin, S.J., et al., *Global honey bee viral landscape altered by a parasitic mite*. Science, 2012. **336**(6086): p. 1304-1306.
124. Moritz, R.F.A., et al., *Research strategies to improve honeybee health in Europe*. Apidologie, 2010. **41**(3): p. 227-242.
125. Budge, G.E., et al., *The occurrence of *Melissococcus plutonius* in healthy colonies of *Apis mellifera* and the efficacy of European foulbrood control measures*. Journal of Invertebrate Pathology, 2010. **105**(2): p. 164-170.
126. Kraus, B. and R.E. Page, *Effect of *Varroa jacobsoni* (Mesostigmata: Varroidae) on feral *Apis mellifera* (Hymenoptera: Apidae) in California*. Environmental Entomology, 1995. **24**(6): p. 1473-1480.
127. McMullan JB and B. MJF, *A qualitative model of mortality in honey bee (*Apis mellifera*) colonies infested with tracheal mites (*Acarapis woodi*)*. Experimental and Applied Acarology, 2009. **47**: p. 225-234.
128. Highfield, A.C., et al., *Deformed wing virus implicated in overwintering honeybee colony losses*. Applied and Environmental Microbiology, 2009. **75**(22): p. 7212-7220.
129. Yang, X.L. and D.L. Cox-Foster, *Impact of an ectoparasite on the immunity and pathology of an invertebrate: evidence for host immunosuppression and viral amplification*. Proceedings of the National Academy of Sciences of the United States of America, 2005. **102**(21): p. 7470-7475.
130. Higes, M., et al., *How natural infection by *Nosema ceranae* causes honeybee colony collapse*. Environmental Microbiology, 2008. **10**(10): p. 2659-2669.
131. Runckel, C., et al., *Temporal analysis of the honey bee microbiome reveals four novel viruses and seasonal prevalence of known viruses, *Nosema*, and *Crithidia**. PLoS ONE, 2011. **6**(6): p. e20656.
132. Cox-Foster, D.L., et al., *A metagenomic survey of microbes in honey bee colony collapse disorder*. Science, 2007. **318**(5848): p. 283-287.

133. Paxton, R.J., et al., *Nosema ceranae* has infected *Apis mellifera* in Europe since at least 1998 and may be more virulent than *Nosema apis*. *Apidologie*, 2007. **38**(6): p. 558-565.
134. Schroeder, D.C. and S.J. Martin, *Deformed wing virus: The main suspect in unexplained honeybee deaths worldwide*. *Virulence*, 2012. **3**(7): p. 589-591.
135. Bromenshenk, J.J., et al., *Iridovirus and Microsporidian Linked to Honey Bee Colony Decline*. *PLoS ONE*, 2010. **5**(10).
136. Martin, S.J., et al., *Do the honeybee pathogens *Nosema ceranae* and deformed wing virus act synergistically?* *Environmental Microbiology Reports*, 2013. **5**(4): p. 506-510.
137. Schmid-Hempel, P. and H.P. Stauffer, *Parasites and flower choice of bumblebees*. *Animal Behaviour*, 1998. **55**: p. 819-825.
138. Shykoff, J.A. and P. Schmidhempel, *Incidence and effects of 4 parasites in natural populations of bumble bees in Switzerland*. *Apidologie*, 1991. **22**(2): p. 117-125.
139. Henson, K.S.E., P.G. Craze, and J. Memmott, *The restoration of parasites, parasitoids, and pathogens to heathland communities*. *Ecology*, 2009. **90**(7): p. 1840-1851.
140. Singh, R., et al., *RNA viruses in hymenopteran pollinators: evidence of inter-taxa virus transmission via pollen and potential impact on non-*Apis* hymenopteran species*. *PLoS ONE*, 2010. **5**(12): p. e14357.
141. Colla, S.R., et al., *Plight of the bumble bee: pathogen spillover from commercial to wild populations*. *Biological Conservation*, 2006. **129**: p. 461-467.
142. Core, A., et al., *A new threat to honey bees, the parasitic phorid fly *Apocephalus borealis**. *PLoS ONE*, 2012. **7**(1): p. e29639.
143. Otterstatter, M.C. and J.D. Thomson, *Does pathogen spillover from commercially reared bumble bees threaten wild pollinators?* *PLoS ONE*, 2008. **3**(7): p. e2771.
144. Szabo, N.D., et al., *Do pathogen spillover, pesticide use, or habitat loss explain recent North American bumblebee declines?* *Conservation Letters*, 2012. **5**(3): p. 232-239.
145. Meeus, I., et al., *Effects of Invasive Parasites on Bumble Bee Declines*. *Conservation Biology*, 2011. **25**(4): p. 662-671.
146. Genersch, E., et al., *Detection of Deformed wing virus, a honey bee viral pathogen, in bumble bees (*Bombus terrestris* and *Bombus pascuorum*) with wing deformities*. *Journal of Invertebrate Pathology*, 2006. **91**(1): p. 61-63.
147. Graystock, P., et al., *The Trojan hives: pollinator pathogens, imported and distributed in bumblebee colonies*. *Journal of Applied Ecology*, 2013. **50**(5): p. 1207-1215.
148. Dormann, C.F., et al., *Prediction uncertainty of environmental change effects on temperate European biodiversity*. *Ecology Letters*, 2008. **11**(3): p. 235-244.
149. Memmott, J., et al., *Global warming and the disruption of plant-pollinator interactions*. *Ecology Letters*, 2007. **10**(8): p. 710-717.
150. Rader, R., et al., *Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops*. *Global Change Biology*, 2013. **19**(10): p. 3103-3110.
151. Baron, G.L., N.E. Raine, and M.J.F. Brown, *Impact of chronic exposure to a pyrethroid pesticide on bumblebees and interactions with a trypanosome parasite*. *Journal of Applied Ecology*, 2014: p. n/a-n/a.
152. Bryden, J., et al., *Chronic sublethal stress causes bee colony failure*. *Ecology Letters*, 2013. **16**(12): p. 1463-1469.
153. Thomson, D., *Competitive interactions between the invasive European honey bee and native bumble bees*. *Ecology*, 2004. **85**(2): p. 458-470.
154. Traveset, A., et al., *Invaders of pollination networks in the Galápagos Islands: emergence of novel communities*. *Proceedings of the Royal Society B: Biological Sciences*, 2013. **280**(1758).
155. Abe, T., et al., *Alien pollinator promotes invasive mutualism in an insular pollination system*. *Biological Invasions*, 2011. **13**(4): p. 957-967.
156. Carvalheiro, L.G., et al., *Pollination services decline with distance from natural habitat even in biodiversity-rich areas*. *Journal of Applied Ecology*, 2010. **47**(4): p. 810-820.
157. Woodcock, B.A., et al., *Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape*. *Agriculture, Ecosystems & Environment*, 2013. **171**(0): p. 1-8.
158. Carvalheiro, L.G., et al., *Natural and within-farmland biodiversity enhances crop productivity*. *Ecology Letters*, 2011. **14**(3): p. 251-259.

159. Brittain, C., et al., *Synergistic effects of non-Apis bees and honey bees for pollination services*. Proceedings of the Royal Society B: Biological Sciences, 2013. **280**(1754).
160. Winfree, R. and C. Kremen, *Are ecosystem services stabilized by differences among species? A test using crop pollination*. Proceedings of the Royal Society B-Biological Sciences, 2009. **276**(1655): p. 229-237.
161. Woodcock, B.A., et al., *National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops* Journal of Applied Ecology, 2013. **51**(1): p. 142-151.
162. Hoyle, M., K. Hayter, and J.E. Cresswell, *Effect of pollinator abundance on self-fertilization and gene flow: Application to GM canola*. Ecological Applications, 2007. **17**(7): p. 2123-2135.
163. Hayter, K.E. and J.E. Cresswell, *The influence of pollinator abundance on the dynamics and efficiency of pollination in agricultural Brassica napus: implications for landscape-scale gene dispersal*. Journal of Applied Ecology, 2006. **43**(6): p. 1196-1202.
164. Bommarco, R., L. Marini, and B.E. Vaissiere, *Insect pollination enhances seed yield, quality, and market value in oilseed rape*. Oecologia, 2012. **169**(4): p. 1025-1032.
165. Rader, R., et al., *Diurnal effectiveness of pollination by bees and flies in agricultural Brassica rapa: Implications for ecosystem resilience*. Basic and Applied Ecology, 2013. **14**(1): p. 20-27.
166. Laliberté, E. and P. Legendre, *A distance-based framework for measuring functional diversity from multiple traits*. Ecology, 2010. **91**: p. 299-305.
167. Hill, M.O., *Local frequency as a key to interpreting species occurrence data when recording effort is not known*. Methods in Ecology and Evolution, 2012. **3**: p. 195-205.
168. Ricketts, T.H., et al., *Landscape effects on crop pollination services: are there general patterns?* Ecology Letters, 2008. **11**(5): p. 499-515.
169. Kennedy, C.M., et al., *A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems*. Ecology Letters, 2013. **16**(5): p. 584-599.
170. Kremen, C., N.M. Williams, and R.W. Thorp, *Crop pollination from native bees at risk from agricultural intensification*. Proceedings of the National Academy of Sciences of the United States of America, 2002. **99**(26): p. 16812-16816.
171. Garrat, M.P., et al., *Avoiding a bad apple: insect pollination enhances fruit quality and economic value*. Agriculture Ecosystems and Environment, 2014. **184**: p. 34-40.
172. Garratt, M.P.D., et al., *Pollination deficits in UK apple orchards*. Journal of Pollination Ecology, 2013. **11**: p. 1-6.
173. Simpson, R.D., *The economics of ecosystem services: the case of pollination.*, in *BioEcon conference 2013*: Cambridge.
174. Hanley, N. and E.B. Barbier, *Pricing Nature 2009*, Cheltenham: Edward Elgar Publishing.
175. Baumgartner, S., *The insurance value of biodiversity in the provision of ecosystem services*. Natural Resource Modelling, 2007. **20**: p. 87-127.
176. Barbier, E.B., *Capitalizing on nature: ecosystems as natural assets 2011*, Cambridge: Cambridge University Press.
177. UNEP, *Inclusive Wealth Report 2012. Measuring progress toward sustainability 2012*, Cambridge: Cambridge University Press.
178. World Bank, *The changing wealth of nations, 2011*, World Bank.: Washington DC.
179. Arrow, K.J., et al., *Sustainability and the measurement of wealth*. Environment and Development Economics, 2012. **17**(3): p. 317-353.
180. Breeze, T.D., et al., *Agricultural policies exacerbate honeybee pollination service supply-demand mismatches across Europe*. PLoS ONE, 2014. **9**(1): p. e82996.
181. Schulp, C.J.E., S. Lautenbach, and P.H. Verburg, *Quantifying and mapping ecosystem services: Demand and supply of pollination in the European Union*. Ecological Indicators, 2014. **36**: p. 131-141.
182. Calderone, N.W., *Insect pollinated crops, insect pollinators and US agriculture: trend analysis of aggregate data for the period 1992-2009*. PLoS One, 2012. **7**((5)): p. e37235.
183. Allsopp, M.H., W.J. de Lange, and R. Veldtman, *Valuing insect pollination services with cost of replacement*. PLoS ONE, 2008. **3**(9).
184. Kempler, C., B. Harding, and D. Ehret, *Out-of-season raspberry production in British Columbia, Canada*, in *Proceedings of the Eighth International Rubus and Ribes*

- Symposium, Vols 1 and 2*, R.M. Brennan, S.L. Gordon, and B. Williamson, Editors. 2002. p. 629-632.
185. Winfree, R., B.J. Gross, and C. Kremen, *Valuing pollination services to agriculture*. Ecological Economics, 2011. **71**: p. 80-88.
186. Freeman, A.M., *The measurement of environmental and resource values*. 2003: Washington DC: Resources for the Future.
187. Hynes, S. and N. Hanley, *The "Crex crex" lament: Estimating landowners willingness to pay for corncrake conservation on Irish farmland*. Biological Conservation, 2009. **142**(1): p. 180-188.
188. Czajkowski, M., M. Buszko-Briggs, and N. Hanley, *Valuing changes in forest biodiversity*. Ecological Economics, 2009. **68**(12): p. 2910-2917.
189. Christie, M., et al., *Valuing the diversity of biodiversity*. Ecological Economics, 2006. **58**(2): p. 304-317.
190. Mwebaze P., et al., *Quantifying the value of ecosystem services: a case study of honeybee pollination in the UK* in *Contributed Paper for the 12th Annual BIOECON Conference 2010*.
191. Franzen, M. and S.G. Nilsson, *How can we preserve and restore species richness of pollinating insects on agricultural land?* Ecography, 2008. **31**(6): p. 698-708.
192. Billeter, R., et al., *Indicators for biodiversity in agricultural landscapes: a pan-European study*. Journal of Applied Ecology, 2008. **45**(1): p. 141-150.
193. Lawton, J.H., et al., *Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest*. Nature, 1998. **391**(6662): p. 72-76.