

The canary in the coalmine; bee declines as an indicator of environmental health

Dave Goulson & Elizabeth Nicholls

School of Life Sciences, University of Sussex, Falmer, Brighton, BN1 9QG

Email: D.Goulson@sussex.ac.uk

Abstract

Bee declines have received much attention of late, but there is considerable debate and confusion as to the extent, significance and causes of declines. In part this reflects conflation of data for domestic honeybees, numbers of which are largely driven by economic factors, with those for wild bees, many of which have undergone marked range contractions but for the majority of which we have no good data on population size. There is no doubt that bees are subject to numerous pressures in the modern world. The abundance and diversity of flowers has declined along with availability of suitable nest sites, bees are chronically exposed to cocktails of agrochemicals, and they are simultaneously exposed to novel parasites and pathogens accidentally spread by humans. Climate change is likely to exacerbate these problems in the future, particularly for cool-climate specialists such as bumblebees. Stressors do not act in isolation; for example pesticide exposure can impair both detoxification mechanisms and immune responses, rendering bees more susceptible to parasites. It seems certain that chronic exposure to multiple, interacting stressors is driving honey bee colony losses and declines of wild pollinators. Bees have a high profile and so their travails attract attention, but these same stressors undoubtedly bear upon other wild organisms, many of which are not monitored and have few champions. Those wild insects for which we do have population data (notably butterflies and moths) are overwhelmingly also in decline. We argue that bee declines are indicators of pervasive and ongoing environmental damage that is likely to impact broadly on biodiversity and the ecosystem services it provides.

Keywords: Apoidea, pollution, pathogens, pesticides, habitat loss, indicator species

Introduction

Declines in insect biodiversity, and particularly declines in pollinator populations, have become a serious cause for concern and a topic debated heavily in both the academic community and wider public arena. Such concerns are justified given our increasing reliance on insect-pollinated crops. Approximately three quarters of crop species benefit from insect pollinators, providing us with just under one third of the food we eat ¹, so that the global value of insect pollinators has been estimated to be worth \$215 billion to food production ². Hence the potential that we may be facing a “pollination crisis” ^{3,4}, in which crop yields begin to fall because of inadequate pollination, has understandably stimulated much research in recent decades. Throughout all of this debate, bees have emerged as the ‘poster child’ of pollinator declines, dominating media coverage of the issue, with many media articles focussing exclusively on just one species of bee, the honeybee *Apis mellifera*. Estimates of media coverage of pollinator declines in four UK broadsheet newspapers, (*Financial Times*, *The Guardian*, *The Independent* and *The Times*) and four US broadsheets (*The New York Times*, *USA Today*, *The Wall Street Journal* and *The Washington Post*) over the past twenty years (1996-2016) using LexisNexis archives⁵, finds that the terms ‘bee’ and ‘decline’ receive a major mention in the headline or lead paragraph of 286 news articles, compared with 142 for ‘butterfly’ and ‘decline’ and just 68 for ‘pollinator’ and ‘decline’. A YouGov poll conducted in 2014 found that 85% of British people surveyed considered ‘bees dying off’ to be one of the most serious environmental issues, similar to that of air pollution (83%) and surpassing concerns about climate change (73%) ⁶. The connection between honeybees, pollination and the production of food is an ecosystem service that seems to be reasonably well understood by the public. Indeed, many lay people are unaware that there are other species of bee, or that other insects can be pollinators, and they assume that all pollination is delivered by honeybees.

While honeybees certainly play a substantial role, the majority of crop pollination at a global scale is delivered by wild pollinators rather than by the domesticated honey bee with which the public are so familiar ⁷⁻⁹. For example in the UK, Breeze *et al.* ⁷ demonstrate that honeybees are responsible for a maximum of 34% of crop pollination, probably much less, with wild pollinators providing the large majority. In a meta-analysis of 29 studies on diverse crops and contrasting biomes, Garibaldi *et al.* ¹⁰ found that wild pollinator visitation and yields generally drop with increasing distance from natural areas, suggesting that yields on some

farms are already being impacted by inadequate pollination by wild insects. Similarly, Garibaldi *et al.*¹¹ showed that yields of pollinator-dependent crops are more variable, and have increased less, than crops that do not benefit from pollinators, to the extent that a shortage of pollinators is undermining the stability of agricultural food production.

Why then has media coverage and public perception focussed so heavily on one managed bee species, overlooking the numerous other flower-visiting insects that play a major role in delivering the vital ecosystem service of pollination? Is there any reason to suggest that the plight of bees, and in particular that of honeybees, is more serious than that of other insects, thus justifying this bee-centric focus? The existence of beekeepers, people with an economic incentive to look after their honeybees and often also an emotional attachment to them means that honeybees have human champions to promote their interests. Honeybees also provide additional tangible benefits in the form of honey and beeswax, thus further endearing these insects to humans.

The same bias is also evident in scientific research. The domestication of honeybees, and more recently the commercial production of bumblebee colonies (of *Bombus terrestris* and *B. impatiens*), has meant that these three bee species are readily accessible for scientific research, and as a result many aspects of their ecology, physiology and behaviour are well studied and understood compared to other pollinating taxa. The focus on these model species has been at the expense of wild bees and other pollinators, which vary a great deal in terms of their ecology and life history strategies. For example, a Web of Science search for all published research articles with the terms ‘Bee’ NOT ‘Apis’, ‘Bombus’, ‘Honey’ or ‘Bumble’ in the title returns 55,230 studies, compared to a search for ‘Bee’ AND any one of the previous terms which returns 80,507 articles in total. There are 28,322 articles with *Apis* in the title alone. Considering that there are approximately 20,000 species of bee, plus countless other pollinating insects, this strong focus on one genus (and very largely on one species) of pollinator is highly disproportionate.

The disappearing bees

The close association of honeybees and humans, and their very visible role in the ‘industrial pollination’ of crops in the US, has meant that this species has served as an early warning system for pollinator population declines, since deleterious effects are more easily detected in a managed species than for other pollinating species for which there are few data on changing

abundance due to a lack of adequate monitoring schemes. Accordingly, the best pollinator population data we have are for numbers of domesticated honey bee colonies, which show that numbers of managed colonies have decreased in Europe (25% loss of colonies in central Europe between 1985 and 2005 ¹²), and declined markedly in North America (59% loss of colonies between 1947 and 2005, although there have been slight increases in the USA in the last decade ^{13,14}). However, overall global stocks actually increased by ~45% between 1961 and 2008, due to a major increase in numbers of hives reported to exist in countries such as China and Argentina ¹⁵. At the same time, there have been widespread reports of unusually high rates of honey bee colony mortality from many parts of the world but especially the US, sometimes ascribed to a syndrome known as Colony Collapse Disorder (CCD) ¹⁶. For example, recent estimates suggest that 44.1% of honeybee colonies in the USA died between April 2015 and April 2016¹⁷.

These figures appear to be somewhat contradictory, and have led skeptics to question whether there is in fact a pollination crisis ¹⁸ but it should be remembered that honeybees are domestic animals and their population dynamics are largely driven by economic factors such as the price of honey and the revenue to be earned from providing pollination ¹⁹. The major increase in area of crops being grown that require pollination¹⁷ means that there is more demand than ever for bees, meaning that beekeepers have a strong financial incentive to maintain or increase hive numbers. High rates of colony loss may thus not result in declining numbers of hives if beekeepers split their hives more frequently and generally work harder to maintain and replace their lost stocks. For example in the USA, high rates of colony loss in the last decade coincide with small *increases* in the total number of hives as the increasing revenue to be earned from almond pollination has incentivised beekeepers to overcome their husbandry problems. However, if bee reproductive rates are not high enough to support splitting then there is a danger that the average strength of colonies may decline over time, something not captured by official monitoring.

One would not judge the status of wild bird populations on the basis of the numbers of domestic chickens, and similarly changes in honeybee populations probably tell us little about the status of wild pollinators. Of the wild bees, we have reasonable measures of the past and present distributions of some of the more distinctive taxa for some developed countries, but almost no data on population sizes or direction of change. The best distribution data available are for bumblebees, of which there are about 250 species in the world ²⁰. In Europe, many bumblebee species have undergone substantial range contractions and localized extinction,

with four species going extinct throughout the continent^{20,21}. In North America, some formerly abundant and widespread species such as *Bombus terricola*, *B. affinis* and *B. occidentalis* underwent severe declines from the late 1990s onwards, and now occupy only a small fraction of their former range^{22,23}. *Bombus franklini*, a species formerly found in California and Oregon, has not been seen since 2006 and is presumed extinct²². For the remaining wild bees data are exceedingly sparse, though they comprise the large majority of the world's bee species. Analysis of historic presence / absence records suggests that diversity of all wild bees declined in the UK, Netherlands and Belgium during the twentieth century, but that these declines have decelerated since 1990^{24–26}. However, in the absence of any systematic monitoring scheme it is very hard to disentangle actual range change from the effects of increasing search effort over time, which could readily mask real declines²⁶. Twenty three bee and flower-visiting wasp species have gone extinct in the UK since 1850²⁷. A recent review of the status of all 1,965 wild bee species in Europe concluded that 9.2% were threaten with extinction, and a further 5.2% were near threatened, but insufficient data were available for 57% of species so that they could not be evaluated (IUCN 2015).

The biggest knowledge gap is regarding pollinator abundance; even in well-studied countries such as the UK we have almost no data on how wild bee populations have changed over time. Hence we do not know whether common species are less abundant than formerly, or whether they are currently in decline. Most pollination is delivered by a small number of these abundant species which tend to have large distributions^{28,29}. Declines in their abundance would not be detected in distribution maps until they become extinct in parts of their range, which is rather late in the day to introduce conservation measures.

Multiple threats to bees

It is abundantly clear that a major driver of pollinator declines is loss and degradation of flower-rich habitats, and their replacement with extensive monocultures of crops (reviewed in³⁰). Modern intensive farming methods provide little food for bees apart from occasional gluts when mass-flowering crops come into flower, so that bees suffer from inadequate food availability for much of the year, gaps in the season continuity of food availability, and they are forced to consume an unnaturally monotonous diet of crop pollen. Crop monocultures also provide few nesting opportunities for most bee species. With nowhere for them to nest and

nothing much for them to eat most of the while we should not be surprised if bees become scarce. However, loss of habitat is far from the only problem bees face.

One drawback of such a close association between bees and humans is the potential for increased exposure of bees to anthropogenic induced stressors. Many of these issues have arisen from human driven movement and trade of these pollinators across the globe. Aside from the stress caused to the domesticated bees that are transported (which in itself has the potential to increase their vulnerability to disease and other stressors), introducing high volumes and/or novel species of bee to an area can have deleterious effects on existing wild pollinators. For example there is evidence to suggest that domesticated honeybees outcompete wild bumblebees foraging on their preferred food plants, which can reduce bumblebee worker size and impair reproductive success of colonies³¹⁻³⁴.

Historic movement of bees by humans is widely accepted as being responsible for the spread of several bee-parasites and pathogens, the best-known example being the mite *Varroa destructor*, originally associated with the Asian honey bee *Apis cerana*. *Varroa* has since jumped hosts to the European honey bee *Apis mellifera*, which has little resistance to this pest. Since the 1960s *Varroa* has spread to most parts of the world (Australia being a notable exception), all of this movement almost certainly resulting from humans transporting honeybees. The mite acts as a vector for pathogens such as deformed wing virus (DWV), and the combined effect of the mite and the diseases it transmits is a major contributor to honey bee colony losses in North America and Europe^{35,36}. Recent evidence strongly suggests that DWV itself has also been spread around the world from Europe with the transport of honeybee colonies by man³⁷, so the blame for this entire issue can be firmly placed on the unwitting (and often careless) actions of humankind.

More recently, trade in commercially reared bumblebee colonies for the pollination of greenhouse crops has also been found to be negatively affecting wild bee populations. Trade began in the 1980s in Europe, and now more than 1 million nests of the European *Bombus terrestris* are reared each year and exported to various countries. Unfortunately, it does not seem possible yet to rear colonies that are free of disease, not least because the bees are reared on honeybee-collected pollen, providing a route for exposure to many bee pathogens³⁸. Commercial colonies of *B. terrestris* are commonly infected with a range of parasites including *Nosema bombi*, *N. ceranae*, *Apicystis bombi* and DWV³⁹. In North America, the accidental importation of a non-native strain of the parasite *Nosema bombi* via commercial bumblebees

has been implicated in the dramatic decline of several bumblebee species, though convincing causal evidence remains elusive^{40,41}. The evidence from South America is clearer; here, *B. terrestris* were deliberately introduced by the Chilean government despite the presence of native *Bombus* species, with *terrestris* spreading rapidly to occupy a vast area of southern South America. The arrival of *B. terrestris* appears to have led to the rapid local extinction of the native *B. dahlbomii* at a speed only plausibly explained by pathogen spillover⁴². Although the parasite(s) responsible has yet to be ascertained with certainty, both *A. bombi* and *C. bombi* have been shown to be highly prevalent in the invasive species^{42,43}.

The economic importance of honeybees has at least meant that the pests and pathogens affecting them have received considerable research interest and funding over recent years. Evidence is accumulating that many so called ‘honeybee pathogens’ have broader host ranges than previously thought⁴⁴, therefore wild bees and other insect taxa may also be affected by the emergence of novel pathogens. In general we know little about the natural geographic range, host range, prevalence or virulence of most bee pathogens, or indeed of the pathogens of insects more generally, and so it would seem wise to take very careful precautions to prevent further spread of pathogens outside of their native range, in addition to minimizing any spillover from commercial pollination operations^{38,41,45}.

As previously discussed, the role of honeybees in the pollination of food crops is well acknowledged and understood, and as a result serious concerns have been raised regarding the risk posed to bees from exposure to agro-chemicals used on those crops. While the same risks are likely to affect other flower-visiting insects, and indeed any organism closely associated with agro-ecosystems, both research and public interest in this topic over recent years has focused primarily on bees, particularly honeybees. According to Web of Science, in the last twenty years almost four times as many articles on bees and pesticides (n= 2,316) have been published compared to those considering the effects of pesticides on butterflies (n=589), another high-profile group of flower-visiting insect. Interestingly, a comparison of Google searches by the global community (via the online tool, ‘Google Insights for Search’, GIFS), a proxy measure for public interest in a topic, reveals that prior to April 2007 searches for the terms ‘butterfly+pesticide’ exceeded that for ‘bees+pesticide’. However since May 2007 onwards, coinciding with large scale reports of honeybee colonies dying in the US and the first coining of the term ‘Colony Collapse Disorder’, searches for the terms ‘bees+pesticide’ have consistently outweighed those for butterflies (Fig. 1). A similar spike in 2007 for searches of the term ‘bee declines’ is also observed, and this specific query outweighs more broad searches

for information on, for example ‘pollinator declines’ (Fig. 2). Evidence suggesting that pesticides may be playing a role in pollinator declines has been met with opposition from the agrochemical industry and farming unions and there is considerable debate concerning the accurate quantification of exposure and the potential for sub-lethal effects to be impacting on bee populations in a more subtle way than just direct mortality from intoxication. As we have seen, intensification of agriculture has also led to a loss of habitat for bees and other pollinators, and reduced diet diversity, and so disentangling the relative contribution of these stress factors can prove difficult.

There is no doubt that bees are exposed to pesticides throughout their development and early life^{46–49}. One hundred and sixty one different pesticides have been detected in honey bee colonies^{46,50}, and between three and ten pesticide compounds were detected in pollen stored in a sample of bumblebee nests placed in the UK countryside⁵¹. However the effects of simultaneous exposure to multiple agrochemicals are not well understood, nor are they examined by current regulatory risk-assessment procedures⁵². Based on their toxicity, frequency in honeybee hives and the concentrations detected, Sanchez-Bayo and Goka⁴⁶ predict that three neonicotinoid insecticides (thiamethoxam, imidacloprid and clothianidin), and the organophosphate insecticides phosmet and chlorpyrifos pose the biggest risk to honey bees at a global scale.

Neonicotinoids are the newest of the main classes of insecticide, and the group most strongly implicated in bee declines^{52,53}. They are neurotoxins that target the insect central nervous system, binding to postsynaptic nicotinic acetylcholine receptors and causing overstimulation, paralysis and death⁵⁴. These insecticides are commonly applied as seed-treatments and are systemic within plants, spreading through plant tissues and into the pollen and nectar of flowering crops such as oilseed rape (canola). They are also found at significant concentrations (up to ~90ppb) in the pollen and nectar of wildflowers growing in field margins and hedgerows near treated crops, sometimes several years after they were applied to the crop, demonstrating high levels of persistence in both soil and within plant tissues^{48,51,55}. Thus there is a clear route for ingestion by bees and other flower-visiting and herbivorous insects. Oral toxicity for bees is high, with the short-term LD₅₀ for the most commonly-used neonicotinoids in the region of 4-5ng/honey bee⁵⁶ (LD₅₀ = Lethal Dose 50%, the dose that kills 50% of test organisms). Long-term chronic exposure to neonicotinoids results in mortality in overwintering honey bees when feeding on food contaminated with concentrations as low as 0.25ppb⁵⁷. Sub-lethal effects of neonicotinoid exposure have also been observed in both honey bees and

bumblebees, including increased susceptibility to disease and a reduction in learning, foraging ability and homing ability, all of which are essential to bee survival^{58–64}. Yang *et al.*⁶⁵ recently showed that even low exposure during the larval stage (to less than 1/100th of the lethal dose) can have a lasting impact on learning in adult honey bees.

Perhaps the biggest long-term future threat to biodiversity worldwide, one which is certainly not unique to bees or even invertebrates, is climate change. Bumblebees are unusual among insects in showing greater species diversity away from the tropics and towards more temperate climates, and are typically poorly adapted to coping with high temperatures and so we might expect these bees to be particularly adversely affected by global warming. A recent comprehensive analysis of the changing distributions of North American and European bumblebees⁶⁷ has found that the southern edges of bumblebee species ranges have tended to contract northwards, but there has been no corresponding shift in the northern edge of the range, so that overall range has declined, a phenomenon the authors liken to a “climate vice”. There is also evidence that the lower altitudinal limit of some montane bumblebees has shifted uphill in Spain⁶⁸. Of course climate change is not solely associated with warming; extreme weather events such as storms, floods and droughts are predicted to increase, and we would expect these to have major impacts on local bee communities. For example, flooding is likely to be harmful to the many bee species that nest or hibernate underground.

The canary in the coalmine

Bees may have become the pin-up girls of the insect world, the focus of a plethora of scientific research and media coverage, but is there any reason to suppose that they are unique in suffering from a range of pressures due to environmental change? The simple answer is no; we may notice loss of bees more quickly than that of other insects, particularly if they are domesticated honey bees whose owner will soon notice if the colony becomes weak or dies, but all of the stressors discussed will impact to varying degrees on other wildlife. **Habitat loss** to intensive monoculture farming or urban sprawl will affect all taxa. Man’s activities have spread **parasites and pathogens** of numerous taxa around the world, leading to a succession of epizootics of emerging diseases in groups as diverse as amphibians, primates, rodents, canids, birds, marsupials, crayfish and snakes^{reviewed in 69}. It would be remarkable if we had not spread other insect diseases around the world in addition to those of bees. The bee diseases that we do know about certainly have host ranges that

extend far beyond bees. For example, Evison et al. ⁷⁰ found a range of diseases normally associated with honey bees in bumblebees, solitary bees, social wasps and hoverflies. It therefore seems probable that the spread of honeybees and their diseases around the globe has exposed wild populations of many other insect species to novel parasites, but what impacts this might have had we will perhaps never know. **Pesticides** undoubtedly impact on all taxa that inhabit farmland and neighboring areas. Widespread contamination of soils, waterways, field margin foliage and pollen and nectar with cocktails of fungicides and insecticides ^{51,55} is certain to impact on a diversity of insects. **Climate change** will undoubtedly exert profound impacts on all forms of life on the planet as its effects become greater in coming decades. Of the stressors faced by bees discussed above, perhaps **monotonous diets** is the issue of least relevance to other taxa, though it may well affect generalist pollinators such as hoverflies.

What evidence is there for widespread decline of wild insects other than bees? Even more so than with bees, we have scant knowledge of the population trajectories of perhaps 99% of the insects with which we share the planet. However, those for which we have data are overwhelmingly in decline. The UK has long-running butterfly and moth recording schemes, and both reveal alarming declines of the majority of species, particularly those associated with farmland habitats. A recent study revealed that 76% of the UK's butterflies declined in abundance, occurrence or both over the last four decades ⁷². Many moths have declined precipitously over the same time period ⁷³, while similar patterns are evident in carabid beetles ⁷⁴. In the Netherlands, total butterfly abundance decreased by about 30% between 1992 and 2007, with 55% of common species suffering severe declines ⁷⁵, while van Swaay et al. ⁷⁶ estimate that European grassland butterflies declined by 50% between 1990 and 2005. Forister et al. ⁷⁷ describe "ubiquitous" declines amongst lowland California butterflies in the period 1975-2009 and numerous studies have observed deleterious effects of habitat loss and agricultural intensification on the richness of tropical butterfly assemblages (reviewed by ^{78,79}).

Just as with bees, the causes of lepidopteran declines are the subject of debate. In the UK farmland butterfly declines have accelerated since the mid-1990s, and rates of declines have been found to correlate with neonicotinoid use ⁶⁶. As previously mentioned, it is very hard to disentangle the effects of other farming practices that may also correlate with neonicotinoid use (which began in 1994 and has increased rapidly since), but there have been few major changes in arable farming practices since 1994 that seem reasonable as alternative explanations for the decline in butterflies. It is highly plausible that the widespread contamination of field

margin vegetation and more broadly of the farmed environment with neonicotinoids is harming either the larval or adult stages of butterflies. A similar correlation between neonicotinoid pollution of freshwater habitats and reduced aquatic insect diversity and abundance has been described⁷¹. We might also expect to find a relationship between insect population change and pesticide use for other insect taxa, but the paucity of long-term population data render analyses difficult or impossible.

Data generated by ‘citizen scientists’ are increasingly being recognised as a potential means to fill some of these knowledge gaps^{80–82}. Using data submitted to the UK Biological Records Centre, Thomas et al.⁸³ recently analysed population trends across 229 insect species, spanning ten invertebrate groups which inhabit the early successional stages of ecosystems. Those species dependent on the early stages of woodland regeneration are seen to have suffered the greatest declines, relative to grass and heathland species, thought to be due to a reduction in the number of clearings found in UK woodlands. Citizen science schemes can be particularly useful for monitoring less well known insect groups, particularly when volunteer training, assistance and species verification is co-ordinated by trained professionals. A recent scheme implemented in Finland to monitor little studied gall wasps increased the number of records by eight-fold and provided useful data on the effects of host-plant distribution on species richness which may inform future conservation efforts⁸⁴.

Patchy though it is, the evidence suggests that bees are indeed the canary in the coal mine; their declines are probably indicative of widespread reductions in insect diversity and abundance, driven by a range of anthropogenic pressures. With the human population continuing to grow, and no signs in any significant shifts away from the current model of intensive, large-scale monoculture agriculture with high chemical inputs, it seems likely that these declines are set to continue. As the biologist E.O. Wilson once observed “*If insects were to disappear, the environment would collapse into chaos*”. Insects deliver not just pollination, but also a raft of other vital ecosystem services, from decomposition to pest control to providing food for a multitude of larger organisms. The rapid, ongoing collapse of insect populations around the globe should be a cause of the gravest concern.

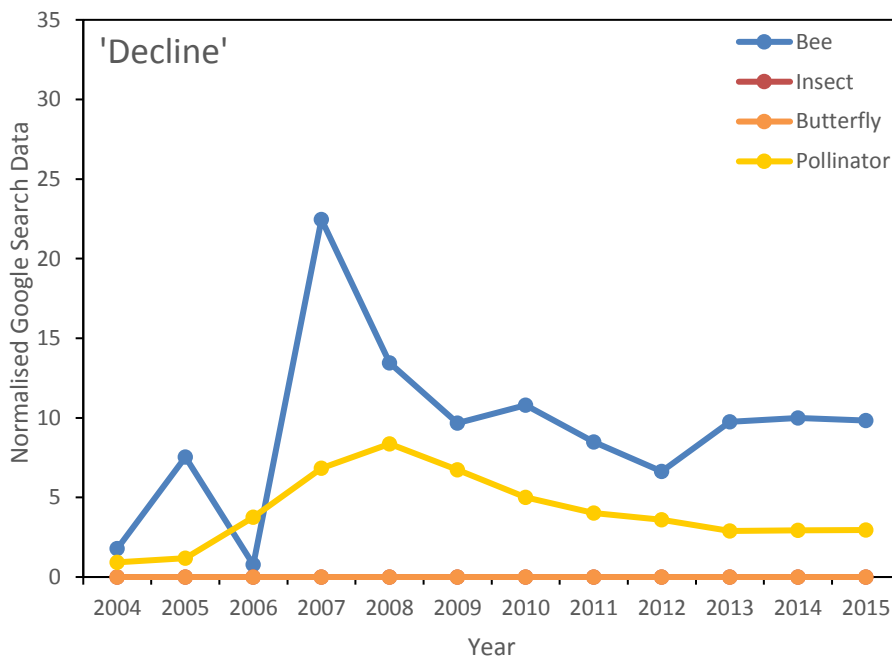
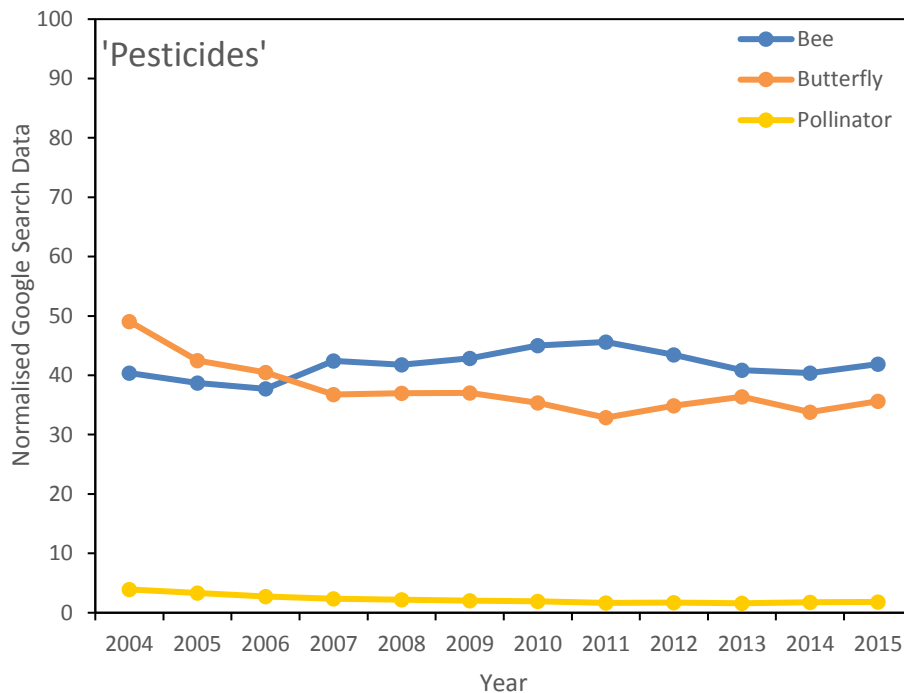


Fig. 1+2 Search data generated using the online tool 'Google Trends' for the term 'Pesticide' AND 'Bee', 'Butterfly' or 'Pollinator' (Fig. 1) and the term 'Decline' AND 'Bee', 'Butterfly', 'Insect' or 'Pollinator' (Fig. 2) from 2004-2015. Data indicate how often worldwide internet users search for a given term in relation to the total number of Google searches conducted in the same period, from 2004 to 2015 (normalised and represented on a scale from 0 to 100). Repeated enquiries from an individual user over a short space of time are omitted to avoid pseudoreplication. Declines in the number of searches for a particular term are thought to reflect waning public interest in a particular topic.

371

372 **References**

- 373 1 Klein, A-M., Steffan-Dewenter, I., Tschamntke, T. (2003) Fruit set of highland coffee
374 increases with the diversity of pollinating bees. *Proc. Biol. Sci.*, **270**, 955–961.
- 375 2 Gallai, N., Salles, J-M., Settele, J., Vaissière, BE. (2009) Economic valuation of the
376 vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.*, **68**,
377 810–821.
- 378 3 Holden, C. (2006) Report warns of looming pollination crisis in North America.
379 *Science*, **314**, 397.
- 380 4 Gross, M. (2008) Bee gloom deepens. *Curr. Biol.*, **18**, 1073.
- 381 5 Verissimo, D., MacMillan, DC., Smith, RJ., Crees, J., Davies, ZG. (2014) Has climate
382 change taken prominence over biodiversity conservation? *Bioscience*, **64**, 625–629.
- 383 6 Dahlgreen, W. (2014) Decline of bees seen as more serious than climate change.
384 YouGov Surv. [https://yougov.co.uk/news/2014/06/27/bees-dying-most-serious-](https://yougov.co.uk/news/2014/06/27/bees-dying-most-serious-environmental-issue/)
385 [environmental-issue/](https://yougov.co.uk/news/2014/06/27/bees-dying-most-serious-environmental-issue/) (accessed 12 Apr2016).
- 386 7 Breeze, TD., Bailey, a. P., Balcombe, KG., Potts, SG. (2011) Pollination services in
387 the UK: How important are honeybees? *Agric. Ecosyst. Environ.*, **142**, 137–143.
- 388 8 Garibaldi, LA., Steffan-Dewenter, I., Winfree, R., Aizen, MA., Bommarco, R.,
389 Cunningham, S a. *et al.* (2013) Wild pollinators enhance fruit set of crops regardless of
390 honey bee abundance. *Science*, **339**, 1608–1611.
- 391 9 Mallinger, RE., Gratton, C. (2014) Species richness of wild bees, but not the use of
392 managed honey bees, increases fruit set of a pollinator-dependent crop. *J. Appl. Ecol.*,
393 323–330.
- 394 10 Garibaldi, LA., Steffan-Dewenter, I., Kremen, C., Morales, JM., Bommarco, R.,
395 Cunningham, S a. *et al.* (2011) Stability of pollination services decreases with isolation
396 from natural areas despite honey bee visits. *Ecol. Lett.*, **14**, 1062–1072.
- 397 11 Garibaldi, LA., Aizen, MA., Klein, AM., Cunningham, SA., Harder, LD. (2011)
398 Global growth and stability of agricultural yield decrease with pollinator dependence.
399 *Proc. Natl. Acad. Sci. U. S. A.*, **108**, 5909–5914.
- 400 12 Potts, SG., Roberts, SPM., Dean, R., Marris, G., Brown, MA., Jones, R. *et al.* (2010)

401 Declines of managed honey bees and beekeepers in Europe. *J. Apic. Res.*, 15–22.

402 13 National Resource Council,. (2007) *Status of Pollinators in North America*. National
403 Academies Press, 2007.

404 14 van Engelsdorp, D., Hayes, J., Underwood, RM., Pettis, J. (2008) A survey of honey
405 bee colony losses in the U.S., fall 2007 to spring 2008. *PLoS One*, **3**, e4071.

406 15 Aizen, MA., Harder, LD. (2009) The global stock of domesticated honey bees is
407 growing slower than agricultural demand for pollination. *Curr. Biol.*, **19**, 915–918.

408 16 vanEngelsdorp, D., Evans, JD., Saegerman, C., Mullin, C., Haubruge, E., Nguyen, BK.
409 *et al.* (2009) Colony collapse disorder: A descriptive study. *PLoS One*, **4**, e6481.

410 17 The Bee Informed Partnership. [https://beeinformed.org/results/colony-loss-2015-2016-](https://beeinformed.org/results/colony-loss-2015-2016-preliminary-results/)
411 [preliminary-results/](https://beeinformed.org/results/colony-loss-2015-2016-preliminary-results/) .

412 18 Ghazoul, J. (2015) Qualifying pollinator decline evidence. *Science*, **348**, 981–2.

413 19 Smith, KM., Loh, EH., Rostal, MK., Zambrana-Torrel, CM., Mendiola, L., Daszak,
414 P. (2013) Pathogens, pests, and economics: drivers of honey bee colony declines and
415 losses. *Ecohealth*, **10**, 434–45.

416 20 Goulson, D., Lye, GC., Darvill, B. (2008) Decline and conservation of bumble bees.
417 *Annu. Rev. Entomol.*, **53**, 191–208.

418 21 Kosior, A., Celary, W., Olejniczak, P., Fijał, J., Król, W., Solarz, W. *et al.* (2007) The
419 decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of
420 Western and Central Europe. *Oryx*, **41**, 79–88.

421 22 Williams, PH., Osborne, JL. (2009) Bumblebee vulnerability and conservation world-
422 wide. *Apidologie*, **40**, 367–387.

423 23 Williams, PH., Thorp, RW., Richardson, LL., Colla, SR. (2014) *Bumble Bees of North*
424 *America: An Identification Guide*. Princeton University Press, 2014.

425 24 Carvalheiro, LG., Kunin, WE., Keil, P., Aguirre-Gutiérrez, J., Ellis, WN., Fox, R. *et*
426 *al.* (2013) Species richness declines and biotic homogenisation have slowed down for
427 NW-European pollinators and plants. *Ecol. Lett.*, **16**, 870–878.

428 25 Biesmeijer, JC., Roberts, SPM., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T.
429 *et al.* (2006) Parallel declines in pollinators and insect pollinated plants in Britain and
430 the Netherlands. *Science*, **313**, 351–354.

- 431 26 Casey, LM., Rebelo, H., Rotheray, E., Goulson, D. (2015) Evidence for habitat and
432 climatic specializations driving the long-term distribution trends of UK and Irish
433 bumblebees. *Divers. Distrib.*, **21**, 864–875.
- 434 27 Ollerton, J., Erenler, H., Edwards, M., Crockett, R. (2014) Pollinator declines.
435 Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural
436 changes. *Science*, **346**, 1360–2.
- 437 28 Scheper, J., Holzschuh, A., Kuussaari, M., Potts, SG., Rundlöf, M., Smith, HG. *et al.*
438 (2013) Environmental factors driving the effectiveness of European agri-
439 environmental measures in mitigating pollinator loss--a meta-analysis. *Ecol. Lett.*, **16**,
440 912–20.
- 441 29 Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, LG., Henry, M., Isaacs, R. *et al.*
442 (2015) Delivery of crop pollination services is an insufficient argument for wild
443 pollinator conservation. *Nat. Commun.*, **6**, 7414.
- 444 30 Goulson, D., Nicholls, E., Botías, C., Rotheray, EL. (2015) Bee declines driven by
445 combined stress from parasites, pesticides, and lack of flowers. *Science*, **347**, 1255957.
- 446 31 Forup, ML., Memmott, J. (2005) The relationship between the abundance of
447 bumblebees and honeybees in a native habitat. *Ecol. Entomol.*, **30**, 47–57.
- 448 32 Walther-Hellwig, K., Fokul, G., Frankl, R., Buchler, R., Ekschmitt, K., Wolters, V.
449 (2006) Increased density of honeybee colonies affects foraging bumblebees.
450 *Apidologie*, **37**, 517–532.
- 451 33 Goulson, D., Sparrow, KR. (2008) Evidence for competition between honeybees and
452 bumblebees; effects on bumblebee worker size. *J. Insect Conserv.*, **13**, 177–181.
- 453 34 Thomson, DM. (2006) Detecting the effects of introduced species: A case study of
454 competition between *Apis* and *Bombus*. *Oikos*, **114**, 407–418.
- 455 35 Rosenkranz, P., Aumeier, P., Ziegelmann, B. (2010) Biology and control of Varroa
456 destructor. *J. Invertebr. Pathol.*, **103**, 96–119.
- 457 36 Nazzi, F., Brown, SP., Annoscia, D., Del Piccolo, F., Di Prisco, G., Varricchio, P. *et al.*
458 (2012) Synergistic parasite-pathogen interactions mediated by host immunity can
459 drive the collapse of honeybee colonies. *PLoS Pathog.*, **8**, e1002735.
- 460 37 Wilfert, L., Long, G., Leggett, HC., Schmid-Hempel, P., Butlin, R., Martin, SJM. *et al.*

461 (2016) Deformed wing virus is a recent global epidemic in honeybees driven by
462 Varroa mites. *Science* (80-.), **351**, 594–597.

463 38 Goulson, D., Hughes, WOH. (2015) Mitigating the anthropogenic spread of bee
464 parasites to protect wild pollinators. *Biol. Conserv.* **191**, 10–19.

465 39 Graystock, P., Yates, K., Darvill, B., Goulson, D., Hughes, WOH. (2013) Emerging
466 dangers: deadly effects of an emergent parasite in a new pollinator host. *J. Invertebr.*
467 *Pathol.*, **114**, 114–119.

468 40 Cameron, SA., Lozier, JD., Strange, JP., Koch, JB., Cordes, N., Solter, LF. *et al.*
469 (2011) Patterns of widespread decline in North American bumble bees. *Proc. Natl.*
470 *Acad. Sci. U. S. A.*, **108**, 662–667.

471 41 Meeus, I., Brown, MJF., De Graaf, DC., Smagghe, G. (2011) Effects of invasive
472 parasites on bumble bee declines. *Conserv. Biol.*, **25**, 662–671.

473 42 Schmid-Hempel, R., Eckhardt, M., Goulson, D., Heinzmann, D., Lange, C., Plischuk,
474 S. *et al.* (2014) The invasion of southern South America by imported bumblebees and
475 associated parasites. *J. Anim. Ecol.*, **83**, 823–837.

476 43 Arbetman, MP., Meeus, I., Morales, CL., Aizen, MA., Smagghe, G. (2013) Alien
477 parasite hitchhikes to Patagonia on invasive bumblebee. *Biol. Invasions*, **15**, 489–494.

478 44 Ravoet, J., De Smet, L., Meeus, I., Smagghe, G., Wenseleers, T., de Graaf, DC. (2014)
479 Widespread occurrence of honey bee pathogens in solitary bees. *J. Invertebr. Pathol.*,
480 **122**, 55–8.

481 45 Goulson, D. (2003) Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol.*
482 *Evol. Syst.*, **34**, 1–26.

483 46 Sanchez-Bayo, F., Goka, K. (2014) Pesticide residues and bees--a risk assessment.
484 *PLoS One*, **9**, e94482–e94482.

485 47 Mullin, CA., Frazier, M., Frazier, JL., Ashcraft, S., Simonds, R., Vanengelsdorp, D. *et*
486 *al.* (2010) High levels of miticides and agrochemicals in North American apiaries:
487 implications for honey bee health. *PLoS One*, **5**, e9754–e9754.

488 48 Krupke, CH., Hunt, GJ., Eitzer, BD., Andino, G., Given, K. (2012) Multiple routes of
489 pesticide exposure for honey bees living near agricultural fields. *PLoS One*, **7**,
490 e29268–e29268.

491 49 Paradis, D., Bérail, G., Bonmatin, JM., Belzunces, LP. (2014) Sensitive analytical
492 methods for 22 relevant insecticides of 3 chemical families in honey by GC-MS/MS
493 and LC-MS/MS. *Anal. Bioanal. Chem.*, **406**, 621–633.

494 50 Chauzat, AM., Faucon, J., Martel, A., Cougoule, N., Aubert, M., Chauzat, M. *et al.*
495 (2006) A survey of pesticide residues in pollen loads collected by honey bees in
496 France. *J. Econ. Entomol.*, **99**, 253–262.

497 51 David, A., Botías, C., Abdul-Sada, A., Nicholls, E., Rotheray, EL., Hill, EM. *et al.*
498 (2016) Widespread contamination of wildflower and bee-collected pollen with
499 complex mixtures of neonicotinoids and fungicides commonly applied to crops.
500 *Environ. Int.*, **88**, 169–178.

501 52 Pisa, LW., Amaral-Rogers, V., Belzunces, LP., Bonmatin, JM., Downs, CA., Goulson,
502 D. *et al.* (2014) Effects of neonicotinoids and fipronil on non-target invertebrates.
503 *Environ. Sci. Pollut. Res. Int.*, **22**, 1–35.

504 53 Goulson, D. (2013) An overview of the environmental risks posed by neonicotinoid
505 insecticides. *J. Appl. Ecol.*, **50**, 977–987.

506 54 Tomizawa, M., Casida, JE. (2005) Neonicotinoid insecticide toxicology: mechanisms
507 of selective action. *Annu. Rev. Pharmacol. Toxicol.*, **45**, 247–268.

508 55 Botías, C., David, A., Horwood, J., Abdul-Sada, A., Nicholls, E., Hill, E. *et al.* (2015)
509 Neonicotinoid Residues in Wildflowers, a Potential Route of Chronic Exposure for
510 Bees. *Environ. Sci. Technol.*, **49**, 12731–40.

511 56 Suchail, S., Guez, D., Belzunces, LP. (2000) Characteristics of imidacloprid toxicity in
512 two *Apis mellifera* subspecies. *Environ. Toxicol. Chem.*, **19**, 1901–1905.

513 57 Rondeau, G., Sánchez-Bayo, F., Tennekes, H a., Decourtye, A., Ramírez-Romero, R.,
514 Desneux, N. (2014) Delayed and time-cumulative toxicity of imidacloprid in bees, ants
515 and termites. *Sci. Rep.*, **4**, 5566.

516 58 Yang, EC., Chuang, YC., Chen, YL., Chang, LH., Yang, AEC. (2008) Abnormal
517 foraging behavior induced by sublethal dosage of imidacloprid in the honey bee
518 (Hymenoptera: Apidae). *J. Econ. Entomol.*, **101**, 1743–1748.

519 59 Mommaerts, V., Reynders, S., Boulet, J., Besard, L., Sterk, G., Smagghe, G. (2010)
520 Risk assessment for side-effects of neonicotinoids against bumblebees with and

521 without impairing foraging behavior. *Ecotoxicology*, **19**, 207–215.

522 60 Henry, M., Béguin, M., Requier, F., Rollin, O., Odoux, J-F., Aupinel, P. *et al.* (2012)

523 A common pesticide decreases foraging success and survival in honey bees. *Science*,

524 **336**, 348–350.

525 61 Feltham, H., Park, K., Goulson, D. (2014) Field realistic doses of pesticide

526 imidacloprid reduce bumblebee pollen foraging efficiency. *Ecotoxicology*, **23**, 317–

527 323.

528 62 Han, P., Niu, CY., Lei, CL., Cui, JJ., Desneux, N. (2010) Quantification of toxins in a

529 Cry1Ac + CpTI cotton cultivar and its potential effects on the honey bee *Apis mellifera*

530 L. *Ecotoxicology*, **19**, 1452–1459.

531 63 Piironen, S., Goulson, D. (2016) Chronic neonicotinoid pesticide exposure and

532 parasite stress differentially affects learning in honeybees and bumblebees. *Proc. Biol.*

533 *Sci.*, **283**, 20160246.

534 64 Piironen, S., Botías, C., Nicholls, E., Goulson, D. (2016) No effect of low-level

535 chronic neonicotinoid exposure on bumblebee learning and fecundity. *PeerJ*, **4**, e1808.

536 65 Yang, EC., Chang, HC., Wu, WY., Chen, YW. (2012) Impaired olfactory associative

537 behavior of honeybee workers due to contamination of imidacloprid in the larval stage.

538 *PLoS One*, **7**, e49472.

539 66 Gilburn, AS., Bunnefeld, N., Wilson, JM., Botham, MS., Brereton, TM., Fox, R. *et al.*

540 (2015) Are neonicotinoid insecticides driving declines of widespread butterflies?

541 *PeerJ*, **3**, e1402.

542 67 Kerr, JT., Pindar, A., Galpern, P., Packer, L., Potts, SG., Roberts, SM. *et al.* (2015)

543 Climate change impacts on bumblebees converge across continents. *Science*, **349**,

544 177–80.

545 68 Ploquin, EF., Herrera, JM., Obeso, JR. (2013) Bumblebee community homogenization

546 after uphill shifts in montane areas of northern Spain. *Oecologia*, **173**, 1649–1660.

547 69 Daszak, P., Cunningham, AA., Hyatt, AD. (2000) Emerging infectious diseases of

548 wildlife - threats to biodiversity and human health. *Science (80-.)*, **287**, 443–449.

549 70 Evison, SEF., Roberts, KE., Laurenson, L., Pietravalle, S., Hui, J., Biesmeijer, JC. *et*

550 *al.* (2012) Pervasiveness of parasites in pollinators. *PLoS One*, **7**, e30641–e30641.

- 551 71 Morrissey, CA., Mineau, P., Devries, JH., Sanchez-Bayo, F., Liess, M., Cavallaro,
552 MC. *et al.* (2015) Neonicotinoid contamination of global surface waters and associated
553 risk to aquatic invertebrates: A review. *Environ. Int.* **74**, 291–303.
- 554 72 Fox, R., Brereton, T.M., Asher, J., August, T.A., Botham, M.S., Bourn, A.N.D.,
555 Cruickshanks, K.L., Bulman, C.R., Ellis, S., Harrower, C.A., Middlebrook, I., Noble,
556 D.G., Powney, G.D., Randle, Z., Warren, M.S. & Roy, D. (2015) The State of the
557 UK's Butterflies 2015. *Butterfly Conserv. Cent. Ecol. Hydrol.*, .
- 558 73 Conrad, KF., Warren, MS., Fox, R., Parsons, MS., Woiwod, IP. (2006) Rapid declines
559 of common, widespread British moths provide evidence of an insect biodiversity crisis.
560 *Biol. Conserv.*, **132**, 279–291.
- 561 74 Brooks, DR., Bater, JE., Clark, SJ., Monteith, DT., Andrews, C., Corbett, SJ. *et al.*
562 (2012) Large carabid beetle declines in a United Kingdom monitoring network
563 increases evidence for a widespread loss in insect biodiversity. *J. Appl. Ecol.*, **49**,
564 1009–1019.
- 565 75 Van Dyck, H., Van Strien, AJ., Maes, D., Van Swaay, CAM. (2009) Declines in
566 Common, Widespread Butterflies in a Landscape under Intense Human Use. *Conserv.*
567 *Biol.*, **23**, 957–965.
- 568 76 Van Swaay, CAM., Nowicki, P., Settele, J., Van Strien, AJ. (2008) Butterfly
569 monitoring in Europe: Methods, applications and perspectives. *Biodivers. Conserv.* **17**,
570 3455–3469.
- 571 77 Forister, ML., Jahner, JP., Casner, KL., Wilson, JS., Shapiro, AM. (2011) The race is
572 not to the swift: Long-term data reveal pervasive declines in California's low-elevation
573 butterfly fauna. *Ecology*, **92**, 2222–2235.
- 574 78 Bonebrake, TC., Ponisio, LC., Boggs, CL., Ehrlich, PR. (2010) More than just
575 indicators: A review of tropical butterfly ecology and conservation. *Biol. Conserv.*,
576 **143**, 1831–1841.
- 577 79 KOH, LP. (2007) Impacts of land use change on South-east Asian forest butterflies: a
578 review. *J. Appl. Ecol.*, **44**, 703–713.
- 579 80 Pocock, MJO., Roy, HE., Preston, CD., Roy, DB. (2015) The Biological Records
580 Centre: a pioneer of citizen science. *Biol. J. Linn. Soc.*, **115**, 475–493.

581 81 Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J. *et al.* (2012)
582 The current state of citizen science as a tool for ecological research and public
583 engagement. *Front. Ecol. Environ.*, **10**, 291–297.

584 82 Silvertown, J. (2009) A new dawn for citizen science. *Trends Ecol. Evol.*, **24**, 467–71.

585 83 Thomas, J.A., Edwards, M., Simcox, D.J., Powney, G.D., August, T.A., Isaac, N.J.B.
586 (2015) Recent trends in UK insects that inhabit early successional stages of
587 ecosystems. *Biol. J. Linn. Soc.*, **115**, 636–646.

588 84 Hardwick, B., Kaartinen, R., Koponen, M., Roslin, T. (2016) A rapid assessment of a
589 poorly known insect group. *Insect Conserv. Divers.*, **9**, 49–62.

590

591