Sciencexpress Reviews

Bee declines driven by combined stress from parasites, pesticides, and lack of flowers

Dave Goulson,* Elizabeth Nicholls, Cristina Botías, Ellen L. Rotheray

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

*Corresponding author. E-mail: d.goulson@sussex.ac.uk

Bees are subject to numerous pressures in the modern world. The abundance and diversity of flowers has declined, bees are chronically exposed to cocktails of agrochemicals, and they are simultaneously exposed to novel parasites accidentally spread by humans. Climate change is likely to exacerbate these problems in the future. 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, but such interactions are not addressed by current regulatory procedures and studying these interactions experimentally poses a major challenge. In the meantime, taking steps to reduce stress on bees would seem prudent; incorporating flower-rich habitat into farmland, reducing pesticide use through adopting more sustainable farming methods, and enforcing effective quarantine measures on bee movements are all practical measures that should be adopted. Effective monitoring of wild pollinator populations is urgently needed to inform management strategies into the future.

Insect pollination is vitally important to terrestrial ecosystems and to crop production. The oft-quoted statistics are that 75% of our crop species benefit from insect pollinators (*1*), which provide a global service 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 generated understandable debate and concern and stimulated much research in recent decades. Nonetheless, knowledge gaps remain substantial, both with regard to the extent and causes of pollinator declines. Indeed, for most regions of the globe and for most wild pollinator taxa, we have no data as to whether there have actually been declines. Our best estimates are for numbers of domesticated honey bee colonies, which can be obtained for many countries with varying reliability. Overall, these suggest that numbers of managed honey bee colonies have decreased in Europe (25% loss of colonies in central Europe between 1985 and 2005 (*5*)), and markedly in North America (59% loss of colonies between 1947 and 2005 (*6*, *7*)). However, overall global stocks actually increased by ~45% between 1961 and 2008, due to a major increase in numbers of hives in countries such as China and Argentina (*8*). Conversely, there are widespread reports of unusually high rates of honey bee colony loss from many parts of the world, sometimes ascribed to a syndrome known as Colony Collapse Disorder (CCD) (*9*). It seems that socioeconomic factors (such as increasing demand for pollination or honey (*10*), are at present sufficient to incentivise beekeepers to overcome problems with bee health, when examined at a global scale (but not locally in North America and Europe).

If we turn to wild pollinators, the best data available are for bumblebees (*11*). In Europe, many species have undergone substantial range contractions and localized extinction, with four species going extinct throughout the continent (*11*, *12*) (Fig. 1A). In North America, some formerly abundant and widespread species such as *Bombus terricola* and *B. occidentalis* underwent severe declines from the late 1990s onwards, and now occupy only a small fraction of their former range (Fig. 1B) (*13*, *14*). *Bombus franklini*, a species formerly found in northern California and Oregon, has not been recorded since 2006 and is presumed extinct. In a study of the bumblebee fauna of Illinois over the past 100 years, Grixti *et al.* (*15*) describe substantial declines in species diversity, particularly in the period 1940-1960, with the extirpation of four species during the 20th century. In South America, the recent invasion by the European species *B. terrestris* is causing precipitous declines in the native *B. dahlbomii* (*16*). There is some evidence of loss of species richness from lowland areas of Sichuan in China (*17*, *18*), and a few reports of declines in Japan from the mid 1990s onwards (*19*, *20*), but elsewhere in the world, few data are available. For the remaining wild bees, data are exceedingly sparse, though they comprise the large majority of the world's approximately 22,000 bee species. Analysis of historic records suggests that diversity of both bumblebees and other wild bees declined in the UK, Netherlands and Belgium during the twentieth century, but that these declines have decelerated since 1990 (*21*, *22*). In surveys in Illinois, 50% of wild bee species went extinct over a 120 year period to 2010 (*23*). Given that bee diversity has declined in both

Europe and the Americas, it is probably reasonable to assume that declines are also occurring elsewhere across the globe.

The biggest knowledge gap is regarding bee abundance; although we have maps of past and present distributions of bees for some well-studied countries such as the UK, we have almost no data on how populations have changed over time. Hence we do not know whether common species such as *Bombus terrestris* in Europe or *Bombus impatiens* in North America 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. Declines in their abundance would not be detected in distribution maps until they become extinct in parts of their range, which is rather late to introduce conservation measures.

Another way to examine the likelihood or proximity of a pollination crisis is to examine delivery of pollination services. Although global honey bee stocks have increased by ~45%, demand has risen more than supply, for the fraction of global crops that require animal pollination has tripled over the same time period (*8*), making food production more dependent on pollinators than before. It has also emerged that the majority of crop pollination, at a global scale, is delivered by wild pollinators rather than honey bees. Yields correlate better with wild pollinators abundance than with abundance of honey bees (*24*–*26*); hence increasing honey bee numbers alone is unlikely to provide a complete solution to the increasing demand for pollination. Reliance on a single species is also a risky strategy (*27*). While Aizen *et al.* (*28*) concluded from a global analysis of changing crop yields over time that there was not yet any clear evidence that a shortage of pollinators was reducing yield, a subsequent analysis of the same data set by Garibaldi *et al.* (*29*) shows 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 reducing the stability of agricultural food production. In a meta-analysis of 29 studies on diverse crops and contrasting biomes, Garibaldi *et al.* (*30*) found that wild pollinator visitation and yields generally drop with increasing distance from natural areas, suggesting that yields on some farms are already impacted by inadequate pollination.

To summarize, in the past 50 years global honey bee stocks have increased, while wild bees appear to have declined substantially, as evidenced by data for bumblebees, and very scant data for other bee species. The demand for insect pollinators in farming has tripled in the same period. There is clearly no major pollination crisis yet, but there is evidence for localized limitation of crop yield as a result of inadequate pollination.

Drivers of wild bee declines and honey bee colony losses

Habitat loss

Bee declines have been attributed to many factors, some more plausible than others; however, the clear consensus is that loss of habitat has been a long-term contributor to declines (*11*, *31*–*33*). Bees require appropriate floral resources during the adult flight season, which may be short for some solitary species or year-long for social species in tropical environments. They also require undisturbed nest sites, with different species occupying diverse locations (e.g., cavities underground, hollow-stemmed twigs, burrows in the soil, even abandoned snail shells). The conversion of natural and semi-natural flower-rich habitat to farmland has been a major driver of long-term declines in bees. For example, in the UK, approximately 97% of flower-rich grasslands were lost in the 20th century (*34*), and this has resulted in major range contractions of bee species associated with this habitat, particularly long-tongued bumblebees (*11*). Declines of similar magnitude have affected the grasslands of North America, although these began in the early 19th century (*35*).

Urbanization also contributes to loss of natural habitat, but the net effect on bees is less clear. Gardens can support high densities of wild bees, particularly bumblebees and some solitary bee species, but highly urbanized environments have few bees (*36*, *37*), and the building of roads and other infrastructure undoubtedly contributes to the ongoing fragmentation and degradation of habitats. Increased traffic can also cause direct mortality through collisions (*38*), although the numbers of bees killed in this way is not known. The planting of road verges and traffic islands with wildflowers is often promoted as a means of boosting urban pollinator populations, but it might increase mortality by vehicle collisions.

Parasites and disease

Bees naturally suffer from a broad range of parasites, parasitoids and pathogens, the latter including protozoans, fungi, bacteria and viruses. By far the majority of research has focused on those associated with honey bees and to a lesser extent with bumblebees, with very little known about the pathogens of other wild bee species. Some bee diseases, such as Deformed Wing Virus (DWV) and *Nosema ceranae*, have broad host ranges and are able to infect both honey bees and bumblebees while others, such as *Crithidia bombi* or *Paenibacillus larvae*, seem to be more host-specific (*39*–*41*). While natural pathogens undoubtedly play an important but poorly-understood role in influencing the population dynamics of their bee hosts, we will focus here on the impacts that non-native parasites and pathogens may have.

The spread of most honey bee parasites and pathogens has occurred inadvertently as a result of transporting honey bees long distances. Much of this happened in historic times, but it continues, despite some improvements in quarantine procedures. The best-known example is 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 from

Asia to Europe, the Americas and most recently to New Zealand. The mite acts as a vector for pathogens such as 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 (*42*, *43*). Fortunately, the mite appears unable to survive on bees outside the genus *Apis*.

A strikingly similar series of events has also seen the microsporidian *N. ceranae* jump from *A. cerana* to *A. mellifera,* and in the past 20 years it has spread to Europe and the Americas, where it is now prevalent at high frequency (Fig. 2) (*44*, *45*). It has also been detected in wild bumblebees in Europe, China and South America (*41*, *46*, *47*), and solitary bees in Europe (*48*). In the lab *N.ceranae* appears to have higher virulence in bumblebees than it does in honey bees (*41*), though the impact it has had on wild populations is unknown. Asia is not the only source of non-native diseases; the African honey bee parasite *Aethina tumida* (small hive beetle) recently invaded North America, Egypt, Australia and Europe, and attacks *B. impatiens* colonies causing considerable damage (*49*, *50*). It seems highly likely that it also attacks other wild bumblebee species that are not so readily cultured and therefore less well studied.

Bee diseases are also being redistributed around the globe by the commercial trade in bumblebee colonies, which are mainly used for pollination of greenhouse crops such as tomatoes. This 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. In North America, the eastern American species *Bombus impatiens* is reared for this purpose. Unfortunately, it does not seem possible yet to rear colonies that are free of disease, not least because the bees are reared on honey-bee collected pollen, providing a route for exposure to many bee pathogens. Commercial colonies of *B. terrestris* are commonly infected with one or more parasites, including *Nosema bombi, N. ceranae, Apicystis bombi* and DWV (*41*).

There is evidence that non-native pathogens or pathogen strains associated with these colonies are having devastating impacts on wild bumblebee populations. 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 (*51*, *52*). 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 spillover (*16*). Although the parasite 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 (*16*, *53*). There is a clear parallel with the devastating impact that the arrival of European diseases had on the native Americans 500 years ago.

Even when commercial bees are free of disease on arrival, or are infected only with indigenous parasites, they can still affect native pollinators. High-density populations of managed bees may provide conditions for the rapid multiplication of parasites that then spill over into wild populations (*54*–*56*). A combination of field observations and modelling suggest that waves of *Crithidia bombi* infection travel outwards from greenhouses containing commercial bumblebees. Prediction indicates that waves can spread at ~2 km per week, with up to 100% of wild bees within the spreading radius becoming infected, although this is not yet well supported by direct evidence (*55*).

In general we know little about the natural geographic range, host range, prevalence or virulence of most bee pathogens, and so it would seem wise to take very careful precautions to prevent further introductions of bee pathogens from outside their native range, in addition to minimizing any spillover from commercial pollination operations (*52*, *57*).

Pesticides

The most controversial and debated cause of bee declines are pesticides. When appropriately used, pesticides provide a clear economic benefit, but bring the welfare of bees into direct conflict with industrial agriculture. Herbicides are highly effective at minimizing weed problems in most cropping systems, enabling farmers to grow near-pure monocultures, but their use inevitably reduces the availability of flowers for pollinators and can contribute substantially to rendering farmland an inhospitable environment for bees (*11*, *58*, *59*). Understandably, most attention has been paid to the direct toxic effects of pesticides on bees, particularly the impacts of insecticides. One hundred and sixty one different pesticides have been detected in honey bee colonies (*60*, *61*) and based on their toxicity, frequency in hives and the concentrations detected, Sanchez-Bayo and Goka (*61*) predict that three neonicotinoids (thiamethoxam, imidacloprid and clothianidin), and the organophosphates phosmet and chlorpyrifos pose the biggest risk to honey bees at a global scale. It is clear that bees are often chronically exposed to cocktails of pesticides throughout their development and adult life (*61*–*64*), but the effects of this are poorly understood and are not examined by current regulatory risk-assessment procedures (*65*).

Neonicotinoids are the newest of the main classes of insecticide, and the group most strongly implicated in bee declines (*65, 66*). They are neurotoxins that target the insect central nervous system, binding to postsynaptic nicotinic acetylcholine receptors and causing over-stimulation, paralysis and death (*67*). 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 canola. They are also water soluble but highly persistent in soil and soil water, and as a result have been found at significant concentrations in the pollen and nectar of wildflowers near crops (*63*). Thus there is a clear route for ingestion by bees. Oral toxicity is high, with the short-term LD_{50} for the most commonly-used neonicotinoids in the region of 4-5ng/honey bee (*68*) (LD_{50} = Lethal Dose 50%, the dose that kills 50% of test organisms). Long-term chronic exposure results in mortality in overwintering honey bees when feeding on food contaminated with concentrations as low as 0.25ppb (*69*). Sub-lethal effects of neonicotinoid exposure have also been observed in both honey bees and bumblebees, including a reduction in learning, foraging ability and homing ability, all of which are essential to bee survival (*70*–*74*). Yang *et al.* (*75*) recently showed that even low exposure during the larval stage (0.04ng/larva equating to less than $1/100^{th}$ of the LC_{50} for adult bees) can have a lasting impact on learning in adult honey bees (LC_{50} = Lethal Concentration 50%, the concentration that kills 50% of test organisms).

It seems very likely that bees living in most arable farmland are routinely exposed to sufficient neonicotinoids to suffer both lethal and sublethal effects. However, whether this translates into a detrimental effect at the colony-level remains disputed. In bumblebees, exposure of colonies to field-realistic concentrations of imidacloprid greatly impaired colony growth and reduced queen production by 85% (*76*). In contrast, field studies with honey bee colonies have proved more challenging to perform convincingly (*77*, *78*), not least because of the huge areas over which honey bees forage, the lack of a clear end-point to colony development, and their long-term storage of food reserves. This lack of clear evidence of harm in the field is often misinterpreted as evidence that toxicological studies on individual bees do not translate into colony losses in the field, rather than as the absence of evidence.

Monotonous diets

Intensively farmed areas provide few wildflowers, but do provide spatially and temporally isolated gluts of flowers in the form of mass-flowering crops such as sunflowers and canola. If a human were to consume nothing but sardines one month, chocolate the next, turnips the month after and so on, one could reasonably expect them to fall ill. This may seem a frivolous example, but it is a reasonable parallel to the experience of some honey bee colonies, particularly those in North America that are transported backward and forward across the continent each year to provide pollination for major crops such as almonds in California, blueberries in Maine and citrus in Florida. Where the nectar or pollen of crop flowers contain toxins, such as the glycoside amygdalin found in almonds (*79*), bees might potentially consume harmful concentrations of such substances.

More generally it seems certain that bees inhabiting intensive farmland have a more monotonous diet than they would have experienced in their evolutionary past, but how this impacts upon their fitness remains unclear. The pollen of different plant species varies greatly in protein content, amino acid composition, lipid, starch, vitamin and mineral content. Nectar commonly contains varying and low concentrations of a range of nutrients and other compounds of largely unknown importance (*80*–*84*). Thus, we might expect the type and range of flowers available will affect individual bee health and colony fitness in multiple ways; for example in honey bees, both pollen quality and diversity influence longevity, physiology and resistance/tolerance to disease (*85*–*88*). However, this topic has been little investigated, particularly for wild bees. The perception that honey bees may be receiving an inadequate diet has led to the development of protein supplements, but once again there has been little research on the long-term effectiveness of such supplements on colony health (*89*, *90*).

Interpreting the effects of availability of mass-flowering crops on bees and their colonies is further complicated since visiting such crops often exposes bees to pesticide residues, so that positive effects of increased food availability may be offset by negative effects of the pesticide. Some studies have found positive effects of proximity to canola on bumblebee colony growth and abundance (*91*, *92*) and on numbers of nesting red mason bees *Osmia bicornis* (*93*, *94*) while others found no relationship for bumblebees (*58*, *95*) nor forsolitary bees (*96*). Interestingly, none of these studies considered what role pesticides might have played in mediating the effect of the crop, or even report which pesticides were applied to crops in the study area, an omission that now seems naive given the recent focus on impacts of neonicotinoid insecticides on bees.

Shipping fever

It seems reasonable to hypothesize that the long-distance transport of bees, as routinely occurs for honey bees in North America and for commercial bumblebee colonies, places stress on the colonies. For several days they may be confined and subject to vibration, high temperatures, high levels of carbon dioxide and irregular disturbance. It has long been known that such stress can activate bacterial and viral infections and generally reduce condition in vertebrate livestock (*97*), but this has not been investigated in bees, although Bakonyi *et al.* (*98*) suggest that shipping stress may have contributed to honey bee colony losses in Hungary. This is clearly an area where further research is needed.

Competition

The role of competition in determining the relative abundance of species is notoriously hard to ascertain in mobile organisms such as bees, but it seems likely that competition for floral resources and perhaps also for nest sites does occur in natural communities, and that it can be exacerbated by the introduction of non-native species, particularly when the latter are present at high densities (*57*). For example, there is evidence that high concentrations of domestic honey bee hives can displace wild bumblebees from their preferred foodplants and from whole areas if hive densities are sufficiently high (*99*, *100*). This can result in a reduction in the size of bumblebee workers (*101*), and reduced reproductive success of bumblebee colonies (*102*). Although in general the interests of honey bee keepers and wild bee conservationists are aligned (all would agree on the benefits of increasing floral resources, reducing exposure to pesticides and preventing invasions of alien pathogens), there may occasionally be conflict where bee keepers wish to place hives in areas with significant populations of rare wild bees (*57*).

Climate change

Climate change is widely accepted to pose one of the largest threats to biodiversity worldwide, but likely impacts on pollinators and pollination are not well understood. One danger is that the phenology of pollinators may diverge from that of the plants they pollinate, with potentially disastrous consequences for both, but there is little evidence that this is happening to a significant extent yet (*103*). Advances in flowering and bee emergence are often broadly similar, and in any case few plants are dependent on a single pollinator so that any mismatch with one pollinator is likely to be compensated by increased availability of another (*103*, *104*).

Another potential effect of climate change is as a driver of range shifts, leading to a spatial mismatch between plants and pollinators. Range shifts in response to climate have been demonstrated in butterflies (*105*) and are to be expected in bees (*13*); for example there is already evidence that the lower altitudinal limit of some montane bumblebees has shifted uphill in Spain (*106*). We would predict declines in bumblebees at the southern edge of their range since they tend to be poorly adapted to high temperatures.

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.

Overall, although there is little strong evidence that climate change has yet had any great effect on bees, it is likely to provide a growing source of stress in the future that would exacerbate the impact of other factors, such as habitat loss.

Interactions between stressors

Unfortunately the public debate on bee health has often become polarized, with claims that, for example, *Varroa* or neonicotinoid insecticides are the sole or primary cause of bee declines or honey bee colony losses. If a middle-aged man who is overweight, does little exercise, and smokes and drinks heavily were to die of a heart attack, we would not be surprised and we might not spend too long arguing over which single risk factor was most important in bringing about his untimely demise. Similarly, wild bee declines and honey bee colony losses are clearly due to multiple, interacting and sometimes synergistic factors, and the combination of factors involved no doubt varies in time and space.

In general, the combined effect of multiple stressors are likely to be more harmful than one stressor alone (*107–109*) (Fig. 3). In the worst-case scenario, sublethal stressors that do not incur any significant harmful effects in isolation could, in combination, result in lethal effects. As we have already seen, bees are often exposed chronically to mixtures of pesticides and other chemicals. Some, such as ergosterol biosynthesis inhibitors (EBI) fungicides, have very low toxicity in themselves but may increase the toxicity of some neonicotinoids and pyrethroids up to 1,000-fold (*110–112*). Piperonyl butoxide is often added to pesticide formulations and also acts synergistically with some neonicotinoids, increasing toxicity up to 244-fold (*111*). Intriguingly, while imidacloprid alone has been shown to impair olfactory learning (*113*), combined exposure to imidacloprid and coumaphos has been shown to result in a slight increase in learning in honey bees (*114*). So while regulatory processes examine the effects on bees of exposure to a single pesticide at a time, in reality bees are simultaneously exposed to many pesticides, some of which have combined effects that cannot be predicted from studies of their effects when used in isolation.

Several recent studies indicate that interactive effects between pesticides and pathogens could be especially harmful for bees (*115–121*). For instance, developmental exposure to neonicotinoid insecticides renders honey bees more susceptible to the impact of the invasive pathogen *N. ceranae* (*122*). Imidacloprid can act synergistically with *Nosema* spp. by increasing the prevalence of *Nosema* infections in hives (*116*) and increasing *Nosema*-induced mortality (*115*). Similarly, Aufauvre *et al.* (*118*) showed that mortality of honey bees was greater when bees were exposed to the insecticide fipronil and infected by *N. ceranae* than when only a single stress factor was present. There is evidence that exposure to pesticides may impair the immune function of insects, which would explain these effects (*43*, *123–125*). For example, Di Prisco *et al.* (*126*) recently showed that exposure to neonicotinoids (clothianidin or imidacloprid) leads to immunosuppression in honey bees, which, in turn, promotes the replication of the deformed wing virus in insects with covert infections. This effect was found at very low concentrations, well below those that bees are likely to encounter in the field.

Interactions between stressors are not confined to pesticides and pathogens. The ability of bees to survive parasite infections is compromised by nutritional stress. For example, *Crithidia bombi* causes little mortality in well-fed bumblebees, but becomes virulent in bumblebees with a restricted diet (*127*). Activating the immune response has a metabolic cost; bumblebees increase their food consumption when immune responses areupregulated (*128*), and artificially stimulating the immune response by injecting latex beads caused mortality in starving bumblebees but not in those that were well fed (*129*). Increased food consumption in infected bees could also increase exposure to pesticides. Activating immunity has been shown to impair learning in both honey bees (*130*) and bumblebees (*131*, *132*), and impaired learning will reduce the bees' ability to locate floral resources and extract rewards, so exacerbating nutritional stresses.

Although to our knowledge this has not yet been examined, it seems highly likely that nutritional stress may also modulate the ability of bees to cope with pesticides, and this may explain in part why the observed LD50 of toxins in bees is highly variable across studies (*65*).

In summary, stressors do not act in isolation. Bees of all species are likely to encounter multiple stressors during their lives, and each is likely to reduce the ability of bees to cope with the others. A bee or bee colony that appears to have succumbed to a pathogen may not have died if it had not also been exposed to a sublethal dose of a pesticide and/or been subject to food stress (which might in turn be due to drought or heavy rain induced by climate change, or competition from a high density of honey bee hives placed nearby). Unfortunately, conducting well-replicated studies of the effects of multiple, interacting stressors on bee colonies is exceedingly difficult. The number of stressor combinations rapidly become large, and exposure to stressors is hard or impossible to control with free-flying bees. Nonetheless, a strong argument can be made that it is the interaction between parasites, pesticides and diet that lies at the heart of current bee health problems.

Sustainable pollination into the future

There is universal agreement that we must ensure adequate pollinator populations into the future if we wish to continue to grow a diversity of insect-pollinated crops and also ensure the integrity of natural ecosystems. It is also clear that moving toward heavy reliance on a few species number of managed pollinators, such as honey bees or one or two species of bumblebee, runs the risk of supply failure; for example, should honey bee stocks in North America fall much further, the viability of almond production in California would be threatened (*133*). Wild pollinators provide a service that is largely free, and globally already contributes to the majority of crop pollination (*24*, *25*, *134*, *135*). Maintaining a diversity of pollinator species improves crop success via functional complementarity; different species visit different parts of the crop or crop plant, at different times of the day or year, and respond differently to environmental perturbations (*1*, *136–141*). A diversity of pollinators can buffer impacts of climate change which might otherwise result in a mismatch in phenology of pollinators with the flowering of crops (*104*). It is thus essential that we take steps to conserve a broad community of pollinators in farmland.

Fortunately, although the causes of pollinator ill-health may be complex and multi-causal, conserving pollinators need not be difficult or expensive. If we accept that declines are due to interacting stressors, then it follows logically that removing or reducing any of the stressors we have described is likely to benefit bee populations. Measures can be taken that are likely to simultaneously benefit a broad suit of species, both domesticated and wild:

Increase abundance, diversity and continuity of floral resources

Schemes such as the sowing of flower-rich field margins or hedgerows, or retaining patches of semi-natural habitat among or near farmland provide clear benefits to bee diversity and abundance (*30*, *141–148*) (Fig. 4A). This in turn increases pollination to nearby crops and provide an economic incentive to farmers growing insect-pollinated crops (*149*). Many countries also offer financial incentives to farmers for taking measures to boost biodiversity that help to offset implementation and opportunity costs. However, take-up of schemes to boost pollinators remains low in most countries, perhaps reflecting a lack of understanding of the economic and environmental benefits, or a lack of familiarity with implementation of such measures. Education and outreach in this area could pay great dividends for pollinator conservation.

Planting of appropriate flowers in gardens and amenity areas can also contribute to pollinator conservation (*150*, *151*) (Fig. 4B). There is evidence that urban areas can support higher populations of some pollinators than farmland e.g., (*36*) and boost bee numbers in adjacent farmland (*58*). Many lists of bee or wildlife-friendly flowers are available on the internet but they tend to be based on anecdote rather than evidence, and there is a need to develop regionally appropriate, evidence-based advice as to the best plants to grow (*152*).

Provide nest sites

Wild bees use a diversity of habitats for nesting, including burrowing into bare soil, using existing cavities underground, holes in wood, or hollow plant stems. Semi-natural habitats, hedgerows and permanently uncropped field margins cater for many of these, meaning that schemes to boost floral diversity are also likely to boost nesting opportunities (*141*). Additional nest sites can also be provided by providing bundles of hollow reeds or canes, or patches of bare soil (*153*).

Reduce exposure to pesticides

Bees are currently chronically exposed to a cocktail of pesticides some of which act synergistically. Since the late 1990s, the cost of pesticides has fallen markedly relative to labor and fuel costs and the value of the crops (*154*). As a result, current levels of pesticide use are generally high, and not always justified by evidence that they are necessary to maintain yield (*66*, *155*). The widespread, prophylactic use of systemic insecticides, such as neonicotinoids as seed dressings, exposes bees and other non-target wildlife, results in accumulation of pesticides in the environment, and places strong selection pressure on pests to evolve resistance. A return to the principles of Integrated Pest Management (*156*), which utilizes preventative methods, such as crop rotation, and views the use of pesticides as a last resort in the battle against insect pests, could greatly reduce exposure of bees, benefit the environment, and improve farming profitability. Some European countries have independently developed national pesticide reduction programs (*156*), and the European Union Sustainable Use of Pesticides Directive ?citation required member states to implement national action plans to minimize pesticide use by January 2014. In most EU states this directive appears to have had little or no impact on farming practices.

Current risk assessment procedures, which examine the short-term impact of a single pesticide in isolation, are clearly not adequate to encapsulate the true scenario faced by bees living in farmland. Improvements are needed to make them more realistic, while keeping the cost of regulatory tests affordable, posing a considerable challenge to the ingenuity of scientists and regulators.

The EU moratorium on the use of three neonicotinoids (which started in December 2013) is an attempt to use policy change to reduce exposure of bees to stressors, following a review by the European Food Standards Agency (*157*–*159*) which declared that neonicotinoids pose an "unacceptable risk" to bees. However, if this simply leads farmers to replace neonicotinoids with other pesticides this may not be of great benefit to bees or the environment. Funding for research and for the provision of clear, independent advice for farmers with regard to how to reduce pesticide use generally by adopting IPM practices might provide a better and more sustainable long-term solution.

Prevent further introductions of non-native bees, parasites and pathogens

The careless disregard with which we ship bees from country to country has resulted in the irreversible spread of many serious parasites and pathogens. Strict quarantine controls should be implemented on the movement of all commercial bees, and there is an urgent need to develop means of rearing commercial bumblebees that are free from disease. Deliberate introductions of non-native bee species (such as the recent introduction of the European *Bombus terrestris* to South America) should of course be prevented. The companies that rear commercial bees should bear some responsibility here, and refuse to sell bees to regions where they are not native. There is clear hypocrisy in the policies of countries that prevent importation of non-native species but allow exportation of species to places where they do not naturally occur.

Develop monitoring programs

We have good distribution maps for pollinators in some countries, particularly for bumblebees, and citizen science schemes such as "Bumble Bee Watch" in North America and "Beewatch" in the UK can help to track changes in these distributions. However, the lack of long-term data on pollinator abundance is a glaring knowledge gap that urgently needs to be filled. It will probably never be possible to monitor all pollinator species at a global scale, but it would be practical to systematically collect data on the abundance of a subset of the more abundant and economically important pollinators. Citizen science surveys can provide a cost effective means for large-scale population monitoring; for example the UK butterfly monitoring scheme employs volunteers to walk regular transects using a standard methodology to count the butterflies seen, and has generated a large and long-term data set which has provided powerful insights into insect population change (*160*, *161*). "Beewalks", a similar scheme to count bumblebees, has been launched by the Bumblebee Conservation Trust to obtain population data for bumblebees in the UK, although it is still in its infancy. In the USA, "The Great Sunflower Project" asks volunteers to count pollinators in flower patches in their local area. However, such schemes are limited by the taxonomic skills of volunteers, particularly for the many pollinator taxa that are hard or impossible to identify in the field. LeBuhn *et al.* (*162*) argue that a pan-tapping network, which could employ citizen scientists to place out the traps but experts to identify the catch, would be the most cost-effective means for monitoring a large cross-section of pollinator species on a large geographic scale. Indeed, for a relatively modest sum it would be possible to set up an international pan-trapping network to monitor pollinators following a standard methodology. Until good population data become available, we cannot identify species or regions under most threat and hence we cannot prioritize management.

In the absence of pollinator monitoring, we have no early warning system to tell us how close we may be to a pollination crisis. With a growing human population and rapid growth in global demand for pollination services, we cannot afford to see crop yields begin to fall, and we would be well advised to take pre-emptive action to ensure that we have adequate pollination services into the future.

REFERENCES AND NOTES

1. A.-M. Klein, I. Steffan-Dewenter, T. Tscharntke, Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. B* 270, 955–961 (2003). Medline doi:10.1098/rspb.2002.2306

2. N. Gallai, J.-M. Salles, J. Settele, B. E. Vaissière, Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* **68**, 810–821 (2009). doi:10.1016/j.ecolecon.2008.06.014

3. C. Holden, Ecology. Report warns of looming pollination crisis in North America. *Science* **314**, 397 (2006). Medline doi:10.1126/science.314.5798.397

4. M. Gross, Bee gloom deepens. *Curr. Biol.* **18**, 1073 (2008).

doi:10.1016/j.cub.2008.11.013

5. S. G. Potts, S. Roberts, R. Dean, G. Marris, M. Brown, R. Jones, P. Neumann, J. Settele, Declines of managed honey bees and beekeepers in Europe. *J. Apic. Res.* **49**, 15–22 (2010). doi:10.3896/IBRA.1.49.1.02

6. National Resource Council, *Status of Pollinators in North America* (National Academies Press, Washington, DC, 2007).

7. D. van Engelsdorp, J. Hayes Jr., R. M. Underwood, J. Pettis, A survey of honey bee colony losses in the U.S., fall 2007 to spring 2008. *PLOS ONE* **3**, e4071 (2008). Medline

8. M. A. Aizen, L. D. Harder, The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Curr. Biol.* **19**, 915–918 (2009). Medline doi:10.1016/j.cub.2009.03.071

9. D. Van Engelsdorp, J. D. Evans, C. Saegerman, C. Mullin, E. Haubruge, B. K. Nguyen, M. Frazier, J. Frazier, D. Cox-Foster, Y. Chen, R. Underwood, D. R. Tarpy, J. S. Pettis, Colony collapse disorder: A descriptive study. *PLOS ONE* **4**, e6481 (2009). Medline doi:10.1371/journal.pone.0006481

10. K. M. Smith, E. H. Loh, M. K. Rostal, C. M. Zambrana-Torrelio, L. Mendiola, P. Daszak, Pathogens, pests, and economics: Drivers of honey bee colony declines and losses. *EcoHealth* **10**, 434–445 (2013). Medline doi:10.1007/s10393-013-0870-2

11. D. Goulson, G. C. Lye, B. Darvill, Decline and conservation of bumble bees. *Annu. Rev. Entomol.* **53**, 191–208 (2008). Medline doi:10.1146/annurev.ento.53.103106.093454

12. A. Kosior, W. Celary, P. Olejniczak, J. Fijal, W. Król, W. Solarz, P. Plonka, The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. *Oryx* **41**, 79–88 (2007). doi:10.1017/S0030605307001597

13. P. H. Williams, J. L. Osborne, Bumblebee vulnerability and conservation world-wide. *Apidologie* **40**, 367–387 (2009). doi:10.1051/apido/2009025

14. P. H. Williams, R. W. Thorp, L. L. Richardson, S. R. Colla, *Bumble Bees of North America: An Identification Guide* (Princeton Univ. Press, Princeton, NJ, 2014).

15. J. C. Grixti, L. T. Wong, S. A. Cameron, C. Favret, Decline of bumble bees (*Bombus*) in the North American Midwest. *Biol. Conserv.* **142**, 75–84 (2009). doi:10.1016/j.biocon.2008.09.027

16. R. Schmid-Hempel, M. Eckhardt, D. Goulson, D. Heinzmann, C. Lange, S. Plischuk, L. R. Escudero, R. Salathé, J. J. Scriven, P. Schmid-Hempel, The invasion of southern South America by imported bumblebees and associated parasites. *J. Anim. Ecol.* **83**, 823–837 (2013). Medline doi:10.1111/1365-2656.12185

17. Z. Xie, P. H. Williams, Y. Tang, The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *J. Insect Conserv.* **12**, 695–703 (2008). doi:10.1007/s10841-008-9180-3

18. P. Williams, Y. Tang, J. Yao, S. Cameron, The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini). *Syst. Biodivers.* **7**, 101–189 (2009). doi:10.1017/S1477200008002843

19. C. Matsumura, J. Yokoyama, I. Washitani, Invasion status and potential ecological impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in Southern Hokkaido, Japan. *Glob. Environ. Res.* **8**, 51–66 (2004).

20. M. N. Inoue, J. Yokoyama, I. Washitani, Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). *J. Insect Conserv.* **12**, 135–146 (2008). doi:10.1007/s10841-007-9071-z

21. L. G. Carvalheiro, W. E. Kunin, P. Keil, J. Aguirre-Gutiérrez, W. N. Ellis, R. Fox, Q. Groom, S. Hennekens, W. Van Landuyt, D. Maes, F. Van de Meutter, D. Michez, P. Rasmont, B. Ode, S. G. Potts, M. Reemer, S. P. Roberts, J. Schaminée, M. F. WallisDeVries, J. C. Biesmeijer, Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecol. Lett.* **16**, 870–878 (2013). Medline doi:10.1111/ele.12121

22. J. C. Biesmeijer, S. P. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, W. E. Kunin, Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**, 351–354 (2006). Medline doi:10.1126/science.1127863

23. L. A. Burkle, J. C. Marlin, T. M. Knight, Plant-pollinator interactions over 120 years: Loss of species, co-occurrence, and function. *Science* **339**, 1611–1615 (2013). Medline

24. T. D. Breeze, P. Bailey, K. G. Balcombe, S. G. Potts, Pollination services in the UK: How important are honeybees? *Agric. Ecosyst. Environ.* **142**, 137–143 (2011). doi:10.1016/j.agee.2011.03.020

25. L. A. Garibaldi, I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, L. G. Carvalheiro, L. D. Harder, O. Afik, I. Bartomeus, F. Benjamin, V. Boreux, D. Cariveau, N. P. Chacoff, J. H. Dudenhöffer, B. M. Freitas, J. Ghazoul, S. Greenleaf, J. Hipólito, A. Holzschuh, B. Howlett, R. Isaacs, S. K. Javorek, C. M. Kennedy, K. M. Krewenka, S. Krishnan, Y. Mandelik, M. M. Mayfield, I. Motzke, T. Munyuli, B. A. Nault, M. Otieno, J. Petersen, G. Pisanty, S. G. Potts, R. Rader, T. H. Ricketts, M. Rundlöf, C. L. Seymour, C. Schüepp, H. Szentgyörgyi, H. Taki, T. Tscharntke, C. H. Vergara, B. F. Viana, T. C. Wanger, C. Westphal, N. Williams, A. M. Klein, Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* **339**, 1608–1611 (2013). Medline doi:10.1126/science.1230200

26. R. E. Mallinger, C. Gratton, Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *J. Appl. Ecol.* 10.1111/1365-2664.12377 (2014). doi:10.1111/1365-2664.12377

27. C. A. Kearns, D. W. Inouye, N. M. Waser, Endangered mutualisms: The conservation of plant-pollinator interactions. *Annu. Rev. Ecol. Syst.* **29**, 83–112 (1998). doi:10.1146/annurev.ecolsys.29.1.83

28. M. A. Aizen, L. A. Garibaldi, S. A. Cunningham, A. M. Klein, Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Curr. Biol.* **18**, 1572–1575 (2008). Medline doi:10.1016/j.cub.2008.08.066

29. L. A. Garibaldi, M. A. Aizen, A. M. Klein, S. A. Cunningham, L. D. Harder, Global growth and stability of agricultural yield decrease with pollinator dependence. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 5909–5914 (2011). Medline doi:10.1073/pnas.1012431108

30. L. A. Garibaldi, I. Steffan-Dewenter, C. Kremen, J. M. Morales, R. Bommarco, S. A. Cunningham, L. G. Carvalheiro, N. P. Chacoff, J. H. Dudenhöffer, S. S. Greenleaf, A. Holzschuh, R. Isaacs, K. Krewenka, Y. Mandelik, M. M. Mayfield, L. A. Morandin, S. G. Potts, T. H. Ricketts, H. Szentgyörgyi, B. F. Viana, C. Westphal, R. Winfree, A. M. Klein, Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* **14**, 1062–1072 (2011). Medline doi:10.1111/j.1461-0248.2011.01669.x

31. M. J. F. Brown, R. J. Paxton, The conservation of bees: A global perspective. *Apidologie* **40**, 410–416 (2009). doi:10.1051/apido/2009019

32. S. G. Potts, J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, W. E. Kunin, Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.* **25**, 345–353 (2010). Medline doi:10.1016/j.tree.2010.01.007

33. A. J. Vanbergen, I. P. Initiative, Threats to an ecosystem service: Pressures on pollinators. *Front. Ecol. Environ* **11**, 251–259 (2013). doi:10.1890/120126

34. D. C. Howard, J. W. Watkins, R. T. Clarke, C. L. Barnett, G. J. Stark, Estimating the extent and change in Broad Habitats in Great Britain. *J. Environ. Manage.* **67**, 219–227 (2003). Medline doi:10.1016/S0301-4797(02)00175-5

35. F. Samson, F. Knopf, Prairie conservation in North America. *Bioscience* **44**, 418–421 (1994). doi:10.2307/1312365

36. J. L. Osborne, A. P. Martin, C. R. Shortall, A. D. Todd, D. Goulson, M. E. Knight, R. J. Hale, R. A. Sanderson, Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *J. Appl. Ecol.* **45**, 784–792 (2008). doi:10.1111/j.1365-2664.2007.01359.x

37. A. J. Bates, J. P. Sadler, A. J. Fairbrass, S. J. Falk, J. D. Hale, T. J. Matthews, Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *PLOS ONE* **6**, e23459 (2011). Medline doi:10.1371/journal.pone.0023459

38. P. Skórka, M. Lenda, D. Moroń, K. Kalarus, P. Tryjanowski, Factors affecting road mortality and the suitability of road verges for butterflies. *Biol. Conserv.* **159**, 148–157 (2013). doi:10.1016/j.biocon.2012.12.028

39. E. Genersch, American Foulbrood in honeybees and its causative agent, *Paenibacillus* larvae. *J. Invertebr. Pathol.* **103** (suppl. 1), S10–S19 (2010). doi:10.1016/j.jip.2009.06.015

40. E. Genersch, C. Yue, I. Fries, J. R. de Miranda, Detection of *Deformed wing virus*, a honey bee viral pathogen, in bumble bees (*Bombus terrestris* and *Bombus pascuorum*) with wing deformities. *J. Invertebr. Pathol.* **91**, 61–63 (2006). Medline doi:10.1016/j.jip.2005.10.002

41. P. Graystock, K. Yates, B. Darvill, D. Goulson, W. O. H. Hughes, Emerging dangers: Deadly effects of an emergent parasite in a new pollinator host. *J. Invertebr. Pathol.* **114**, 114–119 (2013). Medline doi:10.1016/j.jip.2013.06.005

42. P. Rosenkranz, P. Aumeier, B. Ziegelmann, Biology and control of *Varroa destructor*. *J. Invertebr. Pathol.* **103** (suppl. 1), S96–S119 (2010). doi:10.1016/j.jip.2009.07.016

43. F. Nazzi, S. P. Brown, D. Annoscia, F. Del Piccolo, G. Di Prisco, P. Varricchio, G. Della Vedova, F. Cattonaro, E. Caprio, F. Pennacchio, Synergistic parasite-pathogen interactions mediated by host immunity can drive the collapse of honeybee colonies. *PLOS Pathog.* **8**, e1002735 (2012). Medline doi:10.1371/journal.ppat.1002735

44. J. Klee, A. M. Besana, E. Genersch, S. Gisder, A. Nanetti, D. Q. Tam, T. X. Chinh, F. Puerta, J. M. Ruz, P. Kryger, D. Message, F. Hatjina, S. Korpela, I. Fries, R. J. Paxton, Widespread dispersal of the microsporidian *Nosema ceranae*, an emergent pathogen of the western honey bee, *Apis mellifera*. *J. Invertebr. Pathol.* **96**, 1–10 (2007). Medline doi:10.1016/j.jip.2007.02.014

45. Y. Chen, J. D. Evans, I. B. Smith, J. S. Pettis, *Nosema ceranae* is a long-present and wide-spread microsporidian infection of the European honey bee (*Apis mellifera*) in the United States. *J. Invertebr. Pathol.* **97**, 186–188 (2008). Medline doi:10.1016/j.jip.2007.07.010

46. J. Li, W. Chen, J. Wu, W. Peng, J. An, P. Schmid-Hempel, R. Schmid-Hempel, Diversity of *Nosema* associated with bumblebees (*Bombus* spp.) from China. *Int. J. Parasitol.* **42**, 49–61 (2012). Medline doi:10.1016/j.ijpara.2011.10.005

47. S. Plischuk, R. Martín-Hernández, L. Prieto, M. Lucía, C. Botías, A. Meana, A. H. Abrahamovich, C. Lange, M. Higes, South American native bumblebees (Hymenoptera: Apidae) infected by *Nosema ceranae* (Microsporidia), an emerging pathogen of honeybees (*Apis mellifera*). *Environ. Microbiol. Rep.* **1**, 131–135 (2009). Medline doi:10.1111/j.1758-2229.2009.00018.x

48. J. Ravoet, L. De Smet, I. Meeus, G. Smagghe, T. Wenseleers, D. C. de Graaf, Widespread occurrence of honey bee pathogens in solitary bees. *J. Invertebr. Pathol.* **122**, 55–58 (2014). Medline doi:10.1016/j.jip.2014.08.007

49. S. Spiewok, P. Neumann, Infestation of commercial bumblebee (*Bombus impatiens*) field colonies by small hive beetles (*Aethina tumida*). *Ecol. Entomol.* **31**, 623–628 (2006). doi:10.1111/j.1365-2311.2006.00827.x

50. D. Hoffmann, J. S. Pettis, P. Neumann, Potential host shift of the small hive beetle (*Aethina tumida*) to bumblebee colonies (*Bombus impatiens*). *Insectes Soc.* **55**, 153–162 (2008). doi:10.1007/s00040-008-0982-9

51. S. A. Cameron, J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, T. L. Griswold, Patterns of widespread decline in North American bumble bees. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 662–667 (2011). Medline doi:10.1073/pnas.1014743108

52. I. Meeus, M. J. F. Brown, D. C. De Graaf, G. Smagghe, Effects of invasive parasites on bumble bee declines. *Conserv. Biol.* **25**, 662–671 (2011). Medline doi:10.1111/j.1523-1739.2011.01707.x

53. M. P. Arbetman, I. Meeus, C. L. Morales, M. A. Aizen, G. Smagghe, Alien parasite hitchhikes to Patagonia on invasive bumblebee. *Biol. Invasions* **15**, 489–494 (2013). doi:10.1007/s10530-012-0311-0

54. S. R. Colla, M. C. Otterstatter, R. J. Gegear, J. D. Thomson, Plight of the bumble bee: Pathogen spillover from commercial to wild populations. *Biol. Conserv.* **129**, 461–467 (2006). doi:10.1016/j.biocon.2005.11.013

55. M. C. Otterstatter, J. D. Thomson, Does pathogen spillover from commercially reared bumble bees threaten wild pollinators? *PLOS ONE* **3**, e2771 (2008). doi:10.1371/journal.pone.0002771

56. M. Yoneda, H. Furuta, K. Tsuchida, K. Okabe, K. Goka, Commercial colonies of *Bombus terrestris* (Hymenopter: Apidae) are reservoirs of the tracheal mite *Locustacarus buchneri* (Acari: Podapolipidae). *Appl. Entomol. Zool.* **43**, 73–76 (2008). doi:10.1303/aez.2008.73

57. D. Goulson, Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **34**, 1–26 (2003). doi:10.1146/annurev.ecolsys.34.011802.132355

58. D. Goulson, O. Lepais, S. O'Connor, J. L. Osborne, R. A. Sanderson, J. Cussans, L. Goffe, B. Darvill, Effects of land use at a landscape scale on bumblebee nest density and survival. *J. Appl. Ecol.* **47**, 1207–1215 (2010). doi:10.1111/j.1365-2664.2010.01872.x

59. L. A. Morandin, M. L. Winston, Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecol. Appl.* **15**, 871–881 (2005). doi:10.1890/03-5271

60. M. P. Chauzat, J. P. Faucon, A. C. Martel, J. Lachaize, N. Cougoule, M. Aubert, A survey of pesticide residues in pollen loads collected by honey bees in France. *J. Econ. Entomol.* **99**, 253–262 (2006). Medline doi:10.1093/jee/99.2.253

61. F. Sanchez-Bayo, K. Goka, Pesticide residues and bees—a risk assessment. *PLOS ONE* **9**, e94482 (2014). Medline doi:10.1371/journal.pone.0094482

62. C. A. Mullin, M. Frazier, J. L. Frazier, S. Ashcraft, R. Simonds, D. Vanengelsdorp, J. S. Pettis, High levels of miticides and agrochemicals in North American apiaries: Implications for honey bee health. *PLOS ONE* **5**, e9754 (2010). Medline doi:10.1371/journal.pone.0009754

63. C. H. Krupke, G. J. Hunt, B. D. Eitzer, G. Andino, K. Given, Multiple routes of pesticide exposure for honey bees living near agricultural fields. *PLOS ONE* **7**, e29268 (2012). Medline doi:10.1371/journal.pone.0029268

64. D. Paradis, G. Bérail, J. M. Bonmatin, L. P. Belzunces, Sensitive analytical methods for 22 relevant insecticides of 3 chemical families in honey by GC-MS/MS and LC-MS/MS. *Anal. Bioanal. Chem.* **406**, 621–633 (2014). Medline doi:10.1007/s00216-013-7483-z

65. L. W. Pisa, V. Amaral-Rogers, L. P. Belzunces, J. M. Bonmatin, C. A. Downs, D. Goulson, D. P. Kreutzweiser, C. Krupke, M. Liess, M. McField, C. A. Morrissey, D. A. Noome, J. Settele, N. Simon-Delso, J. D. Stark, J. P. Van der Sluijs, H. Van Dyck, M. Wiemers, Effects of neonicotinoids and fipronil on non-target invertebrates. *Environ. Sci. Pollut. Res. Int.* **22**, 68–102 (2015). Medline

66. D. Goulson, An overview of the environmental risks posed by neonicotinoid insecticides. *J. Appl. Ecol.* **50**, 977–987 (2013). doi:10.1111/1365-2664.12111

67. M. Tomizawa, J. E. Casida, Neonicotinoid insecticide toxicology: Mechanisms of selective action. *Annu. Rev. Pharmacol. Toxicol.* **45**, 247–268 (2005). Medline doi:10.1146/annurev.pharmtox.45.120403.095930

68. S. Suchail, D. Guez, L. P. Belzunces, Characteristics of imidacloprid toxicity in two *Apis mellifera* subspecies. *Environ. Toxicol. Chem.* **19**, 1901–1905 (2000). doi:10.1897/1551-5028(2000)019<1901:COITIT>2.3.CO;2

69. G. Rondeau, F. Sánchez-Bayo, H. A. Tennekes, A. Decourtye, R. Ramírez-Romero, N. Desneux, Delayed and time-cumulative toxicity of imidacloprid in bees, ants and termites. *Sci. Rep.* **4**, 5566 (2014). Medline doi:10.1038/srep05566

70. E. C. Yang, Y. C. Chuang, Y. L. Chen, L. H. Chang, Abnormal foraging behavior induced by sublethal dosage of imidacloprid in the honey bee (Hymenoptera: Apidae). *J. Econ. Entomol.* **101**, 1743–1748 (2008). Medline doi:10.1603/0022-0493-101.6.1743

71. V. Mommaerts, S. Reynders, J. Boulet, L. Besard, G. Sterk, G. Smagghe, Risk assessment for side-effects of neonicotinoids against bumblebees with and without impairing foraging behavior. *Ecotoxicology* **19**, 207–215 (2010). Medline doi:10.1007/s10646-009-0406-2

72. M. Henry, M. Béguin, F. Requier, O. Rollin, J. F. Odoux, P. Aupinel, J. Aptel, S. Tchamitchian, A. Decourtye, A common pesticide decreases foraging success and survival in honey bees. *Science* **336**, 348–350 (2012). Medline doi:10.1126/science.1215039

73. H. Feltham, K. Park, D. Goulson, Field realistic doses of pesticide imidacloprid reduce bumblebee pollen foraging efficiency. *Ecotoxicology* **23**, 317–323 (2014). Medline doi:10.1007/s10646-014-1189-7

74. P. Han, C. Y. Niu, C. L. Lei, J. J. Cui, N. Desneux, Quantification of toxins in a Cry1Ac + CpTI cotton cultivar and its potential effects on the honey bee *Apis mellifera* L. *Ecotoxicology* **19**, 1452–1459 (2010). Medline doi:10.1007/s10646-010-0530-z

75. E. C. Yang, H. C. Chang, W. Y. Wu, Y. W. Chen, Impaired olfactory associative behavior of honeybee workers due to contamination of imidacloprid in the larval stage. *PLOS ONE* **7**, e49472 (2012). Medline doi:10.1371/journal.pone.0049472

76. P. R. Whitehorn, S. O'Connor, F. L. Wackers, D. Goulson, Neonicotinoid pesticide reduces bumble bee colony growth and queen production. *Science* **336**, 351–352 (2012). Medline doi:10.1126/science.1215025

77. G. C. Cutler, C. D. Scott-Dupree, Exposure to clothianidin seed-treated canola has no long-term impact on honey bees. *J. Econ. Entomol.* **100**, 765–772 (2007). Medline doi:10.1603/0022-0493(2007)100[765:ETCSCH]2.0.CO;2

78. E. Pilling, P. Campbell, M. Coulson, N. Ruddle, I. Tornier, A four-year field program investigating long-term effects of repeated exposure of honey bee colonies to flowering crops treated with thiamethoxam. *PLOS ONE* **8**, e77193 (2013). Medline doi:10.1371/journal.pone.0077193

79. I. London-Shafir, S. Shafir, D. Eisikowitch, Amygdalin in almond nectar and pollen-facts and possible roles. *Plant Syst. Evol.* **238**, 87–95 (2003).

80. R. G. Stanley, H. F. Linskens, *Pollen: Biology, Biochemistry, Management* (Springer-Verlag, Berlin, 1974).

81. T. H. Roulston, S. L. Buchmann, A phylogenetic reconsideration of the pollen starch-pollination correlation. *Evol. Ecol. Res.* **2**, 627–643 (2000).

82. M. E. Hanley, M. Franco, S. Pichon, B. Darvill, D. Goulson, Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Funct. Ecol.* **22**, 592–598 (2008). doi:10.1111/j.1365-2435.2008.01415.x

83. G. A. Wright, D. D. Baker, M. J. Palmer, D. Stabler, J. A. Mustard, E. F. Power, A. M. Borland, P. C. Stevenson, Caffeine in floral nectar enhances a pollinator's memory of reward. *Science* **339**, 1202–1204 (2013). Medline doi:10.1126/science.1228806

84. W. Mao, M. A. Schuler, M. R. Berenbaum, Honey constituents up-regulate detoxification and immunity genes in the western honey bee *Apis mellifera*. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 8842–8846 (2013). Medline doi:10.1073/pnas.1303884110

85. A. Maurizio, The influence of pollen feeding and brood rearing on the length of life and physiological condition of the honeybee. *Bee World* **31**, 9–12 (1950).

86. L. N. Standifer, A comparison of the protein quality of pollens for growth-stimulation of the hypopharyngeal glands and longevity of honey bees, *Apis mellifera* L. (Hymenoptera: Apidae). *Insectes Soc.* **14**, 415–425 (1967). doi:10.1007/BF02223687

87. L. S. Schmidt, J. O. Schmidt, H. Rao, W. Wang, L. Xu, Feeding preference and survival of young worker honeybees (Hymenoptera: Apidae) fed rape, sesame, and sunflower pollen. *J. Econ. Entomol.* **88**, 1591–1595 (1995). doi:10.1093/jee/88.6.1591

88. G. Di Pasquale, M. Salignon, Y. Le Conte, L. P. Belzunces, A. Decourtye, A. Kretzschmar, S. Suchail, J. L. Brunet, C. Alaux, Influence of pollen nutrition on honey bee health: Do pollen quality and diversity matter? *PLOS ONE* **8**, e72016 (2013). Medline doi:10.1371/journal.pone.0072016

89. M. M. Morais, A. P. Turcatto, T. M. Francoy, L. S. Gonçalves, F. A. Cappelari, D. De Jong, Evaluation of inexpensive pollen substitute diets through quantification of haemolymph proteins. *J. Apic. Res.* **52**, 119–121 (2013). doi:10.3896/IBRA.1.52.3.01

90. R. Kumar, R. C. Mishra, O. P. Agrawal, Effect of feeding artificial diets to honey bees during dearth period under Panchkula (Haryana) conditions. *J. Entomol. Res.* **37**, 41–46 (2013).

91. M. E. Knight, J. L. Osborne, R. A. Sanderson, R. J. Hale, A. P. Martin, D. Goulson, Bumblebee nest density and the scale of available forage in arable landscapes. *Insect Conserv. Divers.* **2**, 116–124 (2009). doi:10.1111/j.1752-4598.2009.00049.x

92. C. Westphal, I. Steffan-Dewenter, T. Tscharntke, Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *J. Appl. Ecol.* **46**, 187–193 (2009). doi:10.1111/j.1365-2664.2008.01580.x

93. F. Jauker, F. Peter, V. Wolters, T. Diekötter, Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outbalance post-flowering disadvantages. *Basic Appl. Ecol.* **13**, 268–276 (2012). doi:10.1016/j.baae.2012.03.010

94. A. Holzschuh, C. F. Dormann, T. Tscharntke, I. Steffan-Dewenter, Mass-flowering crops enhance wild bee abundance. *Oecologia* **172**, 477–484 (2013). Medline doi:10.1007/s00442-012-2515-5

95. F. Herrmann, C. Westphal, R. F. A. Moritz, I. Steffan-Dewenter, Genetic diversity and mass resources promote colony size and forager densities of a social bee (*Bombus pascuorum*) in agricultural landscapes. *Mol. Ecol.* **16**, 1167–1178 (2007). Medline doi:10.1111/j.1365-294X.2007.03226.x

96. A. Kovács-Hostyánszki, S. Haenke, P. Batáry, B. Jauker, A. Báldi, T. Tscharntke, A. Holzschuh, Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales. *Ecol. Appl.* **23**, 1938–1946 (2013). Medline doi:10.1890/12-2012.1

97. W. D. Yates, A review of infectious bovine rhinotracheitis, shipping fever pneumonia and viral-bacterial synergism in respiratory disease of cattle. *Can. J. Comp. Med.* **46**, 225–263 (1982). Medline

98. T. Bakonyi, R. Farkas, A. Szendröi, M. Dobos-Kovács, M. Rusvai, Detection of acute bee paralysis virus by RT-PCR in honey bee and *Varroa destructor* field samples: Rapid screening of representative Hungarian apiaries. *Apidologie* **33**, 63–74 (2002). doi:10.1051/apido:2001004

99. M. L. Forup, J. Memmott, The relationship between the abundance of bumblebees and honeybees in a native habitat. *Ecol. Entomol.* **30**, 47–57 (2005). doi:10.1111/j.0307-6946.2005.00660.x

100. K. Walther-Hellwig, G. Fokul, R. Frankl, R. Büchler, K. Ekschmitt, V. Wolters, Increased density of honeybee colonies affects foraging bumblebees. *Apidologie* **37**, 517–532 (2006). doi:10.1051/apido:2006035

101. D. Goulson, K. R. Sparrow, Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *J. Insect Conserv.* **13**, 177–181 (2008). doi:10.1007/s10841-008-9140-y

102. D. M. Thomson, Detecting the effects of introduced species: A case study of competition between *Apis* and *Bombus*. *Oikos* **114**, 407–418 (2006). doi:10.1111/j.2006.0030-1299.14604.x

103. P. Willmer, Pollinator-plant synchrony tested by climate change. *Curr. Biol.* **22**, R131–R132 (2012). Medline doi:10.1016/j.cub.2012.01.009

104. I. Bartomeus, M. G. Park, J. Gibbs, B. N. Danforth, A. N. Lakso, R. Winfree, Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecol. Lett.* **16**, 1331–1338 (2013). Medline doi:10.1111/ele.12170

105. M. L. Forister, A. C. McCall, N. J. Sanders, J. A. Fordyce, J. H. Thorne, J. O'Brien, D. P. Waetjen, A. M. Shapiro, Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 2088–2092 (2010). Medline doi:10.1073/pnas.0909686107

106. E. F. Ploquin, J. M. Herrera, J. R. Obeso, Bumblebee community homogenization after uphill shifts in montane areas of northern Spain. *Oecologia* **173**, 1649–1660 (2013). Medline doi:10.1007/s00442-013-2731-7

107. A. Sih, A. M. Bell, J. L. Kerby, Two stressors are far deadlier than one. *Trends Ecol. Evol.* **19**, 274–276 (2004). Medline doi:10.1016/j.tree.2004.02.010

108. A. Coors, L. De Meester, Synergistic, antagonistic and additive effects of multiple stressors: Predation threat, parasitism and pesticide exposure in *Daphnia magna*. *J. Appl. Ecol.* **45**, 1820–1828 (2008). doi:10.1111/j.1365-2664.2008.01566.x

109. R. J. Gill, O. Ramos-Rodriguez, N. E. Raine, Combined pesticide exposure severely affects individual- and colony-level traits in bees. *Nature* **491**, 105–108 (2012). Medline doi:10.1038/nature11585

110. R. Schmuck, T. Stadler, H. W. Schmidt, Field relevance of a synergistic effect observed in the laboratory between an EBI fungicide and a chloronicotinyl insecticide in the honeybee (*Apis mellifera* L, Hymenoptera). *Pest Manag. Sci.* **59**, 279–286 (2003). Medline doi:10.1002/ps.626

111. T. Iwasa, N. Motoyama, J. T. Ambrose, R. M. M. Roe, Mechanism for the differential toxicity of neonicotinoid insecticides in the honey bee, *Apis mellifera*. *Crop Prot.* **23**, 371–378 (2004). doi:10.1016/j.cropro.2003.08.018

112. E. D. Pilling, P. C. Jepson, Synergism between EBI fungicides and a pyrethroid insecticide in the honeybee (*Apis mellifera*). *Pestic. Sci.* **39**, 293–297 (1993). doi:10.1002/ps.2780390407

113. A. Decourtye, C. Armengaud, M. Renou, J. Devillers, S. Cluzeau, M. Gauthier, M.-H. Pham-Delègue, Imidacloprid impairs memory and brain metabolism in the honeybee (*Apis mellifera* L.). *Pestic. Biochem. Physiol.* **78**, 83–92 (2004). doi:10.1016/j.pestbp.2003.10.001

114. S. M. Williamson, G. A. Wright, Exposure to multiple cholinergic pesticides impairs olfactory learning and memory in honeybees. *J. Exp. Biol.* **216**, 1799–1807 (2013). Medline doi:10.1242/jeb.083931

115. C. Alaux, J. L. Brunet, C. Dussaubat, F. Mondet, S. Tchamitchan, M. Cousin, J. Brillard, A. Baldy, L. P. Belzunces, Y. Le Conte, Interactions between *Nosema* microspores and a neonicotinoid weaken honeybees (*Apis mellifera*). *Environ. Microbiol.* **12**, 774–782 (2010). Medline doi:10.1111/j.1462-2920.2009.02123.x

116. J. S. Pettis, D. vanEngelsdorp, J. Johnson, G. Dively, Pesticide exposure in honey bees results in increased levels of the gut pathogen *Nosema*. *Naturwissenschaften* **99**, 153–158 (2012). Medline doi:10.1007/s00114-011-0881-1

117. C. Vidau, M. Diogon, J. Aufauvre, R. Fontbonne, B. Viguès, J. L. Brunet, C. Texier, D. G. Biron, N. Blot, H. El Alaoui, L. P. Belzunces, F. Delbac, Exposure to sublethal doses of fipronil and thiacloprid highly increases mortality of honeybees previously infected by *Nosema ceranae*. *PLOS ONE* **6**, e21550 (2011). Medline doi:10.1371/journal.pone.0021550

118. J. Aufauvre, D. G. Biron, C. Vidau, R. Fontbonne, M. Roudel, M. Diogon, B. Viguès, L. P. Belzunces, F. Delbac, N. Blot, Parasite-insecticide interactions: A case study of Nosema ceranae and fipronil synergy on honeybee. *Sci. Rep.* **2**, 326 (2012). Medline doi:10.1038/srep00326

119. G. L. Baron, N. E. Raine, M. J. F. Brown, Impact of chronic exposure to a pyrethroid pesticide on bumblebees and interactions with a trypanosome parasite. *J. Appl. Ecol.* **51**, 460–469 (2014). doi:10.1111/1365-2664.12205

120. A. Fauser-Misslin, B. M. Sadd, P. Neumann, C. Sandrock, Influence of combined pesticide and parasite exposure on bumblebee colony traits in the laboratory. *J. Appl. Ecol.* **51**, 450–459 (2014). doi:10.1111/1365-2664.12188

121. V. Doublet, M. Labarussias, J. R. de Miranda, R. F. A. Moritz, R. J. Paxton, Bees under stress: Sublethal doses of a neonicotinoid pesticide and pathogens interact to elevate honey bee mortality across the life cycle. *Environ. Microbiol.* 10.1111/1462-2920.12426 (2014). Medline doi:10.1111/1462-2920.12426

122. J. Y. Wu, M. D. Smart, C. M. Anelli, W. S. Sheppard, Honey bees (*Apis mellifera*) reared in brood combs containing high levels of pesticide residues exhibit increased susceptibility to *Nosema* (Microsporidia) infection. *J. Invertebr. Pathol.* **109**, 326–329 (2012). Medline doi:10.1016/j.jip.2012.01.005

123. R. R. James, J. Xu, Mechanisms by which pesticides affect insect immunity. *J. Invertebr. Pathol.* **109**, 175–182 (2012). Medline doi:10.1016/j.jip.2011.12.005

124. F. S. Brunner, P. Schmid-Hempel, S. M. Barribeau, Immune gene expression in *Bombus terrestris*: Signatures of infection despite strong variation among populations, colonies, and sister workers. *PLOS ONE* **8**, e68181 (2013). Medline doi:10.1371/journal.pone.0068181

125. H. Boncristiani, R. Underwood, R. Schwarz, J. D. Evans, J. Pettis, D. vanEngelsdorp, Direct effect of acaricides on pathogen loads and gene expression levels in honey bees *Apis mellifera*. *J. Insect Physiol.* **58**, 613–620 (2012). Medline doi:10.1016/j.jinsphys.2011.12.011

126. G. Di Prisco, V. Cavaliere, D. Annoscia, P. Varricchio, E. Caprio, F. Nazzi, G. Gargiulo, F. Pennacchio, Neonicotinoid clothianidin adversely affects insect immunity and promotes replication of a viral pathogen in honey bees. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 18466–18471 (2013). Medline doi:10.1073/pnas.1314923110

127. M. J. F. Brown, R. Loosli, P. Schmid-Hempel, Condition-dependent expression of virulence in a trypanosome infecting bumblebees. *Oikos* **91**, 421–427 (2000). doi:10.1034/j.1600-0706.2000.910302.x

128. E. R. Tyler, S. Adams, E. B. Mallon, An immune response in the bumblebee, *Bombus terrestris* leads to increased food consumption. *BMC Physiol.* **6**, 6 (2006). Medline doi:10.1186/1472-6793-6-6

129. Y. Moret, P. Schmid-Hempel, Survival for immunity: The price of immune system activation for bumblebee workers. *Science* **290**, 1166–1168 (2000). Medline doi:10.1126/science.290.5494.1166

130. E. B. Mallon, A. Brockmann, P. Schmid-Hempel, Immune response inhibits associative learning in insects. *Proc. R. Soc. B* **270**, 2471–2473 (2003). Medline doi:10.1098/rspb.2003.2456

131. C. E. Riddell, E. B. Mallon, Insect psychoneuroimmunology: Immune response reduces learning in protein starved bumblebees (*Bombus terrestris*). *Brain Behav. Immun.* **20**, 135–138 (2006). Medline doi:10.1016/j.bbi.2005.06.008

132. A. Alghamdi, L. Dalton, A. Phillis, E. Rosato, E. B. Mallon, Immune response impairs learning in free-flying bumble-bees. *Biol. Lett.* **4**, 479–481 (2008). Medline doi:10.1098/rsbl.2008.0331

133. D. Van Engelsdorp, M. D. Meixner, A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *J. Invertebr. Pathol.* **103** (suppl. 1), S80–S95 (2010). Medline doi:10.1016/j.jip.2009.06.011

134. R. Winfree, C. Kremen, Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc. R. Soc. B* **276**, 229–237 (2009). Medline doi:10.1098/rspb.2008.0709

135. R. Rader, B. G. Howlett, S. A. Cunningham, D. A. Westcott, W. Edwards, Spatial and temporal variation in pollinator effectiveness: Do unmanaged insects provide consistent pollination services to mass flowering crops? *J. Appl. Ecol.* **49**, 126–134 (2012). doi:10.1111/j.1365-2664.2011.02066.x

136. P. Hoehn, T. Tscharntke, J. M. Tylianakis, I. Steffan-Dewenter, Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. B* **275**, 2283–2291 (2008). Medline

137. J. K. Tuell, R. Isaacs, Community and species-specific responses of wild bees to insect pest control programs applied to a pollinator-dependent crop. *J. Econ. Entomol.* **103**, 668–675 (2010). Medline doi:10.1603/EC09314

138. N. Blüthgen, A. M. Klein, Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. *Basic Appl. Ecol.* **12**, 282–291 (2011). doi:10.1016/j.baae.2010.11.001

139. C. Brittain, N. Williams, C. Kremen, A. Klein, Synergistic effects of non-*Apis* bees and honey bees for pollination services. *Proc. R. Soc. B* **280**, 20122767 (2013). doi:10.1098/rspb.2012.2767

140. I. Steffan-Dewenter, U. Münzenberg, C. Bürger, C. Thies, T. Tscharntke, Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**, 1421–1432 (2002). doi:10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

141. L. A. Garibaldi *et al*., From research to action: Enhancing crop yield through wild pollinators. *Front. Ecol. Environ.* **12**, 439–447 (2014). doi:10.1890/130330

142. R. F. Pywell, E. A. Warman, L. Hulmes, S. Hulmes, P. Nuttall, T. H. Sparks, C. N. R. Critchley, A. Sherwood, Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biol. Conserv.* **129**, 192–206 (2006). doi:10.1016/j.biocon.2005.10.034

143. R. F. Pywell, E. A. Warman, C. Carvell, T. H. Sparks, L. V. Dicks, D. Bennett, A. Wright, C. N. R. Critchley, A. Sherwood, Providing foraging resources for bumblebees in intensively farmed landscapes. *Biol. Conserv.* **121**, 479–494 (2005). doi:10.1016/j.biocon.2004.05.020

144. C. Carvell, W. R. Meek, R. F. Pywell, D. Goulson, M. Nowakowski, Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J. Appl. Ecol.* **44**, 29–40 (2006). doi:10.1111/j.1365-2664.2006.01249.x

145. M. Rundlöf, H. Nilsson, H. G. Smith, Interacting effects of farming practice and landscape context on bumble bees. *Biol. Conserv.* **141**, 417–426 (2008). doi:10.1016/j.biocon.2007.10.011

146. C. M. Kennedy, E. Lonsdorf, M. C. Neel, N. M. Williams, T. H. Ricketts, R. Winfree, R. Bommarco, C. Brittain, A. L. Burley, D. Cariveau, L. G. Carvalheiro, N. P. Chacoff, S. A. Cunningham, B. N. Danforth, J. H. Dudenhöffer, E. Elle, H. R. Gaines, L. A. Garibaldi, C. Gratton, A. Holzschuh, R. Isaacs, S. K. Javorek, S. Jha, A. M. Klein, K. Krewenka, Y. Mandelik, M. M. Mayfield, L. Morandin, L. A. Neame, M. Otieno, M. Park, S. G. Potts, M. Rundlöf, A. Saez, I. Steffan-Dewenter, H. Taki, B. F. Viana, C. Westphal, J. K. Wilson, S. S. Greenleaf, C. Kremen, A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* **16**, 584–599 (2013). Medline doi:10.1111/ele.12082

147. S. D. Wratten, M. Gillespie, A. Decourtye, E. Mader, N. Desneux, Pollinator habitat enhancement: Benefits to other ecosystem services. *Agric. Ecosyst. Environ.* **159**, 112–122 (2012). doi:10.1016/j.agee.2012.06.020

148. L. A. Morandin, M. L. Winston, V. A. Abbott, M. T. Franklin, Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic Appl. Ecol.* **8**, 117–124 (2007). doi:10.1016/j.baae.2006.06.003

149. B. R. Blaauw, R. Isaacs, Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.* **51**, 890–898 (2014). doi:10.1111/1365-2664.12257

150. D. Goulson, *Bumblebees: Behaviour, Ecology, and Conservation* (Oxford Univ. Press, Oxford, 2010).

151. L. M. Blackmore, D. Goulson, Evaluating the effectiveness of wildflower seed mixes for boosting floral diversity and bumblebee and hoverfly abundance in urban areas. *Insect Conserv. Divers.* **7**, 480–484 (2014). doi:10.1111/icad.12071

152. M. Garbuzov, F. L. W. Ratnieks, Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. *Funct. Ecol.* **28**, 364–374 (2014). doi:10.1111/1365-2435.12178

153. I. Steffan-Dewenter, S. Schiele, Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology* **89**, 1375–1387 (2008). Medline doi:10.1890/06-1323.1

154. C. D. Osteen, J. Fernandez-Cornejo, Economic and policy issues of U.S. agricultural pesticide use trends. *Pest Manag. Sci.* **69**, 1001–1025 (2013). Medline doi:10.1002/ps.3529

155. S. Stevens, P. Jenkins, "Heavy costs: Weighing the value of neonicotinoid insecticides in agriculture" (Center for Food Safety, Washington, DC, 2014).

156. B. Freier, E. F. Boller, Integrated pest management in Europe—history, policy, achievements and implementation. In *Integrated Pest Management: Dissemination and Impact*, R. Peshin, A. K. Dhawan, Eds. (Springer, New York, 2009), pp. 435–454.

157. EFSA, Conclusion on the peer review of the pesticide risk assessment for bees for the active substance thiamethoxam. *EFSA J.* **11**, 3067 (2013); www.efsa.europa.eu/en/efsajournal/pub/3067.htm.

158. EFSA, Conclusion on the peer review of the pesticide risk assessment for bees for the active substance clothianidin. *EFSA J.* **11**, 3066 (2013); www.efsa.europa.eu/en/efsajournal/pub/3066.htm.

159. EFSA, Conclusion on the peer review of the pesticide risk assessment for bees for the active substance imidacloprid. *EFSA J.* **11**, 3068 (2013); www.efsa.europa.eu/en/efsajournal/pub/3068.htm.

160. M. S. Warren, J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, D. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S. G. Willis, J. N. Greatorex-Davies, D. Moss, C. D. Thomas, Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69 (2001). Medline doi:10.1038/35102054

161. R. M. Pateman, J. K. Hill, D. B. Roy, R. Fox, C. D. Thomas, Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science* **336**, 1028–1030 (2012). Medline doi:10.1126/science.1216980

162. G. Lebuhn, S. Droege, E. F. Connor, B. Gemmill-Herren, S. G. Potts, R. L. Minckley, T. Griswold, R. Jean, E. Kula, D. W. Roubik, J. Cane, K. W. Wright, G. Frankie, F. Parker, Detecting insect pollinator declines on regional and global scales. *Conserv. Biol.* **27**, 113–120 (2013). Medline doi:10.1111/j.1523-1739.2012.01962.x

163. I. Fries, F. Feng, A. da Silva, S. B. Slemenda, N. J. Pieniazek, *Nosema ceranae* n. sp. (Microspora, Nosematidae), morphological and molecular characterization of a microsporidian parasite of the Asian honey bee *Apis cerana* (Hymenoptera, Apidae). *Eur. J. Protistol.* **32**, 356–365 (1996). doi:10.1016/S0932-4739(96)80059-9

164. M. Higes, R. Martín, A. Meana, *Nosema ceranae*, a new microsporidian parasite in honeybees in Europe. *J. Invertebr. Pathol.* **92**, 93–95 (2006). Medline doi:10.1016/j.jip.2006.02.005

165. C. M. Aurori, D. S. Dezmirean, L. A. Mărghitaş, R. F. A. Moritz, *Nosema apis* and *N. ceranae* in western honeybee (*Apis mellifera*)—geographical distribution and current methods of diagnosis. *Bull. UASVM Anim. Sci. Biotechnol.* **68**, 63–70 (2011).

166. J. Roberts, D. Anderson, Establishing the disease status of the Asian honeybee in the Cairns region Rural Industries Research and Development Corporation (RIRDC Publ. No. 13/082, RIRDC Proj. No. PRJ-008433, Aust. Gov., 2013).

167. J. Martínez, G. Leal, P. Conget, *Nosema ceranae* an emergent pathogen of *Apis mellifera* in Chile. *Parasitol. Res.* **111**, 601–607 (2012). Medline doi:10.1007/s00436-012-2875-0

168. Y. Chen, J. D. Evans, L. Zhou, H. Boncristiani, K. Kimura, T. Xiao, A. M. Litkowski, J. S. Pettis, Asymmetrical coexistence of *Nosema ceranae* and *Nosema apis* in honey bees. *J. Invertebr. Pathol.* **101**, 204–209 (2009). Medline doi:10.1016/j.jip.2009.05.012

169. V. Chaimanee, N. Warrit, P. Chantawannakul, Infections of *Nosema ceranae* in four different honeybee species. *J. Invertebr. Pathol.* **105**, 207–210 (2010). Medline doi:10.1016/j.jip.2010.06.005

170. C. Botías, D. L. Anderson, A. Meana, E. Garrido-Bailón, R. Martín-Hernández, M. Higes, Further evidence of an oriental origin for *Nosema ceranae* (Microsporidia: Nosematidae). *J. Invertebr. Pathol.* **110**, 108–113 (2012). Medline doi:10.1016/j.jip.2012.02.014

ACKNOWLEDGMENTS

Thanks are due to Rich Hatfield and Sarina Jepsen for their help with Fig. 1B.

10.1126/science.1255957

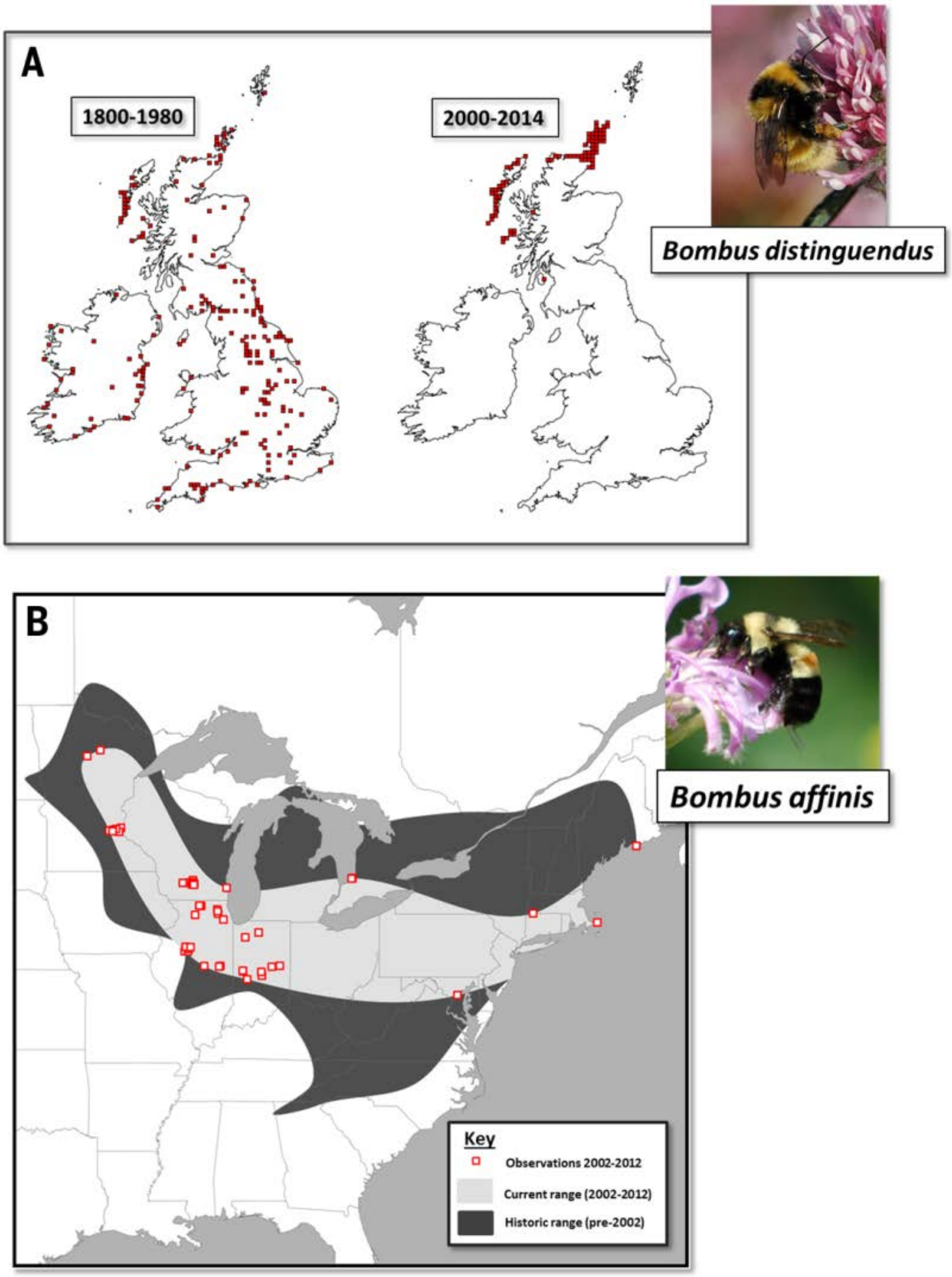

Fig. 1. Some wild bee species have undergone major range contractions. Shown here for (**A**) the bumblebee *Bombus distinguendus* in the UK (data from the National Biodiversity Network, UK) and (**B**) *Bombus affinis* in North America (Map produced by the Xerces Society, list of data providers can be found at www.leifrichardson.org/bbna.html). Photo credit: Dave Goulson, Johanna James-Heinz.

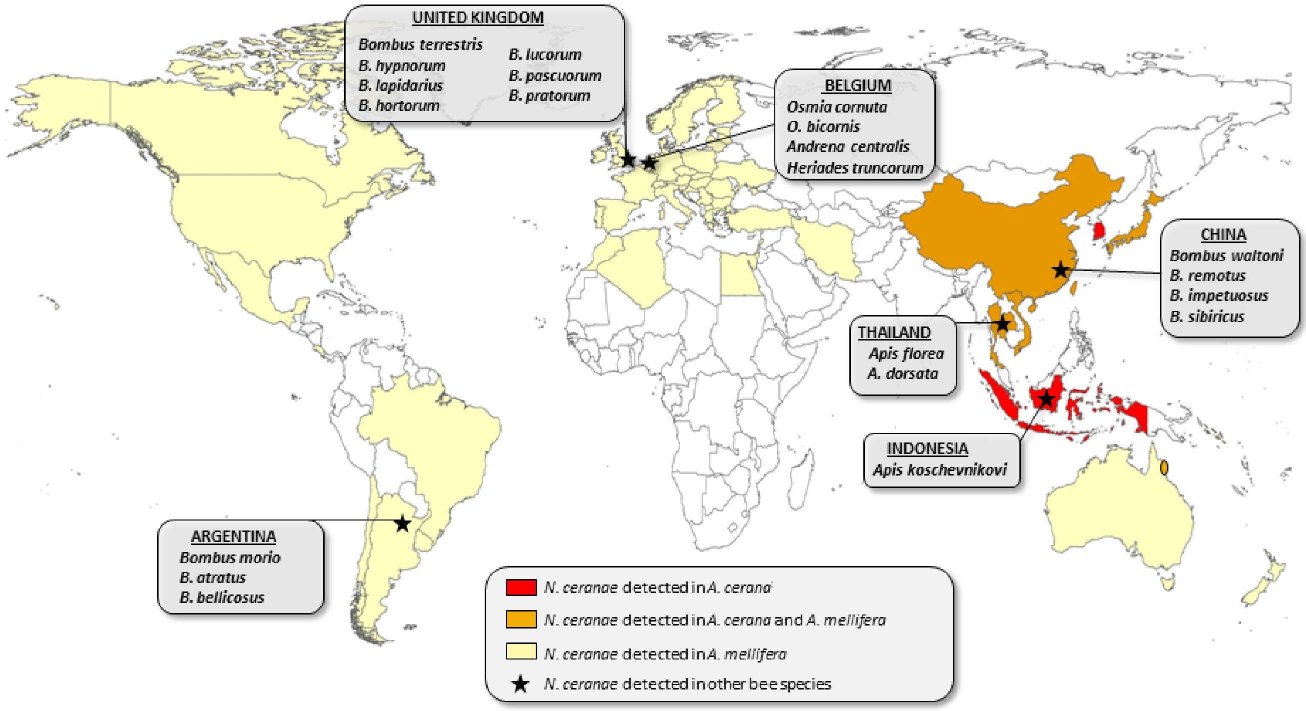

Fig. 2. World distribution of the microsporidian pathogen *Nosema ceranae* in different bee hosts. This parasite was first isolated from the Eastern honeybee (*A. cerana*) collected in China in 1996 (*163*), and was subsequently found infecting Western honey bees (*A. mellifera*) in Europe in 2005 (*164*). Soon after *N.ceranae* was detected in *A.mellifera* in many regions of the world including Africa, Asia, the Americas and Oceania (*44*, *45*, *165–168*), and more recently in other bee species including several Asian *Apis* species (*169*, *170*) and wild bumblebees species from Europe, China and South America (*41*, *46*, *47*). *N.ceranae* has also now been detected in solitary bees from Europe (*48*), confirming a very wide range of hosts and high dispersal rate. Although the origins and primary host of *N. ceranae* are yet to be accurately established, the apparent late and gradual invasions of *N. ceranae* into different *A. mellifera* populations have led some authors to suggest that *A. cerana* may be the primary host of *N. ceranae* and that it may have only recently emerged as a parasite of Western bees (*170*). The mechanism by which *N. ceranae* broadened its host range from an Asian bee species to other bee species across the world is unknown, but there has been human-mediated contact between Asian and Western bees for at least a century. It should be noted that regions in the figure where *Nosema* appears to be absent (white) may be due to a lack of sampling in these areas.

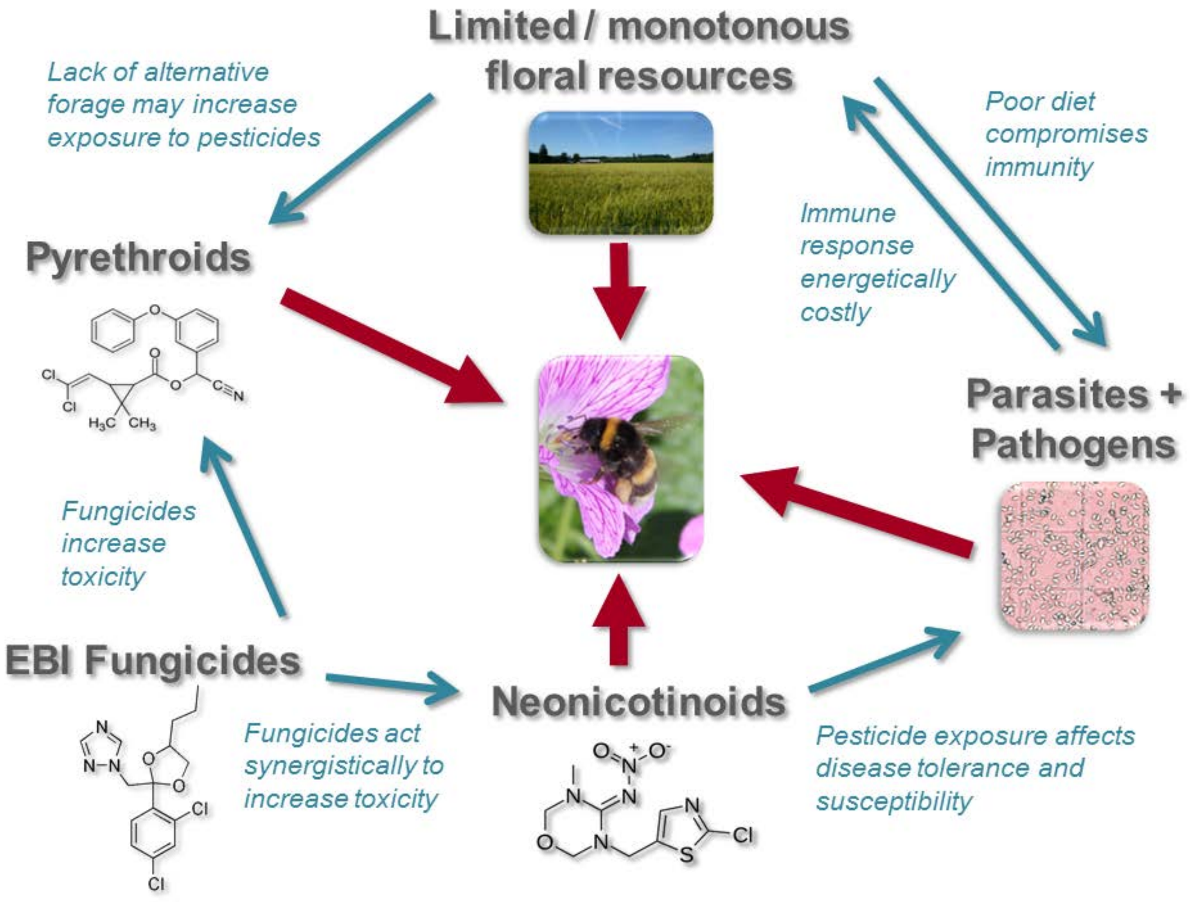

Fig. 3. Both wild and managed bees are subject to a number of significant and interacting stressors. For example, exposure to some fungicides can greatly increase toxicity of insecticides (*110*–*112*), whereas exposure to insecticides reduces resistance to diseases (*115*–*123*, *125*, *126*). Dietary stresses are likely to reduce the ability of bees to cope with both toxins and pathogens (*127*–*129*). Photo credit: Beth Nicholls; Flickr Commons, AJC1 (https://creativecommons.org/licenses/by-nc-sa/2.0/legalcode_).

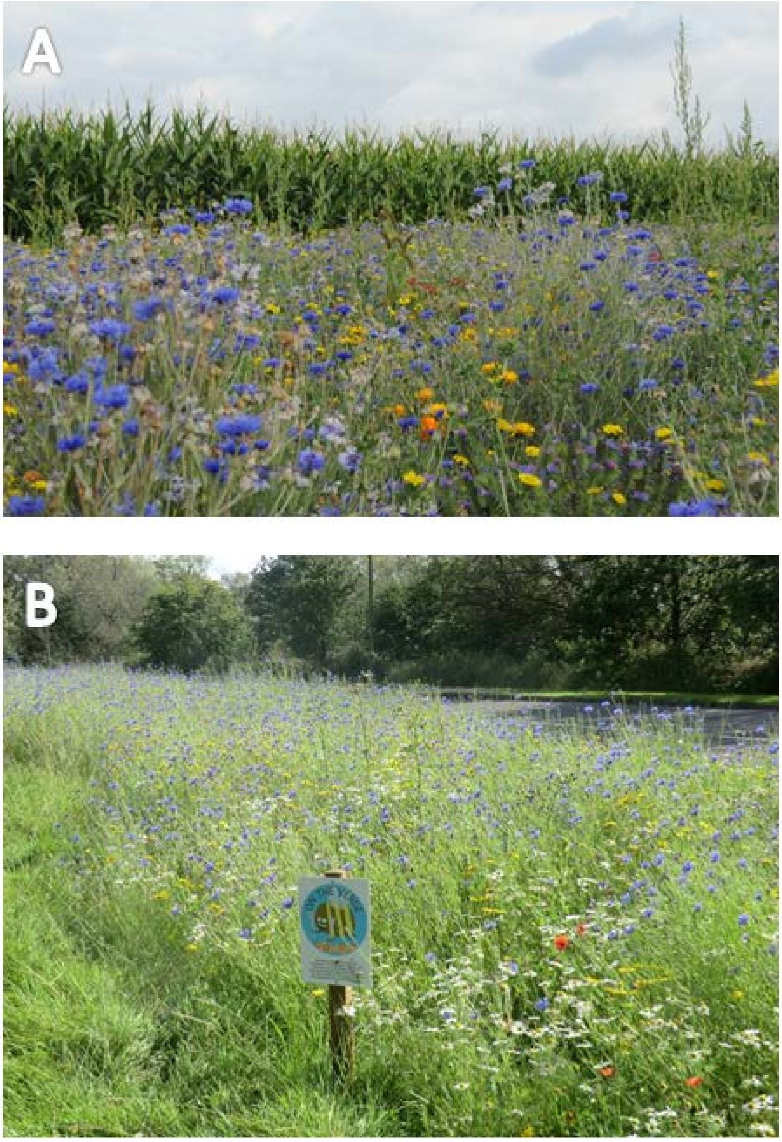

Fig. 4. Increasing floral abundance in the landscape is very likely to benefit pollinator populations. (**A**) Schemes to boost flower abundance in farmland, such as this wildflower strip along a field margin, have been demonstrated to provide clear benefits for wild bee populations [e.g., (*140*–*145*)]. (**B**) Urban areas can support high populations of pollinators, which may spill over into neighboring farmland. Conversion of amenity grasslands in urban areas to wildflower patches has been shown to greatly boost numbers of wild pollinators (*151*).