Threats to an ecosystem service: pressures on pollinators

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Insect pollinators of crops and wild plants are under threat globally and their decline or loss could have profound economic and environmental consequences. Here, we argue that multiple anthropogenic pressures – including land-use intensification, climate change, and the spread of alien species and diseases – are primarily responsible for insect-pollinator declines. We show that a complex interplay between pressures (eg lack of food sources, diseases, and pesticides) and biological processes (eg species dispersal and interactions) at a range of scales (from genes to ecosystems) underpins the general decline in insect-pollinator populations. Interdisciplinary research on the nature and impacts of these interactions will be needed if human food security and ecosystem function are to be preserved. We highlight key areas that require research focus and outline some practical steps to alleviate the pressures on pollinators and the pollination services they deliver to wild and crop plants.

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Human population growth and industrial development have led to increased and unsustainable consumption of natural resources. The resulting interrelated environmental pressures threaten global biodiversity and jeopardize the provision of crucial ecosystem services. Insect pollination is a high-profile example. Social and solitary bees, wasps, flies, beetles, butterflies, and moths comprise the vast majority of the world's pollinators. Many are crucial for the pollination of fruit, vegetable, oil, seed, and nut crops (Free 1993). The global economic value of wild and managed pollination services was US$215 billion in 2005, representing 9.5% of global food production value when calculated as the increase in crop production attributable to insect pollination (Gallai *et al.* 2009). Insect-pollinated crops provide vital human nutrition worldwide (Eilers *et al.* 2011). Insect pollination of wild plants (Ollerton *et al.* 2011) is also a critical life-support mechanism underpinning biodiversity and ecosystem services. Insect pollinators face growing pressure from the effects of intensified land use, climate change, alien species, and the spread of pests and pathogens (Kearns *et al.* 1998; Potts *et al.* 2010a); this has serious implications for human food security and health, and ecosystem function.

While these different threats to pollinators have long been recognized (eg Kearns *et al.* 1998), most research has focused on their individual impacts and has overlooked the complex nature of the problem (Alaux *et al.* 2010a; Runckel *et al.* 2011), thereby only partially explaining the causes and consequences of pollinator declines. Here, we consider managed (mainly honey bees [*Apis* spp] but also some captive-reared bumblebee and solitary bee species) and wild (bumblebees, solitary bees, flies, butterflies, etc) insects with the potential to pollinate crops or wild plants. As the evidence for pollinator decline has been thoroughly reviewed elsewhere (Kearns *et al.* 1998; Potts *et al.* 2010a), we only give a brief update, highlighting recent studies and the challenges involved in detecting these losses (Panel 1). We assess the implications of pollinator decline for ecosystem functioning and the services such insects deliver, and present a synthesis of recent advances in understanding of the individual and interacting impacts of different pressures on pollinators. We then suggest integrated research approaches and list several questions that need to be addressed to better understand the many threats facing insect pollinators (also see Panels 2 and 3). We conclude with a perspective on practical steps to conserve insect pollinators and their associated ecosystem services.

In a nutshell:

- Globally, insects supply pollination services, valued at US$215 billion in 2005, to about 75% of crop species and enable reproduction in up to 94% of wild flowering plants
- Pollinator populations are declining in many regions, threatening human food supplies and ecosystem functions
- A suite of interacting pressures are having an impact on pollinator health, abundance, and diversity
- Interdisciplinary research and stakeholder collaboration are needed to help unravel how these multiple pressures affect different pollinators and will provide evidence-based solutions
- Current options to alleviate the pressure on pollinators include establishment of effective habitat networks, broadening of pesticide risk assessments, and the development and introduction of innovative disease therapies

Implications of pollinator losses

Pollinators provide a crucial ecosystem service by improving or stabilizing yields of approximately 75% of crop-plant species globally (Klein *et al.* 2007). The cultivated area of insect-dependent crops has increased world-

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Panel 1. The evidence for pollinator declines

Are insect pollinators declining?

- There have been declines throughout Europe of wild bee (Biesmeijer *et al.* 2006) and hoverfly (Keil *et al.* 2011) species richness
- Extinctions, reduced abundance, and range contractions of butterfly (Warren *et al.* 2001; Forister *et al.* 2010) and bumblebee (Williams and Osborne 2009; Bommarco *et al.* 2011; Cameron *et al.* 2011) species have occurred across the Northern Hemisphere
- Wild, feral, and managed honey bees have declined over the past few decades in Europe and North America (Potts *et al.* 2010b; vanEngelsdorp *et al.* 2011), although managed honey bees have increased elsewhere (Aizen and Harder 2009)
- Threats in tropical regions are real and pressing, but data on insect pollinator declines are sparse (Aizen and Feinsinger 1994; Freitas *et al.* 2009)

Why are pollinator declines hard to prove?

- Species differences and multiple biological interactions (Keil *et al.* 2011) complicate the scenario by producing winners (eg generalist and highly dispersive species) and losers (eg specialists) in response to environmental change (Warren *et al.* 2001; Bommarco *et al.* 2011; Cameron *et al.* 2011)
- Lack of pollinator abundance data (including managed bees in some regions) and limited taxonomic and geographic coverage imply that researchers rely on sparse species occurrence data or inference from environmental impact studies

How can the extent of pollinator decline be determined?

- Systematic and standardized monitoring of pollinators within and across regions
- Greater focus on developing regions undergoing rapid anthropogenic changes (Freitas *et al.* 2009)
- Improved taxonomic capacity through molecular systematic and DNA barcoding initiatives (eg Global Biodiversity Information Facility, International Barcode of Life Project collaboration)

wide, raising demand for insect pollination threefold since 1961 (Aizen and Harder 2009). This demand is unlikely to be met by managed honey bees alone, given that their activity is often insufficient to deliver adequate quantity and quality of pollen at the appropriate time and place (Garibaldi *et al.* 2011). There is a clear link, however, between pollinator diversity and sustainable crop pollination. Natural habitats support many wild pollinators, providing a resilient and complementary pollination service that increases crop yields (Kremen *et al.* 2002; Carvalheiro *et al.* 2011; Garibaldi *et al.* 2011). In the face of multiple threats to pollinators, any reliance on a single species for pollination services is a risky agricultural strategy (Kearns *et al.* 1998). If demand for insect-pollinated crops continues to rise while pollinator numbers persistently fall (see Panel 1), then crop shortages will likely ensue in the absence of compensatory technical or economic responses (Aizen and Harder 2009; Gallai *et al.* 2009). This will have worldwide consequences for human health. Although wind-pollinated or largely self-pollinated staple crops supply the vast majority of human foods by volume, insect-pollinated crops contribute vital micronutrients (eg vitamins, folic acid) and dietary variety (Free 1993; Klein *et al.* 2007; Eilers *et al.* 2011). For example, vitamin A deficiency in humans is already common in many parts of the world and plants

Panel 2. Research priorities for unraveling the multifactorial pressures on insect pollinators

The italicized text indicates areas where some research has been published but is restricted in taxonomic or geographic scope.

(1) Improve understanding of basic pollinator ecology

- *Identify key pollinators of dominant and rare wild plant species (eg Kleijn and Raemakers 2008)*
- Establish a causal link between floral resource availability and pollinator abundance/diversity at landscape scales
- *Improve measurement of pollinator species movement and pollination success among patchily distributed plants (eg Carvell* et al. *2012)*

(2) Unravel complex pollinator–disease–environment interactions

- Disentangle the interactive effects of multiple pests and pathogens on pollinators from gene to organism scales
- Measure molecular-level interactions between pathogens, environmental toxins, and malnutrition in model social and solitary pollinators
- Establish pathology and epidemiology of shared pathogens within a community of social and solitary pollinators

(3) Understand anthropogenic impacts on pollinators

- Evaluate pollinator metapopulation and metacommunity dynamics across fragmented landscapes
- Assess the landscape-scale impacts of multiple interactions (eg ecosystem fragmentation, disease, alien species) on pollinator densities and behavior
- Couple simulation modeling with field experiments to incorporate insect behavior and demography into prediction of climate-change impacts
- *Understand chronic effects of industrial chemicals on pollinators (eg Gill* et al. *2012) and wild plant reproduction*
- *Compare pollinator species endurance across different gradients of habitat degradation (eg Forister* et al. *2010)*

that depend partially or wholly on insect pollinators provide 70% of this micronutrient, with pollination increasing yields by about 43% in plant species able to self-fertilize (Eilers *et al.* 2011). Human health impacts will be magnified in developing countries, where insect-pollinated crops (eg beans) supply crucial subsistence calories and nutrients.

Pollinator declines could also have serious consequences for natural ecosystems. Estimates of flowering plant dependence on animal pollination vary between 78% and 94% in temperate and tropical ecosystems, respectively (Ollerton *et al.* 2011). While the properties of pollinator networks (species redundancy, network structure, and behavioral flexibility) make them relatively robust, simulation models indicate that continued pollinator extinctions could lead to sudden crashes in plant diversity when highly connected species (ie that interact with many other species) go extinct (Kaiser-Bunbury *et al.* 2010). Reduced pollinator abundance and extinction (Panel 1) would have serious ecological and evolutionary implications for plants, food webs, and ecosystem function. These consequences would be particularly severe in the tropics, where much of the Earth's biodiversity resides and where dependence on animal pollination is highest (Ollerton *et al.* 2011). The extent of tropical pollinator decline is unclear, but threats to these species in the tropics are considered genuine and pressing, and are expected to produce similar outcomes to those seen in more developed regions (Panel 1; Aizen and Feinsinger 1994; Freitas *et al.* 2009). Such ecological changes could further affect human health, given that tropical plants are the source of many commercial nutritional supplements and could possess undiscovered medicinal properties as well (Eilers *et al.* 2011).

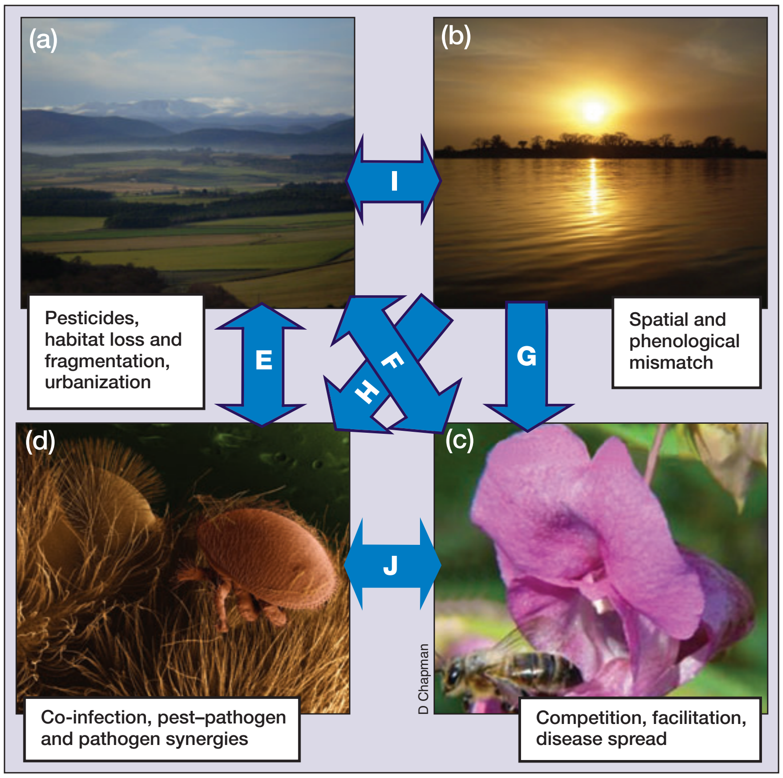

Figure 1. *Conceptual framework illustrating (panels, a–d) the key pressures and (arrows, E–J) their interactions, as they affect pollinators. (a) Land-use intensification; (b) climate change; (c) alien species; (d) pests and pathogens (*Varroa destructor *on a honey bee).*

■ Key pressures on pollinators

Land-use intensification

Urbanization and increasing agricultural intensification have destroyed and fragmented many natural habitats (Figure 1a) that pollinators rely on for forage and nesting resources (Kleijn and Raemakers 2008; Garibaldi *et al.* 2011). Overall, the more specialized pollinator species tend to be most vulnerable to habitat change (Biesmeijer *et al.* 2006; Williams and Osborne 2009). In addition, the ability to locate and move between dispersed resources in different landscapes varies between species (Lepais *et al.* 2010; Rader *et al.* 2011; Carvell *et al.* 2012). Changes in land use can often lead to the elimination of certain pollinator species at local and regional scales, thereby altering the structure and function of plant–pollinator communities (Williams and Osborne 2009; Burkle *et al.* 2013). Although mass flowering crops (eg canola) may offer alternative pollinator food in intensively managed landscapes (Westphal *et al.* 2003), they may compete with wild plants for pollinators and could alter pollinator communities by favoring those species able to exploit such flowering crops more effectively (Pleasants 1980). Furthermore, these types of crops often supply a short, synchronous pulse of floral resources that do not provide adequate nutrition for pollinators, especially those species with longer activity periods (Pleasants 1980).

Intensive crop management often includes the use of pesticides that can harm pollinators (Figure 1a; Scott-Dupree *et al.* 2009; Cresswell 2011; Gill *et al.* 2012). Landscape-scale surveys of wild bees and butterflies show that species richness tends to be lower where pesticide loads and cumulative exposure risk are high (Brittain *et al.* 2010). Used widely in the developed world, systemic pesticides (eg neonicotinoids) spread throughout plant tissues and can accumulate in plant nectar and pollen, thereby producing sublethal negative effects on pollinator performance and behavior (Cresswell 2011; Gill *et al.* 2012). Sublethal neonicotinoid exposure can impair brain function (Palmer *et al.* 2013) and the learned ability of foraging workers to relocate the hive in honey bees (Henry *et al.* 2012), and reduce the foraging performance, growth rate (Gill *et al.* 2012), and queen production of bumblebee (*Bombus terrestris*) colonies (Whitehorn *et al.* 2012).

Panel 3. Research priorities to demonstrate how pollination functions differ across species and crops

The italicized text indicates areas where some research has been published but is restricted in taxonomic or geographic scope.

- *Quantify the contribution to the yield and/or quality of multiple crops from (1) individual pollinator species and (2) pollinator communities (eg Garibaldi* et al. *2011)*
- *Obtain direct evidence of how changes in managed and wild pollinator densities impact crop and wild plant pollination (eg Kremen* et al. *2002)*
- Determine how regional changes in crop and pollinator distributions may produce pollination deficits as a result of climate change
- Estimate pollination deficits in relation to abundance, composition, and pollination efficiency of taxonomic and functional pollinator groups
- Reveal the socioeconomic and environmental influences on beekeeping decisions that affect crop pollination services
- Evaluate the efficacy of mitigation measures (eg agri-environment schemes) on crop and wild plant productivity

Individual behavioral changes resulting from combined field-level exposure to a neonicotinoid and pyrethroid insecticides both reduced bumblebee colony productivity and increased the chances of colony failure (Gill *et al.* 2012). Integrated pest management approaches aim to maximize toxicity to diseases and parasites of humans, animals, and plants by combining different biological control agents (eg pathogens) with judicious doses of chemical insecticides. It would be surprising if beneficial insects were not similarly vulnerable to the combined effects of different mortality agents. For instance, the collective foraging, processing, and storage of food by the social honey bee (*Apis mellifera*) leads to the accumulation of agricultural pesticides, in addition to the acaricides used by beekeepers to combat parasitic mites in the hive (Johnson *et al.* 2009; Mullin *et al.* 2010). Managed honey bees are thus chronically exposed to a cocktail of different chemicals that can subtly interact, sometimes synergistically, with detrimental effects on bee survival, learning, and navigation behaviors (Johnson *et al.* 2009; Cresswell 2011; Henry *et al.* 2012).

Climate change

Plant and pollinator ranges are shifting, causing changes in pollinator populations that inhabit the edges of their species' climatic range, so that they become more susceptible to population declines and even extinction as a result of climate change (Figure 1b; Williams and Osborne 2009; Forister *et al.* 2010). Differential migration rates of co-occurring plants and insects as a result of changing climatic conditions (Schweiger *et al.* 2008) may lead to a spatial dislocation of processes like pollination. As well as affecting distributions, climate change may alter the synchrony between plant flowering and pollinator flight periods. Phenological mismatches probably contribute to pollinator losses that subsequently disrupt pollination of plants that flower later in the season (Pleasants 1980; Memmott *et al.* 2007; Burkle *et al.* 2013). This affects specialist pollinators most severely but may also reduce the breadth of diet among generalists (Warren *et al.* 2001; Memmott *et al.* 2007). For example, climate change could curtail the bumblebee foraging season by reducing the availability of early- or late-season forage for queens establishing colonies (Memmott *et al.* 2010). However, where evolutionary histories have produced robust or flexible species, plant–pollinator interactions may persist during – or even benefit from – new climate regimes (Rafferty and Ives 2010; Stelzer *et al.* 2010).

Alien species

Non-native plant species may co-opt pollinators and come to dominate plant–pollinator interactions by providing abundant foods for those pollinators that are pre-adapted to exploit them (Kleijn and Raemakers 2008; Pyšek *et al.* 2011). Depending on the overlap in flower phenology, alien plants may compete for (Dietzsch *et al.* 2011) or facilitate (McKinney and Goodell 2011) native plant pollination (Figure 1c). While there is little available evidence that alien plants are detrimental to pollinator diversity (Moron *et al.* 2009), the community-level consequences are relatively unknown. However, alien pollinators – introduced accidentally or for agricultural purposes – can disrupt native pollinator communities by outcompeting indigenous insects for resources or by spreading pests and disease (Figure 1j; Aizen and Feinsinger 1994; Le Conte *et al.* 2010; Singh *et al.* 2010).

Pests and pathogens

Mortality due to pests and pathogens (Figure 1d) dominates explanations of honey bee decline in the developed world. The *Varroa destructor* mite is the primary vector of many viruses (*Picornavirales*) implicated in honey bee colony losses (Le Conte *et al.* 2010). By feeding on bee hemolymph, *V destructor* suppresses host immunity and increases host virus load (Yang and Cox-Foster 2005; Highfield *et al.* 2009). Co-infection with a diverse array of pathogens (viruses, bacteria, microsporidians) is the rule rather than the exception (eg Runckel *et al.* 2011), potentially explaining the difficulty in identifying a single agent behind honey bee losses (Le Conte *et al.* 2010; Potts *et al.* 2010a). Furthermore, pathogens associated with colony mortality vary spatially (Higes *et al.* 2008; Highfield *et al.* 2009; Runckel *et al.* 2011). Multiple co-infections over time and space, interacting in complex, non-linear ways, are likely the root cause of pathogen-induced honey bee losses.

Many pests and pathogens also spread within and between populations of wild and managed bee species, and perhaps other pollinating insects as well (Singh *et al.* 2010; Cameron *et al.* 2011; Core *et al.* 2012). Pathogen-associated declines of generalist bumblebee species

(Cameron *et al.* 2011) increase the potential for pollination-network collapse, with serious ecosystem consequences (Kaiser-Bunbury *et al.* 2010) that may be exacerbated by intensified land use and climate change.

Interacting pressures on pollinators

There is no single, overriding cause of pollinator declines. Land-use intensification (and its concomitant impacts) and disease have long driven pollinator losses. Globalization and climate change may extend these impacts to developing regions, increasing the translocation of plants, pollinators, pests, and pathogens worldwide. The interplay between these different pressures is also likely contributing to pollinator declines. Hitherto, our understanding of these multiple impacts was mainly based on the combined effects of malnutrition, disease, and pesticides on honey bee physiology, but it is crucial that wild pollinator responses to multiple pressures are also investigated. Using four examples, we highlight the current understanding of how different pressures can interact to affect pollinators.

(1) Climate change and habitat fragmentation

Pollinators currently at the limits of their climatic range may, under climate change and where suitable habitat is available, colonize new regions, thereby increasing the abundance and diversity of recipient communities (Warren *et al.* 2001; Forister *et al.* 2010). However, compensatory species migration as a result of climate change might be inhibited by habitat loss and fragmentation (Figure 1i; Williams and Osborne 2009). In general, low connectivity between habitat remnants is likely to reduce population sizes and increase extinction likelihoods of pollinators that are poor dispersers or habitat specialists (Warren *et al.* 2001). Pollinator communities might therefore become progressively species-poor and dominated by mobile, habitat generalists. Recent evidence suggests that continuing land-use intensification (Forister *et al.* 2010), combined with stochastic events or disease (Cameron *et al.* 2011), may eliminate even these generalists. In addition, climate-driven changes in pollinator food availability (Memmott *et al.* 2010) may interact with diminishing nutritional resources (Kleijn and Raemakers 2008) in intensively managed landscapes to further stress pollinators.

(2) Nutrition and pathogens

Global land-use changes have led to declining diversity and abundance of flowering plants and the foods they provide to pollinators (Biesmeijer *et al.* 2006; Kleijn and Raemakers 2008). This has potentially damaging consequences, as pollinators require an optimum nutrient balance to support their growth and reproduction. Nutritional regulation in worker honey bees is biased toward carbohydrates (Altaye *et al.* 2010), but we do not know how bees – and other pollinators – balance their nutrition by foraging on different nectar and pollen sources. Furthermore, parasite and pathogen infections increase metabolic demands for specific nutrients; for instance, worker honey bees infected with the gut parasite *Nosema ceranae* increase their daily carbohydrate intake (Mayack and Naug 2009). Poor nutrition reduces honey bee immunity (Alaux *et al.* 2010b), so loss of food sources will increase individuals' vulnerability to infection (Figure 1e) and the effects will be amplified at colony or population scales.

(3) Nutrition and pesticides

The molecular mechanism (ie cytochrome P450 enzymes) by which honey bees can detoxify certain acaricides (eg tau-fluvalinate, coumaphos used for *Varroa* control) known to reduce bee survival has recently been reported (Johnson *et al.* 2009; Mao *et al.* 2011). These enzymes evolved to break down dietary plant chemicals (flavonoids) and the number of P450 enzymes is increased by feeding bees some of the chemical constituents of honey (Mao *et al.* 2011). As these biochemical mechanisms appear to be sensitive to variations in diet, changes in beekeeping practices or land-use management that affect bee nutrition have the potential to reduce or enhance the honey bees' ability to detoxify pesticides.

(4) Pesticides and pathogens

The combined impacts of pathogens and pesticides (Figure 1e) have physiological implications for bee health at both individual and colony levels. Recent laboratory studies have shown increased worker honey bee mortality and energetic stress due to the additive and synergistic interactions between *N ceranae* infection and sublethal doses of a neonicotinoid (Alaux *et al.* 2010a; Vidau *et al.* 2011) or phenylpyrazole pesticide (Vidau *et al.* 2011). The neonicotinoid–*N ceranae* interaction also reduces the activity of an enzyme used by worker bees to sterilize colony food stores and broods and to combat pathogen transmission (Alaux *et al.* 2010a). This potential for negative effects to cascade from individuals through the colony was confirmed by studies demonstrating that previous exposure to sublethal doses of neonicotinoid led to higher *N ceranae* infection levels (Pettis *et al.* 2012). Such findings illustrate the importance of studying impacts across levels of biological organization to obtain insight into pollinator losses.

Integrated research across biological scales

Looking ahead, an urgent research challenge will be to establish how multiple pressures affect pollinators and pollination under continuing environmental change. This requires a research approach that integrates work across biological scales, interdisciplinarity, and the use of model species, similar to the systems-biology approaches

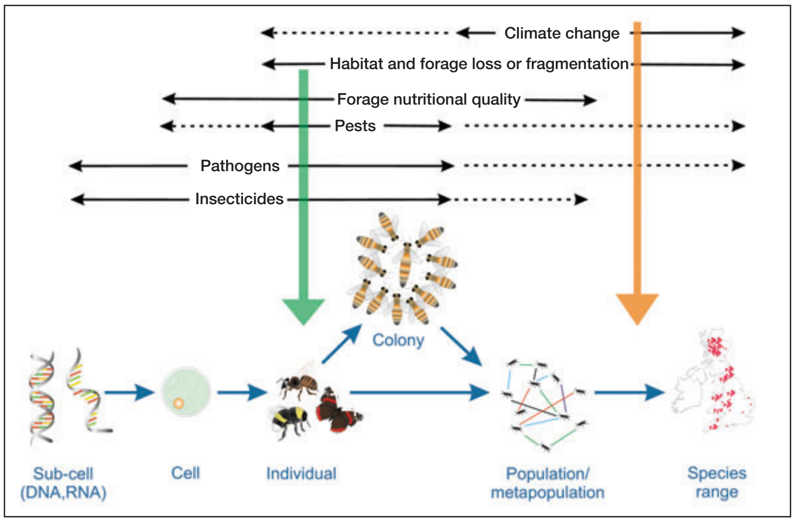

Figure 2. *The impact of multiple pressures (black text) on pollinator species across levels of biological organization (blue text). Black arrows span the levels at which each stressor has direct (solid) and indirect (dotted) effects. Vertical arrows show the most practical scale at which to study interactions between pressures. Green arrow = pesticide–pathogen–nutrition interactions at individual or colony scales; orange arrow = climate change–habitat interactions at population or species scale.*

used to tackle human diseases (eg Marino *et al.* 2011), enabling the emergent properties of complex biological systems to be uncovered.

Investigation across the full range of biological scales will improve our understanding of how various pressures interact to affect pollinators (Figure 2). Scientists need to determine the molecular, physiological, and ecological mechanisms by which combined pathogen–pesticide–nutritional challenges influence pollinator health and, ultimately, population size (Moritz *et al.* 2010). For honey bees, deleterious impacts may stem from subcellular-level (eg neurological damage, decreased detoxification abilities, immunological deficiencies) and insect-level (eg exposure during feeding, malnutrition) effects that become amplified at the colony level through alterations in social behavior, communication, and hive hygiene, or antisepsis (Figure 3). Building on such honey bee research, it is essential to investigate how pathogen–toxin–nutrition impacts affect different pollinator populations and species and how these impacts affect [meta]community dynamics in different landscapes and land-use situations (Figure 3). Finally, we need to know how pollinator populations and communities will respond to direct (eg temperature) and indirect (eg plant and insect dispersal) climate-change effects. Integrating new understanding of the interactions between pathogens, toxins, and nutrition across levels of biological organization and ecological processes up to global scales (Figure 2) will better inform models that will enable the prediction of changes in pollination services under different scenarios.

Interdisciplinarity is central to working across biological scales. For instance, recent collaborations between ecologists, geneticists, and mathematicians have advanced our knowledge of the impacts of landscape structure on bumblebee foraging and dispersal (Carvell *et al.* 2012). This new knowledge could be refined by the addition of data on the nutritional value of mass-flowering crops (Westphal *et al.* 2003), flower margins sown as part of agri-environment schemes (Memmott *et al.* 2010), and alien (and horticultural) plants (Stelzer *et al.* 2010; Dietzsch *et al.* 2011), thereby helping us to understand their potential to alleviate pollinator stress in intensively farmed landscapes. Neurologists, physiologists, ecologists, and mathematical modelers need to collaborate in an investigation of how nutrient availability and quality interacts with pollinator movements in influencing vulnerability to diseases or pesticides.

Such biological findings then need to be coupled with information on how socioeconomic drivers of land-use change affect resource fragmentation and the dynamics of pollination services (eg www.ceh.ac.uk/farmcat/index.html). Such a systems approach, incorporating natural and socioeconomic sciences, will improve our understanding of the drivers of pollinator declines.

The use of model insect pollinator species, such as the honey bee, will help to elucidate these mechanisms in laboratory and field settings, and reveal whether combinations of pressures result in abrupt, non-linear impacts (eg tipping points) on bee health or abundance. For instance, a better understanding of how *V destructor* alters honey bee gene expression to reduce immunity (Yang and Cox-Foster 2005) will aid in the exploration of immune responses to different pathogens (Alaux *et al.* 2010b), thereby revealing molecular mechanisms of disease resistance and their modulation by malnutrition and pesticides (Figure 3; Mao *et al.* 2011). The honey bee is a suitable experimental species because it can be manipulated at many biological scales and its genome has been mapped (http://hymenopteragenome.org/). However, this eusocial insect is unlike most wild pollinators, so there is an urgent need to develop molecular tools (eg genomic and transcriptomic resources) for other pollinators (eg *Bombus* spp, *Megachile* spp, and *Osmia* spp; Moritz *et al.* 2010). This will facilitate answering community-level questions, such as which pollinator species harbor which pests and pathogens (Singh *et al.* 2010; Runckel *et al.* 2011; Core *et al.* 2012), and which share gene expressions and biochemical responses to particular pathogens and environmental toxins.

Perspectives for decision making

Despite the aforementioned knowledge gaps, the pressure on pollinators can be reduced by promoting knowledge exchange, improving landscape management, reducing pesticide impacts, and combating diseases.

Knowledge exchange

Changes in policies and practices aimed at slowing or even halting pollinator losses will require information and data acquired from professional and citizen-science initiatives worldwide (WebTable 1) to be exchanged through closer collaboration between scientists, conservationists, farmers, industry, and governments (Moritz *et al.* 2010; Dicks *et al.* 2012).

Landscape management

Habitat creation and restoration for pollinators will lessen the combined impacts of agricultural intensification, climate change, and – to some extent – pesticides and pathogens. The challenge, during strategic planning at the landscape level, will be to devise appropriate incentives for land managers to engage with one another to ensure an effective spatial and temporal network of food and nest sites for pollinators. Landscapers working in urban areas should include initiatives for "re-wilding" green spaces and promoting wildlife-friendly gardening and beekeeping to better support pollinators (Stelzer *et al.* 2010). Effective networks of food and nest habitat must account for differences in mobility among pollinators (Lepais *et al.* 2010; Rader *et al.* 2011; Carvell *et al.* 2012) while providing a diversity of food sources in time and space (Pleasants 1980; Memmott *et al.* 2010). Aiding species dispersal with habitat networks and sowing flowering plants to minimize temporal and spatial gaps in pollinator sustenance will also lessen the impacts of climate change (Warren *et al.* 2001; Memmott *et al.* 2010). Enhancement of pollinator nutrition will help buffer populations against the combined detrimental effects of nutritional stress, pathogen infection, and pesticide exposure (Mayack and Naug 2009; Alaux *et al.* 2010b; Mao *et al.* 2011).

Pesticide risks

Although designed to minimize lethal impacts on honey bees, pesticide application guidelines provide less protection to wild pollinators with different physiologies, behaviors, and phenologies (Scott-Dupree *et al.* 2009). To avoid non-target and multiplicative impacts, pesticide risk assessment protocols must incorporate a greater range of pollinator taxa (Scott-Dupree *et al.* 2009; Brittain *et al.* 2010; Gill *et al.* 2012) and methods (eg bee learning and behavioral assays) to assess sublethal interactions with other stressors, such as nutrition and pathogens.

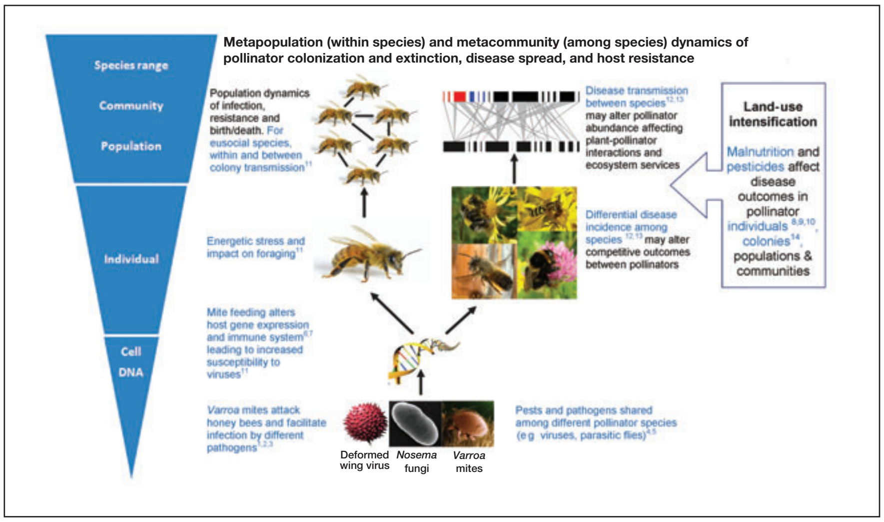

Figure 3. *Interactions between pests and pathogens, malnutrition, and pesticide exposure affecting pollinators across levels of biological organization; blue text indicates where some knowledge is available, and black text indicates knowledge gaps. See WebReferences for associated citations (indicated by superscripts).*

Disease management on multiple fronts

Mitigation of disease impacts on bees will require an integrated understanding of host–pathogen interactions and the role of vectors and alternative hosts (wild bees and other pollinators) in disease epidemiology. Surveillance programs of beekeeping operations remain crucial for combating disease spread and outbreaks that result from the movement of colonies and their products (Moritz *et al.* 2010). Interventions such as improved bee husbandry (eg nutritional supplements) and innovative disease treatments (eg inoculation of bees with lactic-acid bacteria that inhibit gut pathogens or molecular technology, such as RNA interference, to treat virus infection) could help limit pest and pathogen virulence (Moritz *et al.* 2010). Targeted use of other bee species (eg *Bombus* spp, *Megachile* spp, *Osmia* spp) for crop pollination services will reduce agricultural dependence on honey bees and thus minimize the risk of disease outbreaks compromising the ecosystem services that bees deliver (Kearns *et al.* 1998).

■ Conclusions

Multiple pressures that interact with biological processes at scales from genes to ecosystems threaten pollinator health, abundance, and diversity. Implementation of the practical steps described above, backed by interdisciplinary research, is necessary to limit the negative consequences of ongoing pollinator declines for ecological function, agricultural production, and human health.

Evidence on the multiple threats to pollinators must be included in joint decision making by government agencies, non-governmental organizations, and agrichemical, food production, and retail industries. This is achievable (see Dicks *et al.* 2012) and vital as we move toward integrated approaches to landscape management, which balance provisioning (eg food and timber supply) and other ecosystem services (eg pollination, pest regulation, water purification) to improve sustainable resource security.

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