

Global pollinator declines: trends, impacts and drivers

Simon G. Potts¹, Jacobus C. Biesmeijer², Claire Kremen³, Peter Neumann⁴, Oliver Schweiger⁵ and William E. Kunin²

¹ Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, Reading, UK, RG6 6AR

² Earth and Biosphere Institute and Institute of Integrative and Comparative Biology, University of Leeds, Leeds, UK, LS2 9JT

³ Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3114, USA

⁴ Swiss Bee Research Centre, Agroscope Liebefeld-Posieux, Research Station ALP, Schwarzenburgstrasse 161, CH-3003 Bern, Switzerland

⁵ Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Theodor-Lieser-Strasse 4, 06120 Halle, Germany

Pollinators are a key component of global biodiversity, providing vital ecosystem services to crops and wild plants. There is clear evidence of recent declines in both wild and domesticated pollinators, and parallel declines in the plants that rely upon them. Here we describe the nature and extent of reported declines, and review the potential drivers of pollinator loss, including habitat loss and fragmentation, agrochemicals, pathogens, alien species, climate change and the interactions between them. Pollinator declines can result in loss of pollination services which have important negative ecological and economic impacts that could significantly affect the maintenance of wild plant diversity, wider ecosystem stability, crop production, food security and human welfare.

Importance of pollinator declines

Pollinators play an important functional role in most terrestrial ecosystems and represent a key ecosystem service that is vital to the maintenance of both wild plant communities [1,2] and agricultural productivity [3,4]. Insects, particularly bees, are the primary pollinators of most agricultural crops and wild plants and so our review will focus on insects. Pollination services depend on both domesticated and wild pollinator populations, both of which might be affected by a range of recent and projected environmental changes, such as habitat loss and climate change, with unknown consequences for pollination service delivery. Growing concern about the fate of both domesticated and wild pollinators has resulted in the establishment of special initiatives by the Convention on Biological Diversity (International Pollinator Initiative, <http://www.cbd.int/decision/cop/?id=7147>) and several continental, national and regional programmes to tackle the issues of pollinator declines.

However, whether substantial evidence exists for widespread declines and negative impacts on pollination services was recently questioned [5], although since then published literature on the subject has greatly expanded. Here we review our current understanding of the status and trends of pollinators, and how pollinator declines and

associated loss of pollination services impact floral biodiversity and human livelihoods. We assemble and appraise a diverse set of studies addressing the question of what are the actual drivers of observed pollinator declines and what are the consequences. Finally, we identify the most important future research directions.

Current status and trends of pollinators

Globally, the pollinator that is predominantly managed to enhance agricultural production is the honey bee (*Apis mellifera*), although other species of bee are used in specialist contexts (e.g. the leafcutter bee *Megachile rotundata*) [6]. The honey bee, which has been well studied compared to other bee species, has been documented to be capable of increasing yield in 96% of animal-pollinated crops (Appendix 1 and 2 in [3]). The honey bee also provides pollination services to many wild plants, but the amount they contribute is not always well supported by empirical data, and the contribution of wild pollinators might be higher than previously acknowledged [3]. There is clear evidence for severe regional declines in domestic honey bee stocks in the USA (59% loss of colonies between 1947 and 2005, [6,7]) and Europe (25% loss of colonies in central Europe between 1985 and 2005, [8]) making the dependence of agricultural crops, and possibly wild plants, on a single species worrisome. Substantial concerns have been raised about the future availability of honeybee pollination services. Indeed, owing to the ectoparasitic mite *Varroa destructor*, an invasive species from Asia [9], most wild and feral honey bee colonies in Europe and the USA have vanished, leaving only those kept by beekeepers [10–12]. Unfortunately, in recent decades beekeeping has been an industry in decline in the USA [6,7] and most European countries [8]. Despite these regional losses, worldwide the number of honey bee hives have increased by ~45% since 1961, however, the proportion of agricultural crops depending on pollinators is increasing much more rapidly (>300%) so that the demand for pollination services could outstrip the increase in hive numbers [13].

Honey bee population shifts are poorly documented, but even less is known about recent changes in wild pollinator populations and communities. Until recently there was

Corresponding author: Potts, S.G. (s.g.potts@reading.ac.uk).

Box 1. Declines in wild bees and hoverflies in the UK and Holland

Biesmeijer and colleagues [18] analyzed species diversity change utilizing the accumulation of records in national entomological databases, collected largely by amateur naturalists from societies such as the Bees Wasps and Ants Recording Society in the UK (www.bwars.com) and the Netherlands Entomological Society. Although not representing systematic sampling programmes, these databases contain hundreds of thousands of carefully collected records. Rarefaction analysis was used to provide a robust measure of species diversity change despite uneven sampling effort. The results show that, in both countries, bee diversity has fallen significantly in most landscapes (pre- versus post-1980), whereas hoverfly diversity increased in the Netherlands, with a mixed response in the UK (Figure 1). Analyses of pollinator traits demonstrated that in bees and hoverflies, specialist (diet and/or habitat) and sedentary species tended to decline, whereas mobile generalists tended to thrive.

In addition, parallel losses were demonstrated in wild plant communities. In the UK, animal-pollinated plants have declined more (mean relative change according to UK plant atlas: -0.22) than self-pollinating (-0.003) and wind-pollinated species ($+0.18$). However, in the Netherlands, where bee diversity declines were accompanied by increased hoverfly richness, only bee-pollinated plants declined; plants pollinated by hoverflies and other pollinators have continued to thrive. The parallel dynamics between plants and their pollinators suggest a link between the two, although this is correlative and the mechanism is as yet unknown. It could be that plant declines are caused, in part, by a lack of pollination services, or bees could be declining owing to a lack of floral resources, or indeed both could be declining owing to shared sensitivity to environmental changes.

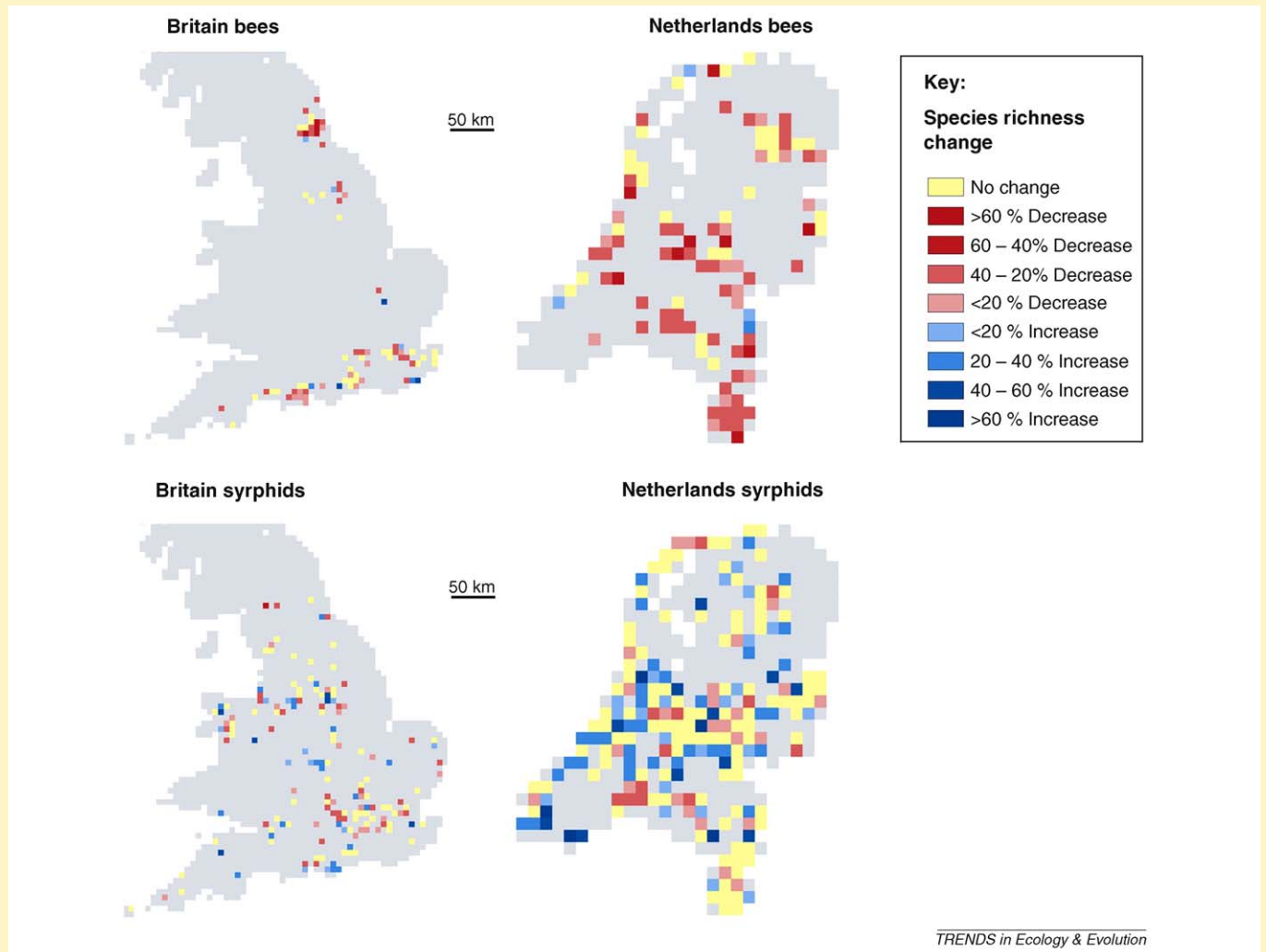


Figure 1. Changes in species richness since 1980 in 10×10 km grid cells for British bees (top left) and syrphids (top right) and Dutch bees (bottom left) and syrphids (bottom right). Data used are available from the Bees Wasps and Ants Recording Society (UK bees, www.bwars.com), the Hoverfly Recording Scheme (UK syrphids, www.hoverfly.org.uk) and the European Invertebrate Survey (Dutch data, www.eis-international.org/index.php). Bee diversity has overwhelmingly declined in landscapes of both countries. Hoverfly diversity has increased in many Dutch landscapes, whereas we find balanced increases and declines of British hoverfly species richness. Grey cells indicate cells with insufficient data for analysis. Adapted with permission from Ref. [18].

little firm evidence of geographically widespread declines for most groups [5]. Among bees, the best documented group are the bumblebees (*Bombus* sp.), which have shown evidence of an ongoing decline in diversity over much of Belgium and the UK [14,15]. For example, in the UK 6 of the 16 non-parasitic bumblebees have declined considerably (including *B. subterraneus* which has become extinct), 4 might be declining and 6 are stable or increasing [16].

With the exception of butterflies [17], data for other pollinators, including other bee species, are fragmentary because of the lack of coordinated monitoring programmes. Consequently, scientists have had to rely on data collected in less standardized ways to test for changes in the pollinator community, such as comparing recording frequencies between time periods or comparing species richness ([18], Box 1).

Indirect evidence of pollinator loss comes from studies of pollinator communities along gradients of agricultural intensification and habitat fragmentation as proxies for temporal change [6,19–21]. Quantitative syntheses of these local-scale studies suggest a widespread pattern of loss of pollinator richness and abundance as a result of agricultural intensification and habitat loss [4,21]. As most natural landscapes around the world have been anthropogenically modified, it is likely that pollinator abundance and richness has declined in many parts of the world. There is also evidence that pollinator losses are biased towards species with particular traits: for example, bumblebees with narrow pollen specialisation [22], and dietary and habitat specialists among pollinators in general [18]. Such biased extinctions raise concerns that important functional roles, such as long-distance pollen dispersal, will be lost, reducing the resilience of pollination services across species, time and space [20].

Ecological and economic consequences of pollinator declines

Pollinator loss will impact two broad groups of pollinator-dependent flowering plants: wild flowers and cultivated crops.

Impacts of pollinator declines on wild flower pollination

The decline in pollinator diversity and abundance can bring with it a decline in pollination services for wild plant populations, potentially affecting populations of animal-pollinated plants (and thus potentially further reducing floral resources for the pollinators). Most wild plant species (80%) are directly dependent on insect pollination for fruit and seed set, and many (62–73%) of the plant populations investigated showed pollination limitation, at least some of the time [1,23], although this may vary markedly between sites and seasons. Obligate outcrossing animal-pollinated plants are particularly vulnerable to declines in pollination services [2], and such species have generally declined in parallel with their pollinators (at least in Western Europe, [18]). Such correlative approaches should ideally be backed up by more mechanistic evidence, but there are few studies that have explored the consequences of pollen limitation on plant survival and plant community composition [24,25]. Although there might be many ways for short-term compensation for poor pollination (e.g. clonal propagation), this cannot compensate in the long-term for a chronic loss of pollination services [26]: in a meta-analysis of 54 studies (covering 89 plant species), the most frequent proximate cause of reproductive impairment of wild plant populations in fragmented habitats was pollination limitation [2].

Among animal-pollinated species, those with the most specialised pollination requirements might be expected to be most at risk, but there is little evidence of this [2]; it may be that the redundancy that is built in to most plant–pollinator networks can provide some buffering capacity against pollinator species losses. Usually, plant–pollinator interactions are asymmetric and generally nested [27], with a core set of generalist species having key roles and specialist pollinators often relying on generalist plants and specialist plants often relying on generalist pollinators [28]. Since generalist species are often less vulnerable to

change than specialist species [e.g. [18]18], they might partly sustain network structure under changed conditions. However, generalist species are still vulnerable. For example, local extinction of the supergeneralist honeybee as a result of disease is not unlikely and could lead to considerable species loss of plants [29]. Asymmetric and nested network patterns are widespread and largely independent of community composition, geographic location and other factors [27]; asymmetric networks are also suggested to have a high level of redundancy [29,30] making them relatively robust to the loss of species and interactions. However, ongoing global change affects not only species occurrences, but also species interactions and interaction pathways [25,31,32]. Thus, in the face of severe disturbance, plant–pollinator networks could also reach a tipping point and collapse despite their seemingly robust structure [29,30].

Impacts of pollinator declines on crop production

Insect pollination, mostly by bees, is necessary for 75% of all crops that are used directly for human food worldwide [3]. Although many of the highest volume crops (e.g. rice and wheat) are wind-pollinated [5], a large proportion of fruit crops (e.g. apple, melon and berry) are potentially vulnerable to declines in apiculture and wild pollinator stocks. The cultivation of pollinator-dependent crops steadily increased between 1961 and 2006 [33]. Although the average yield increase over time is no lower than for pollinator-independent crops [33], a more detailed analysis has revealed that a large proportion of this annual yield increase can be explained by the use of commercial pollinators (usually honey bees) or hand pollination (a relatively rare practice) [34]. Until now, most growers have either matched their pollinator needs by renting honey bees, or utilized the ‘free’ services of wild bee species foraging in farm fields, a component of pollination services that has largely been overlooked in economic calculations (but see [35]). Despite the importance of pollination for crop production, there is still a lack of basic information about how species diversity, and the abundance and community composition of pollinating insects, contributes to seed and fruit yield and quality in most crops [but see [36,37]36,37].

The global annual economic value of insect pollination was estimated to be €153 billion during 2005 (i.e. 9.5% of the total economic value of world agricultural output considering only crops that are used directly for human food (Box 2; [38]). Complete pollinator loss would translate into a production deficit over current consumption levels of -12% for fruits and -6% for vegetables [38]. Although this scenario is unrealistic, the purpose of such calculations is to demonstrate the relative importance of insect pollination as an important agricultural input. This calculation takes into account the fact that production of most crops is only partially reduced in the absence of insect pollinators, and a pollinator dependence ratio (compiled in Ref. [3]) was utilized to derive calculations of economic value [38]. Different crop varieties can have different yield responses to changes in animal pollination, but little information exists on these differences [3]. Accordingly, global economic calculations of the value of pollination services could change substantially if the true dependencies associated

Box 2. Economic value of pollination and vulnerability of global agriculture

Gallai *et al.* [38] estimate insect pollination economic value (IPEV) as a product of the proportional contribution of biotic pollination to production (dependence ratio from Ref. [3]) and the total economic value (EV) of the 100 most important commodity crops used for human food (2005 FAO crop database, <http://www.fao.org>), summed across crops. For all included crops, the global IPEV was estimated at €153 billion per annum, which is equivalent to 9.5% of the value of world agricultural production.

The IPEV:EV ratio provides a measure of the economic vulnerability of each crop to the loss of pollinators and was found to vary widely across crop categories. Globally, vulnerability was high for fruits (23%), vegetables (12%), nuts (31%), edible oil crops (16%) and stimulants (39%), lower for pulses (4%) and spices (3%) and 0% for cereals, roots and tubers and sugar crops (Table 2 in Ref. [38]). Whereas staple crops, being primarily wind-pollinated, have low vulnerabilities, those crops providing much of the proteins, vitamins and minerals in human diets are more reliant on biotic pollination. Vulnerability values were heterogeneous across the globe, with some regions more at risk of pollinator loss than were others (Table 1, adapted from Table 3 in Ref. [38]).

The reliance of Gallai *et al.* [38] on market data for determining pollination value has five caveats: (i) it assumes accurate pricing of crops by the market; (ii) it attributes the full value of crops to pollination processes, rather than utilizing the net value that subtracts the cost of other inputs; (iii) it does not capture crop varietal differences that alter yield responses to pollination services; (iv) it does not include subsistence farming where data for agricultural goods is never captured; and (v) it takes no account of other benefits provided by pollination services, such as contribution to non-timber forest products, indirect value of livestock reliant on pollination products, maintenance of wider ecosystem functions and aesthetic and cultural value [63]. Even though the analysis represents a situation in which all biotic pollination services are lost, there is no human adaptation, and the costs of other inputs are not accounted for (therefore providing an upper-bound impact assessment) this total value is still likely to be an underestimate if the values for (iv) and (v) were included.

Table 1. Geographical distribution of the economic value of insect pollination and crop vulnerability^a. Insect pollination economic value (IPEV) is the proportional contribution of biotic pollination to production multiplied by the total economic value (EV) of the 100 most important commodity crops, summed for all crops in a region. The ratio of IPEV to the EV indicates the economic vulnerability of crops to pollinator loss.

Geographical region (following FAO, http://www.fao.org)	Insect Pollination Economic Value (IPEV) in 10 ⁹ €	Vulnerability of region (IPEV/EV) ^b
Africa	11.9	8
Central Africa	0.7	7
East Africa	0.9	5
North Africa	4.2	11
South Africa	1.1	6
West Africa	5.0	10
Asia	89.4	10
Central Asia	1.7	14
East Asia	51.5	12
Middle East Asia	9.3	15
Oceania	1.3	7
South Asia	14.0	6
South East Asia	11.6	7
Europe	22.0	11
European Union (25 members)	14.2	10
Non EU	7.8	12
North America (Bermuda, Canada and USA)	14.4	11
South and Central America	15.1	6
Central America and Caribbean	3.5	7
South America	11.6	6

^aBased on data from Ref. [38].

^bMean vulnerability for region calculated as unweighted mean of vulnerability of sub-regions.

with each variety, and the area cultivated per variety, were accounted for.

Potential drivers of pollinator declines

There are many potential drivers that affect biodiversity in general and pollinator abundance and diversity in particular [6], and different environmental drivers rarely act in isolation [e.g. [39]39]. Interactive, non-additive effects, where one sub-lethal driver increases the severity of another driver, can help explain ongoing declines in wild and managed pollinators (Box 3; [17,31,40]). However, while awareness of the importance of interacting drivers is increasing [32], most studies have analysed the impacts of specific drivers in isolation, and therefore evidence of interactive effects is scant (but see [41]). Among the most important drivers are land-use change with the consequent loss and fragmentation of habitats [15,21,42,43]; increas-

ing pesticide application and environmental pollution [44,45]; decreased resource diversity [18]; alien species [46,47]; the spread of pathogens [48,49]; and climate change [50,51].

Land-use change: habitat loss, fragmentation, degradation and resource diversity

Habitat loss is generally thought to be the most important factor driving bee declines [52]. In a quantitative review (meta-analysis) of 54 studies on the effects of different types of disturbances on bee communities, Winfree *et al.* [21] found a significant, but relatively small, negative effect, of various types of disturbance on wild bee abundances and species richness, of which habitat loss and/or fragmentation was the most important contributor. Similarly, in a quantitative synthetic analysis of 23 studies of 17 crops in agricultural landscapes from around the globe,

Ricketts *et al.* [4] found a strongly significant negative effect of distance from natural habitat (due to habitat loss and/or conversion) on the richness and abundance of wild bees. In both quantitative reviews, no such effects were found on honey bees, which occurred as managed species in many of the studies considered. In summary, the bulk of evidence from quantitative synthesis supports the hypothesis that habitat loss reduces bee diversity and abundance.

Nonetheless, several studies demonstrate positive effects of urbanization or agriculture on selected bee guilds (e.g. cavity-nesters within urban areas, [53,54]) or bee abundance and richness [55]. Various factors might be responsible for a positive effect of habitat conversion, including intermediate levels of disturbance that promote availability of resources for pollinators across multiple partial habitats [53,56] and the introduction of novel foraging and/or nesting resources or micro-habitats [53,55]. In addition, because bees are highly mobile organisms adapted to using patchy resources, certain bee species can tolerate or benefit from a moderate level of disturbance [54], including moderate levels of habitat loss [21].

Habitat fragmentation is also postulated to negatively affect wild pollinator populations, but to date, relatively few studies exist on effects of fragmentation on pollination, *per se* (i.e. addressing habitat isolation effects independently of habitat area effects) [21,57,58]. Several studies have not found an effect of fragment area on overall community richness or abundance of bee pollinators, although they have detected differential responses among

tribes or guilds, with some favoured by increased native habitat, and others favored by increased (non-native) matrix area [53,58,59]. Other studies report declining species richness and abundance with decreased fragment size for bees [57] and butterflies [60]. As for the previous group of studies, results varied by guild, with stronger effects of fragmentation on richness and abundance for bees that were solitary, parasitic and/or collected specialized pollen resources (oligoleges) [57], and for butterflies that were monophagous [60]. The variance in response to fragmentation among studies and guilds within studies may relate to the quality of the matrix surrounding habitat fragments [61] and the dispersal abilities of pollinators [57]. An important outstanding question is whether there is a critical threshold of habitat area required to maintain viable bee populations? In the Cape Floral region, a study of pollination failure in an orchid, *Ptergodium catholicum*, suggested that habitats of 385 ha or less, when separated by an urban, but not a rural matrix, were too small to maintain populations of its sole bee pollinator, *Rediviva peringueyi* [62]. However, little additional information is available to answer this critical question since the rural matrix can both provide nesting and foraging resources for bees and facilitate movements between patches of natural or semi-natural habitat; it could be that urban landscapes that provide hard boundaries between habitat fragments will provide the best places for investigation [61,63].

Habitat degradation might affect bee species primarily by the loss of floral and nesting resources, and the introduction of insecticides with lethal or sub-lethal effects. To

Box 3. Multiple drivers of honey bee loss

Despite comprehensive research efforts on the recent major honey bee colony losses, no single driver has emerged as the definitive cause of the phenomenon [48,80]. Instead, interactions between multiple drivers are the most probable explanation for elevated overwintering mortality in honey bee colonies. At a global scale, most managed honey bee, *Apis mellifera*, colonies are infected by the ectoparasitic mite, *Varroa destructor* (with few exceptions (e.g. Australia, some isolated islands such as Fiji and Réunion, and possibly some central African countries such as the Democratic Republic of Congo [97]), facilitating the potential interaction between this driver and multiple potential drivers almost anywhere in the world. Moreover, many other prominent honey bee pathogens, such as *Nosema* spp. and several viruses, now have almost global distributions [97]. Therefore, multiple pathogen infections and interactions between pathogens and other the suspected drivers of honey bee loss are inevitable, at least in areas with established mite populations. Whereas the list of potential drivers is not new, the evidence of interactive effects, though limited, is important and growing. These interactions are particularly worrying as sub-lethal effects of one driver could make another driver more lethal.

Potential drivers can be grouped into pests and pathogens, environmental stressors (e.g. malnutrition, exposure to agrochemicals and apicultural mismanagement) and lack of genetic diversity and vitality [49]. As shown in Figure 1, Interactions can occur within each group (blue arrows), such as between agrochemicals ('Environmental stressors' arrow, [98]) or among honey bee pathogens ('Pests and pathogens' arrow, such as between *V. destructor* and viruses [99]), resulting in lethal effects for individual bees and whole colonies. Moreover, interactions might also occur between groups of drivers (green arrows). For example, a sub-lethal and chronic exposure to pesticides, that causes no harm to healthy colonies, might enhance pathogen replication by compromising the immune competence of individual honey bees, thereby resulting in lethal consequences for entire colonies already weakened by disease (arrow between

'Environmental stressors' and 'Pests and pathogens'). Likewise, a reduced genetic diversity may result in higher susceptibility to pathogens (arrow between 'Pests and Pathogens' and 'Genetic diversity and Vitality'). Although some drivers and a few of the interactions are at least partly understood (e.g. between *V. destructor* and viruses, [99]), most of these interactions remain poorly studied. Indeed, very little is known about the nature (additive vs. non-additive), mode of action (e.g. immune compromised) and the magnitude of these interactions in the field. In light of the similar life histories of many insect pollinators, it appears likely that the underlying interactions are similar for wild bees (except apicultural drivers). Therefore, a much better understanding of these interactions between multiple drivers would be essential if we are aiming for sustainable pollination.

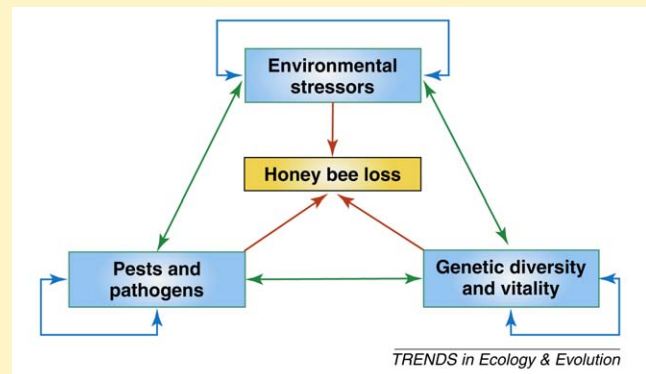


Figure 1. Interactions among multiple drivers of honeybee loss. Blue boxes represent the three main groups of drivers associated with honeybee loss; red arrows represent direct pressures on honeybees from drivers; green arrows represent interactions between drivers; and blue arrows represent interactions within drivers.

date, studies of drivers potentially leading to habitat degradation (grazing, fire, urbanization, agricultural intensification) are few, and findings from a recent meta-analysis did not find these disturbances to have an overall significant impact on bees, although this might simply reflect low statistical power [21]. However, we know that agricultural intensification has increased the use of agrochemicals, resulting in potential habitat degradation within agricultural areas. Insecticides can cause mortality by direct intoxication [64] and can result in local shifts in wild bee diversity and abundance [65], whereas herbicides and fertilisers can affect pollinators indirectly by decreasing floral resource availability [66,67]. Risk assessment procedures for pesticides usually only consider effects on honey bees even though the effects of pesticide exposure varies between pollinator taxa [68]. Sub-lethal effects of pesticides have been demonstrated [69] with implications for the longer term survival of populations. A comparison of fallow strips next to organic versus conventional wheat fields found that both adjacency to organic fields and the proportion of the landscape that was farmed organically significantly increased bee diversity and abundance [67]. In addition, the effects of agrochemicals might not be restricted to agricultural lands themselves because agrochemicals can drift into semi-natural habitats where pollinators nest and forage.

Plant biodiversity in most regions of the world has also undergone rapid change in recent decades. Where high-quality data sets have been compiled [70], local plant diversity appears to have declined in most sites and most habitats. These declines seem to have affected obligately outcrossing animal-pollinated plant populations in particular as they rely entirely on insect pollen vectors [18], suggesting a general decline in floral resources for pollinators. Indeed, in the UK, there is evidence that 76% of forage plants used by bumblebees declined in frequency between 1978 and 1998 [71]. Recent research has begun linking these floral shifts to pollinator dynamics, both in controlled experiments [24] and in the field [22,71]. If wild floral resources have decreased, the planting of mass-flowering crops such as oilseed rape and sunflowers could provide valuable resources for pollinators [72]. However, such superabundant resources are only available for brief periods of time and as a consequence they might have little effect in sustaining viable pollinator populations [63].

Introduction of alien species: plants, pollinators, pests and pathogens

There is empirical evidence that entomophilous alien plants are readily integrated into native plant–pollinator networks, and can act as additional pollen and nectar sources [47]. In this case alien plants can buffer against potential shortages in nectar (and pollen) supply under environmental change [41]. For instance, the alien plant *Impatiens glandulifera* facilitated the survival of native bumblebees when native nectar sources were scarce [22]. Therefore, alien plants with showy floral displays and/or large rewards decrease the dependence of native bees on native plants. In Europe, a significant proportion of entomophilous alien plants are ornamentals with long flower-

ing seasons, appealing scent or showy flowers [73] and so facilitate interactions with native bees. However, the positive effects of alien plants might be limited to generalist pollinators, and indirect effects can disrupt native plant–pollinator interactions. For instance, competitive displacement of the preferred hosts of native pollinators can lead to declines in native pollinator populations, particularly specialist species [74].

Introduction of managed pollinators for crop pollination and honey production can impact on native pollinators [46] through competition for resources or direct interaction. A high level of overlap in plant use (up to 90%) was reported for alien *Apis mellifera* and native *Bombus* species in the USA, [46] and up to 70% overlap for alien *Bombus terrestris* and native *Bombus* species in Japan, [75], indicating high potential for competition. However, it still remains controversial whether competition actually occurs and impacts native pollinator population viability [47]. Whereas several studies show no support for negative effects of domesticated alien pollinators [76,77], others report impacts on reproductive success and body size [46,78]. Alien pollinators can also have negative effects through genetic dilution, for instance, sub-species of managed honey bees and several bumblebees can interbreed with endemic populations, thereby eroding genetic diversity of native populations or even leading to the extinction of local sub-species [79].

There is good evidence that translocated alien bees can increase the risk of pathogen spread [47], including further spread of the ubiquitous *Varroa* mite into new areas such as Hawaii. Infection of colonies by multiple pathogens, and the resultant interactions between pathogens and other environmental stressors, is proposed as one of the reasons for the recently observed honeybee colony collapse disorder [48,80,81], a phenomenon which the authors expect new studies to support. Climate change can affect the spread and virulence of pests and pathogens [31,41], whereas other factors such as land-use change, pesticide load, or decreased resource availability might increase bee susceptibility to pests and pathogens or *vice versa* (see Box 3).

Although little is known about the potential for inter- and intra-specific transfer of pathogens in bee communities, there is evidence that the extent and role of host shifts and shared pathogens has been underestimated [82]. This is particularly true for honey bee viruses, including the widespread deformed wing virus [83], which is able to replicate within its mite vector [84]. Honey bee viruses can invade multiple host species [85] and are thus likely to infect non-*Apis* wild bees and wild bee viruses may be able to infect honey bees. Indeed, preliminary data suggest that the virulence of deformed wing virus might be higher in bumblebees than in its original host, honey bees [86]. Non-native domestic bees can also act as dispersal vectors for parasites and associated diseases, leading to the infection of congeners (e.g. *Varroa* mites in *Apis*, *Nosema* spp. in *Bombus* and *Ascospaera apis* fungus in *Megachile* [87]). Whereas the introduction of pest species (e.g. small hive beetle, *Aethina tumida*) and various pathogenic viruses have been shown to pose significant threats to feral and managed honey bees [88], their effects on wild native

pollinators remain unknown. There is, however, evidence suggesting a host shift of *A. tumida* in the USA to commercial bumblebee colonies [89].

Climate change

Most evidence for climate change impacts on pollinators comes from butterflies, though studies on other pollinators remain scant. Recent climate change has already affected butterfly distributions [90], and future changes, which are predicted to be greater in extent than recent historical changes, are likely to have even more severe impacts [17]. These patterns are consistent with the few studies on bees; Williams *et al.* [50] found a relationship between climatic niche and declines in British bumblebees, whereas Dormann *et al.* [51] projected general declines in future bee species richness in Europe. Such impacts of climate change occur at all organisational levels from the individual level (e.g. changing the temporal activity of bees [91]), through population genetics (e.g. evolutionary change in butterflies [94]), species level shifts (e.g. changes in phenology [92], bumblebee declines due to narrower climatic niches [50], or local or regional extinction of butterfly species [93,94]), to the community level (e.g. changing composition and functioning of pollinator communities [95]). In addition to such direct impacts, indirect effects, when climate change affects interacting species, might be equally important but is poorly studied. Climate change-induced mismatches in temporal [92] and spatial co-occurrence [96], and morphological and physiological interdependencies of differently responding animal-pollinated plants and pollinators can potentially disrupt their interactions [95].

Multiple drivers and pressures

The drivers described above act simultaneously and could act synergistically on pollinator communities [32]. Based on theoretical considerations and supported by evidence from a broad range of organisms, including pollinators such as butterflies, Didham *et al.* [39] conclude that non-additive effects of multiple drivers and pressures can be particularly important. However, most studies to date addressing effects of multiple drivers have been relatively limited in scope. The potential for interacting effects requires that multiple drivers be simultaneously considered if we are to understand how pollinators and animal-pollinated plants will respond to global change [32,95,96]. One of the few insights into the interacting effects of multiple pressures is for domesticated honey bees (Box 3).

Conclusion and future directions

Growing evidence points to substantial losses of pollinators in many regions of the globe, with the strongest evidence coming from Europe and North America. Further studies on other continents are needed to map the ubiquity of the phenomenon. The integration of existing national and local monitoring schemes and the establishment of a global programme could yield important data to help direct policy decisions regarding pollinators. Threats to pollinators are diverse, and might interact; the current challenge is to better quantify the relative importance of a range of drivers and in particular their synergistic effects. With con-

tinued pressure from known drivers such as habitat loss and pathogens, coupled with the clear ecological and economic risks associated with pollinator loss, there is a continued need to improve our understanding of the nature, causes and consequences of declines in pollinator services at local, national, continental and global scales. Given the weight of evidence of pollinator loss and associated risks, investment in developing mitigation options such as agri-environment schemes, protected area networks and alternative managed pollinators is essential to ensure sustainable pollination services in a changing world.

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References

- Ashman, T.L. *et al.* (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85, 2408–2421
- Aguilar, R. *et al.* (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.* 9, 968–980
- Klein, A.M. *et al.* (2007) Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. London B. Biol. Sci.* 274, 303–313
- Ricketts, T.H. *et al.* (2008) Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* 11, 499–515
- Ghazoul, J. (2005) Buzziness as usual? Questioning the global pollination crisis. *Trends Ecol. Evol.* 20, 367–373
- Natural Research Council (2006) *Status of Pollinators in North America*, National Academic Press
- vanEngelsdorp, D. *et al.* (2008) A survey of honey bee colony losses in the U.S., Fall 2007 to Spring 2008. *PLoS ONE* 3, e4071. DOI:10.1371/journal.pone.0004071
- Potts, S.G. *et al.* (2010) Declines of managed honeybees and beekeepers in Europe? *J. Apic. Res.* 49, 15–22
- Sammataro, D. *et al.* (2000) Parasitic mites of honey bees: life history, implications, and impact. *Annu. Rev. Entomol.* 45, 519–548
- Kraus, B. and Page, R.E. (1995) Effect of *Varroa jacobsoni* (Mesostigmata: Varroidae) on feral *Apis mellifera* (Hymenoptera: Apidae) in California. *Environ. Entomol.* 24, 1473–1480
- Moritz, R.F.A. *et al.* (2007) The size of wild honeybee populations (*Apis mellifera*) and its implications for the conservation of honeybees. *J. Insect Conserv.* 11, 391–397
- Jaffée, R. *et al.* (2010) Estimating the density of honeybee colonies across their natural range to fill the gap in pollinator decline censuses. *Conserv. Biol.* 24, 583–593
- Aizen, M.A. and Harder, L.D. (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Curr. Biol.* 19, 1–4
- Rasmont, P. and Mersch, P. (1988) Première estimation de la derive faunique chez les bourdons de la Belgique (Hymenoptera, Apidae). *Ann. Soc. R. Zool. Belg* 118, 141–147
- Goulson, D. *et al.* (2008) Decline and conservation of bumble bees. *Annu. Rev. Entomol.* 53, 191–208
- Williams, P.H. and Osborne, J.L. (2009) Bumblebee vulnerability and conservation world-wide. *Apidologie* 40, 367–387
- Settele, J. *et al.* (2008). Climatic risk atlas of European butterflies. *BioRisk* 1, 1–710, DOI:10.3897/biorisk.1

- 18 Biesmeijer, J.C. *et al.* (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313, 351–354
- 19 Kremen, C. *et al.* (2002) Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. U. S. A.* 99, 16812–16816
- 20 Larsen, T.H. *et al.* (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol. Lett.* 8, 538–547
- 21 Winfree, R. *et al.* (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90, 2068–2076
- 22 Kleijn, D. and Raemakers, I. (2008) A retrospective analysis of pollen host plant use by stable and declining bumblebee species. *Ecology* 89, 1811–1823
- 23 Burd, M. (1994) Bateman principle and reproduction—the role of pollen limitation in fruit and seed set. *Bot. Rev.* 60, 83–139
- 24 Fontaine, C. *et al.* (2006) Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biol.* 4, e1 DOI:10.1371/journal.pbio.0040001
- 25 Hegland, S.J. and Totland, Ø. (2008) Is the magnitude of pollen limitation in a plant community affected by pollinator visitation and plant species specialisation levels? *Oikos* 117, 883–891
- 26 Bond, W.J. (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Proc. R. Soc. Lond. B Biol. Sci.* 344, 83–90
- 27 Bascompte, J. *et al.* (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433
- 28 Bascompte, J. *et al.* (2003) The nested assembly of plant animal mutualistic networks. *Proc. Natl. Acad. Sci. U. S. A.* 100, 9383–9387
- 29 Memmott, J. *et al.* (2004) Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B Biol. Sci.* 271, 2605–2611
- 30 Fortuna, M.A. and Bascompte, J. (2006) Habitat loss and the structure of plant–animal mutualistic networks. *Ecol. Lett.* 9, 278–283
- 31 Le Conte, Y. and Navajas, M. (2008) Climate change: impact on honey bee populations and diseases. *Rev. Sci. Tech. Off. Int. Epizoot.* 27, 499–510
- 32 Tylianakis, J.M. *et al.* (2008) Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363
- 33 Aizen, M.A. *et al.* (2008) Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Curr. Biol.* 18, 1–4
- 34 Garibaldi, L.A. *et al.* (2009) Pollinator shortage and global crop yield - Looking at the whole spectrum of pollinator dependency. *Commun. Integr. Biol.* 2, 37–39
- 35 Losey, J.E. and Vaughan, M. (2006) The economic value of ecological services provided by Insects. *BioScience* 311–323
- 36 Hoehn, P. *et al.* (2008) Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. Lond. B Biol. Sci.* 275, 2283–2291
- 37 Winfree, R. and Kremen, C. (2009) Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc. R. Soc. Lond. B Biol. Sci.* 276, 229–237
- 38 Gallai, N. *et al.* (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* 68, 810–821
- 39 Didham, R.K. *et al.* (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* 22, 489–496
- 40 Oldroyd, B.P. (2007) What's killing American honey bees? *Plos Biol.* 5, 1195–1199
- 41 Schweiger, O. *et al.* Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biol. Rev.* DOI:10.1111/j.1469-185X.2010.00125.x
- 42 Steffan-Dewenter, I. *et al.* (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432
- 43 Hendrickx, F. *et al.* (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J. Appl. Ecol.* 44, 340–351
- 44 Kevan, P.G. *et al.* (1997) Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystemic health: pesticide stress on pollinators on blueberry heaths. *J. Appl. Ecol.* 34, 1122–1136
- 45 Rortais, A. *et al.* (2005) Modes of honeybees exposure to systemic insecticides: estimated amounts of contaminated pollen and nectar consumed by different categories of bees. *Apidologie* 36, 71–83
- 46 Thomson, D.M. (2006) Detecting the effects of introduced species: a case study of competition between. *Apis and Bombus*. *Oikos* 114, 407–418
- 47 Stout, J. and Morales, C.L. (2009) Ecological impacts of invasive alien species on bees. *Apidologie* 40, 388–409
- 48 Cox-Foster, D.L. *et al.* (2007) A metagenomic survey of microbes in honey bee colony collapse disorder. *Science* 318, 283–287
- 49 Neumann, P. and Carreck, C. (2010) Honey bee colony losses: a global perspective. *J. Apic. Res.* 49, 1–6
- 50 Williams, P.H. *et al.* (2007) Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biol. Conserv.* 138, 493–505
- 51 Dormann, C.F. *et al.* (2008) Prediction uncertainty of environmental change effects on temperate European biodiversity. *Ecol. Lett.* 11, 235–244
- 52 Brown, M.J.F. and Paxton, R.J. (2009) The conservation of bees: a global perspective. *Apidologie* 40, 410–416
- 53 Cane, J.H. *et al.* (2006) Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecol. Appl.* 16, 632–644
- 54 Carré, G. *et al.* (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agric. Ecosyst. Environ.* 133, 40–47
- 55 Winfree, R. *et al.* (2007) Effect of human disturbance on bee communities in a forested ecosystem. *Conserv. Biol.* 21, 213–223
- 56 Winfree, R. *et al.* (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J. Appl. Ecol.* 45, 793–802
- 57 Steffan-Dewenter, I. *et al.* (2006) Bee diversity and plant-pollinator interactions in fragmented landscapes. In *Specialization and Generalization in Plant-Pollinator Interactions* (Waser, N.M. and Ollerton, J., eds), pp. 387–410, University of Chicago Press
- 58 Brosi, B.J. *et al.* (2008) The effects of forest fragmentation on bee communities in tropical countryside. *J. Appl. Ecol.* 45, 773–783
- 59 Donaldson, J. *et al.* (2002) Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. *Conserv. Biol.* 16, 1267–1276
- 60 Tschamtké, T. *et al.* (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecol. Appl.* 12, 354–363
- 61 Westrich, P. (1996) Habitat requirements of central European bees and the problems of partial habitats. In *The Conservation of Bees* (Matheson, A., *et al.* eds), pp 1–16, Academic Press
- 62 Pauw, A. (2007) Collapse of a pollination web in small conservation areas. *Ecology* 88, 1759–1769
- 63 Kremen, C. *et al.* (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land use change. *Ecol. Lett.* 10, 219–314
- 64 Alston, D.G. *et al.* (2007) Effects of the insecticide Phosmet on solitary bee foraging and nesting in orchards of Capitol Reef National Park, Utah. *Environ. Entomol.* 36, 811–816
- 65 Brittain, C.A. *et al.* (2010) Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic Appl. Ecol.* 11, 106–115
- 66 Gabriel, D. and Tschamtké, T. (2007) Insect pollinated plants benefit from organic farming. *Agric. Ecosyst. Environ.* 118, 43–48
- 67 Holzschuh, A. *et al.* (2008) Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* 117, 354–361
- 68 Thompson, H.M. and Hunt, L.V. (1999) Extrapolating from honeybees to bumblebees in pesticide risk assessment. *Ecotoxicology* 8, 147–166
- 69 Morandin, L.A. *et al.* (2005) Lethal and sub-lethal effects of spinosad on bumble bees (*Bombus impatiens* Cresson). *Pest Manag. Sci.* 61, 619–626
- 70 Lavergne, S. *et al.* (2006) Fingerprints of environmental change on the rare Mediterranean flora: a 115-year study. *Glob. Change Biol.* 12, 1466–1478
- 71 Carvell, C. *et al.* (2006) Declines in forage availability for bumblebees at a national scale. *Biol. Conserv.* 132, 481–489
- 72 Westphal, C. *et al.* (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6, 961–965
- 73 Lambdon, P.W. *et al.* (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80, 101–149
- 74 Traveset, A. and Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol. Evol.* 21, 208–216

- 75 Matsumura, C. *et al.* (2004) 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
- 76 Steffan-Dewenter, I. and Tschardt, T. (2000) Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia* 122, 288–296
- 77 Roubik, D.W. and Wolda, H. (2001) Do competing honey bees matter? Dynamics and abundance of native bees before and after honey bee invasion. *Popul. Ecol.* 43, 53–62
- 78 Goulson, D. and Sparrow, K. (2009) Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *J. Insect Conserv.* 13, 177–181
- 79 Franck, P. *et al.* (1998) The origin of west European subspecies of honeybees (*Apis mellifera*): new insights from microsatellite and mitochondrial data. *Evolution* 52, 1119–1134
- 80 Anderson, D. and East, I.J. (2008) The latest buzz about Colony Collapse Disorder. *Science* 319, 724–725
- 81 Watanabe, M.E. (2008) Colony collapse disorder: many suspects, no smoking gun. *Bioscience* 58, 384–388
- 82 Woolhouse, M.E.J. *et al.* (2005) Emerging pathogens: the epidemiology and evolution of species jumps. *Trends Ecol. Evol.* 20, 238–244
- 83 Ribière, M. *et al.* (2008) Natural history and geographical distribution of honey bee viruses. In *Virology and the Honey Bee* (Aubert, M.F.A. *et al.*, eds), pp. 15–84, European Commission
- 84 Ongus, J.R. *et al.* (2004) Complete sequence of a picorna-like virus of the genus *Iflavirus* replicating in the mite *Varroa destructor*. *J. Gen. Virol.* 85, 3747–3755
- 85 Eyer, M. *et al.* (2009) Small hive beetle, *Aethina tumida*, as a potential biological vector of honeybee viruses. *Apidologie* 40, 419–428
- 86 Genersch, E. *et al.* (2006) 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
- 87 Goulson, D. (2003) Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Syst.* 34, 1–26
- 88 Neumann, P. and Elzen, P.J. (2004) The biology of the small hive beetle (*Aethina tumida*, Coleoptera: Nitidulidae): gaps in our knowledge of an invasive species. *Apidologie* 35, 229–247
- 89 Spiewok, S. and Neumann, P. (2006) Infestation of commercial bumblebee (*Bombus impatiens*) field colonies by small hive beetles (*Aethina tumida*). *Ecol. Entomol.* 31, 623–628
- 90 Hickling, R. *et al.* (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Change Biol.* 12, 450–455
- 91 Stone, G.N. and Willmer, P.G. (1989) Warm-up rates and body temperatures in bees - the importance of body size, thermal regime and phylogeny. *J. Exp. Biol.* 147, 303–328
- 92 Hegland, S.J. *et al.* (2009) How does climate warming affect plant–pollinator interactions? *Ecol. Lett.* 12, 184–195
- 93 Parmesan, C. *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399, 579–583
- 94 Thomas, C.D. *et al.* (2001) Ecological and evolutionary processes at expanding range margins. *Nature* 411, 577–581
- 95 Memmott, J. *et al.* (2007) Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* 10, 710–717
- 96 Schweiger, O. *et al.* (2008) Climate change can cause spatial mismatch of trophic interacting species. *Ecology* 89, 3472–3479
- 97 Ellis, J.D. and Munn, P.A. (2005) The worldwide health status of honey bees. *Bee World* 86, 88–101
- 98 Pilling, E.D. and Jepson, P.C. (1993) Synergism between EBI fungicides and a pyrethroid insecticide in the honeybee (*Apis mellifera*). *Pestic. Sci.* 39, 293–297
- 99 Chen, Y.P. and Siede, R. (2007) Honeybee viruses. *Adv. Virus Res.* 70, 33–80