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Protecting pollinators and our food supply: understanding and managing threats to pollinator health

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Abstract

Global pollinator declines threaten food production and natural ecosystems. The drivers of declines are complicated and driven by numerous factors such as pesticide use, loss of habitat, rising pathogens due to commercial bee keeping and climate change. Halting and reversing pollinator declines will require a multidisciplinary approach and international cooperation. Here, we summarize 20 presentations given in the symposium ‘Protecting pollinators and our food supply: Understanding and managing threats to pollinator health’ at the 19th Congress of the International Union for the Study of Social Insects in San Diego, 2022. We then synthesize the key findings and discuss future research areas such as better understanding the impact of anthropogenic stressors on wild bees.

Introduction

Pollinators are vital to the health of natural ecosystems and global crop production, but many species are in decline (Powney et al. 2019; Wagner et al. 2021; Zattara and Aizen 2021). Certain wild bees, such as bumblebees and solitary bees, are experiencing range contractions (Biesmeijer et al. 2006; Kerr et al. 2015; Powney et al. 2019; Soroye et al. 2020) and localized declines in managed honey bee colonies are occurring particularly in North America (Aizen and Harder, 2009; van Engelsdorp and Meixner 2010). The drivers of bee declines are complex and multifaceted (Goulson et al. 2015; Siviter Bailes et al. 2021a, b; Vanbergen and Insect Pollinators Initiative 2013). Intensive agricultural practices reduce floral resources and rely heavily on pesticides (Tilman et al. 2002). The commercial honey bee and bumblebee trade can increase bee pathogens and diseases (Cameron et al. 2011), and has led to the spread of invasive species (Cameron et al. 2016; Schmid-Hempel et al. 2014). Climate change can directly harm pollinators through

extreme weather events and also disrupt flowering times which can lead to nutritional stress on pollinators (Miller-Struttman et al. 2015; Soroye et al. 2020; Zaragoza-Trello et al. 2021). Furthermore, bees are simultaneously exposed to multiple anthropogenic stressors which may result in synergistic effects (Goulson et al. 2015; Siviter Bailes et al. 2021a, b; Vanbergen and Insect Pollinators Initiative 2013). While complicated, determining the drivers of pollinators declines is of utmost importance to inform policy.

Identifying the drivers of global pollinator declines is complicated by the fact that managed and wild pollinators are challenged by an overlapping, yet unique, set of threats. These threats are best understood for managed bees, but are likely different for unmanaged wild pollinators, which are also effective and important pollinators in both agricultural and natural landscapes (Cusser et al. 2021; Dainese et al. 2019; Garibaldi et al. 2013; MacInnis and Forrest 2019; Rader et al. 2016). Understanding how common and unique threats impact pollinator populations is further complicated by variation in the social biology of pollinators. Most managed pollinators are eusocial insects (honey bees, bumblebees and stingless bees) with very different social dynamics and life cycles from each other and solitary species. Nevertheless, solitary species, such as leafcutting and mason

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bees, are becoming increasingly important in commercial agriculture (Horth and Campbell 2018; Motzke et al. 2016; Pitts-Singer and Cane 2011). Sustaining effective pollination services thus requires understanding how environmental stressors (e.g., pesticides, habitat loss, diseases, climate change) impact both managed and wild pollinators across a range of sociality.

This global and multifaceted problem requires a multi-disciplinary approach rooted in international cooperation. To promote international and interdisciplinary study of pollinator decline, especially among scientists studying social insects, we organized a symposium at the 19th Congress of the International Union for the Study of Social Insects in San Diego, 2022. This symposium brought together 20 scientists studying pollinator decline in many different taxa and at a variety of disciplinary levels. Here, we present an overview of 20 presentations given at the symposium 'Protecting pollinators and our food supply: Understanding and managing threats to pollinator health', and synthesize key findings and future research directions.

Pesticides: understanding pollinator exposure to pesticides

Kirsten Traynor: pesticides in pollen: real-world exposure in stored pollen of *Apis mellifera*

High levels of honey bee (*Apis mellifera*) colony mortality in the USA (2006–2007) increased interest in the risk factors honey bees experience. As such, the Animal Plant Health Inspection Service National Honeybee Disease Survey incorporated pesticide residue analysis into long-term monitoring of honey bee colonies. Traynor presented pesticide residue data collected from honey bee colonies over 7 years from 2011 to 2017. The dataset looked at 218 different active ingredients and their metabolites in 1055 apiary samples of bee bread, investigating five different ways to estimate risk: (1) pesticide prevalence, which looks at absence or presence in an apiary sample, (2) pesticide diversity, how many different residues are detected in an apiary sample, (3) pesticide concentration in parts per billion (ppb) summed across all products found, (4) relevant pesticides that contribute a minimum of 50 points when the detected concentration is divided by the pesticide product's LD₅₀, and (5) the pollen hazard quotient. In the USA, 82.1% of samples contained at least one pesticide per sample, with 2.78 different pesticide residues detected per sample on average (Traynor et al. 2021). The mean concentration of pesticides in colonies was high in the USA at 600.32 ppb. Altogether, 5.4% of

samples ($N = 54$) exceed the Hazard Quotient threshold of 1000 points (Traynor et al. 2021). Pesticide use in the USA occurs at concerning levels in some apiary samples and was correlated with colony risk factors such as brood disease and queen losses.

Jessica Cole: investigating wildflowers as a route of pesticide exposure to bees

Loss of habitat is undoubtedly a driver of wild bee declines and as such agri-environmental schemes encourage the planting of wildflowers to promote pollinator health (Stout and Dicks 2022). However, wildflowers can be contaminated with pesticides, creating a potential trade-off (David et al. 2016). Here, Cole presented data determining (i) the species of wildflowers most frequently visited by bees in agricultural environments and (ii) if they expressed pesticides. Floral abundance, diversity and visitation were surveyed at 9 transect sites at the University of Vermont Horticultural Center. *Plantago lanceolata* was preferentially visited by both honey bees and wild bees and *Trifolium pratense* was preferentially visited by wild bees, but not honey bees. These flowers (*P. lanceolata* & *T. pratense*) were subsequently grown in greenhouses in one of four treatment groups: control (no pesticides), insecticide (imidacloprid), fungicide (difenoconazole) and insecticide + fungicide (imidacloprid + difenoconazole). High concentrations of imidacloprid were expressed in pollen of both plant species, but difenoconazole was higher in *T. pratense* compared to *P. lanceolata*. Furthermore, difenoconazole concentrations in the pollen were higher when the flower was treated with both the insecticide and fungicide. When toxicity is considered, and hazard quotient calculated, difenoconazole exposure posed a relatively low risk to wild bees, but imidacloprid led to an increased risk of bee mortality.

Pesticides: Determining the impact of pollinator exposure to pesticides

Julia Fine: Indirect exposure to insect growth disruptors affects honey bee reproductive behaviors and ovarian protein expression

Insect growth disruptors (IGD's) are pesticides that inhibit the growth and development of insect pests, but beneficial insects can also be exposed (Fine and Corby-Harris 2021). Here, Fine presented data on the potential impact that IGD's have on honey bee (*Apis mellifera*) egg production

and embryo viability. Honey bee queens were exposed to 3 different IGD's (methoxyfenozide, novaluron and diflubenzuron) at 10 parts per million (ppm) for two weeks. In all treatment groups, the proportion of eggs that successfully hatched was significantly lower when compared to controls. There was no evidence of reduced oviposition, suggesting a transovarial route of pesticide exposure (Fine 2020). To determine if transovarial effects occurred at lower concentrations, the experiment was repeated at 1 ppm (diflubenzuron, methoxyfenozide and pyriproxyfen). Methoxyfenozide lowered daily egg production compared to controls, but there was no difference in the total number of eggs laid between different treatment groups and no difference in queen-worker interactions. Surprisingly, pyriproxyfen treatment resulted in a higher hatching rate compared to controls. There were also 55 differentially expressed proteins in the ovaries of queens exposed to pyriproxyfen compared to control queens. Lastly, worker bees reared in foster colonies from eggs laid by queens exposed to pyriproxyfen were more responsive to novel queens relative to workers from control queens. This suggests that at least in this setup, low concentrations (1 ppm) of IGD's do not have negative transovarial effects on honey bees, and further work is needed to explore the possible hormetic effects of transovarial pyriproxyfen exposure.

Walter Farina: glyphosate exposure in honey bee colonies: effects on brood and social implications

The development of GM crops which are herbicide tolerant has resulted in the herbicide glyphosate becoming the most used agrochemical in the world. Farina summarized recent developments on the impact of glyphosate on honey bee health. Glyphosate can have indirect effects on pollinators by reducing flowering weed species, but can also change gut microbiota and make bees more susceptible to pathogens (Motta et al. 2018). The herbicide can impair honey bee behavior, influencing navigation, orientation, learning and even sleep (Balbuena et al. 2015; Herbert et al. 2014; Mengoni Goñalons and Farina 2018; Vázquez Balbuena et al. 2020a, b). Honey bee larvae chronically exposed to glyphosate can have lower survival and a reduced likelihood of molting. There are also colony level differences, with some colonies more vulnerable to glyphosate exposure than others (Vázquez et al. 2018). However, even when larvae are asymptomatic, differences in gene expression are still observed (Vázquez Latorre-Estivalis et al. 2020a, 2020b). Follow-up experiments in agricultural settings showed that honey bee larvae are more vulnerable than adult workers to glyphosate (Macri et al. 2021). The

data summarized demonstrate that glyphosate exposure poses a significant threat to honey bees and their pollination services.

Adrian Fisher II: a widely used mito-toxic fungicide negatively affects honey bee (*Apis mellifera*) hemolymph protein levels and ontogeny

Pesticides are a major environmental stressor for pollinator health but among the various pesticide categorizations, fungicides may be particularly insidious due to their traditional designation as safe for pollinators (Rondeau et al. 2022). The approval of several fungicides for application during the blooming period of major crops contributes to the potential risk of fungicides relative to other pesticides. Fisher examined the impact of a widely used fungicide, Pristine (25.2% boscalid, 12.8% pyraclostrobin), on honey bee health at field-relevant concentrations. Chronic Pristine consumption negatively impacted honey bee colony health by reducing population levels, inducing precocious foraging, and reducing worker lifespan (Fisher et al. 2021). Analysis of fungicide effects in different seasons and over a shorter exposure duration supported the findings that field-relevant exposure to a fungicide can negatively affect honey bee health (Fisher et al. 2022). Furthermore, the underlying physiological mechanism by which Pristine fungicide adversely affects honey bees may be its premature reduction of vitellogenin concentration. These findings suggest that current laboratory assessment procedures do not reflect field-relevant exposure effects and adjustments are needed to adequately assess pesticide toxicity.

Liliana Fischer: the novel insecticide flupyradifurone impairs collective brood care in bumble bee microcolonies

Bees are routinely exposed to multiple pesticides simultaneously (Mitchell et al. 2017; Traynor et al. 2021) and synergistic interactions may amplify the impact of individual pesticides. Fischer investigated how long-term simultaneous exposure to the novel insecticide flupyradifurone and the herbicide, glyphosate, influenced bumblebee (*Bombus terrestris*) microcolonies. Glyphosate in isolation or combination did not influence the bumblebee microcolonies, yet long-term exposure to flupyradifurone significantly impaired brood thermoregulation. This led to a longer development time of brood and lower reproductive output of the microcolonies. As a result, drone production and colony growth were over fifty percent lower when microcolonies were exposed to flupyradifurone. This suggests that current risk assessments are not protecting bees from the unwanted consequences of pesticide use by overlooking such sub-lethal but fitness relevant effects. The effect on brood thermoregulation is worth

noting as active and passive thermoregulation is an important aspect of insect life, especially in a warming global climate (Wagner et al. 2021) and for wild pollinators with a short colony cycle. Brood thermoregulation and temperature therefore marks a suitable readout to track such sub-lethal effects of pesticides in social insect pollinators.

Harry Siviter: does the novel pesticide flupyradifurone have sub-lethal effects on non-*Apis* bees?

Bumblebees visit thousands of flowers daily collecting nectar and pollen. In an ever-changing floral marketplace, bumblebees need to quickly learn and retain information about rewarding flowers. Here, Siviter presented data that demonstrated that the novel insecticide flupyradifurone impaired the feeding motivation of bumblebees (*Bombus impatiens*) as well as color/olfactory learning and memory (Siviter and Muth 2020). This suggests that these novel insecticides have similar sub-lethal effects on bees to those observed with neonicotinoids (Samuelson et al. 2016; Siviter Koricheva et al. 2018a, b; Stanley et al. 2015a, b). Siviter also presented preliminary data suggesting that Sivanto (commercial formula containing flupyradifurone as an active ingredient) can have both lethal and sub-lethal effects on solitary bees (*Osmia lignaria*). These data add to a growing body of data demonstrating that flupyradifurone pose a threat to bees in general and their pollination services (Siviter and Muth 2020; Stanley, Garratt et al. 2015a, b).

Isabella Fernanda Camargo: toxicity of clothianidin pesticide in the development of larval *Scaptotrigona postica*

Brazil has the greatest diversity of stingless bees in the world, yet the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA) uses honey bees as a model species for conducting pesticide risk assessments. Clothianidin, a neonicotinoid which is banned from use in the Europe Union due to negative impacts on bees (Di Prisco et al. 2013; Rundlöf et al. 2015; Tsvetkov et al. 2017), was recently assessed by IBAMA, and the report highlighted an absence of data on native stingless bee adults and larvae. Camargo presented data that assessed the impact of clothianidin on the development and survival of the stingless bee (*Scaptotrigona postica*) larvae. Bees were reared in vitro and exposed to field-realistic concentrations of clothianidin. Larvae exposed to clothianidin had reduced survival, pupation rates and emergence when compared to control bees. This suggests that stingless bee larvae are more vulnerable to clothianidin than honey bees (Tadei et al. 2019) and suggests that more attention should be given to stingless bees in pesticide risk assessments (Cham et al. 2019).

Nigel Raine: muddying the waters? The risks of exposure to pesticide residues in soil for bees

Pesticide risk assessments use honey bees as a model-system; however, this is not representative of all bee species which differ in many aspects of their life-history (Chan et al. 2019; Franklin and Raine 2019; Sgolastra et al. 2019). For example, pesticide residues in soil are not currently considered as they are seldom encountered by honey bees (Gradish et al. 2019). Here, Raine presented data on the potential impact of pesticide exposure through soil on ground nesting bees. In a semi-field experiment using hoop-houses, soil applied imidacloprid reduced the nesting success of Hoary Squash bees (*Eucera pruinosa*) by 85% and reduced offspring production by 89% (Willis Chan and Raine 2021). A follow-up experiment using a similar experimental design demonstrated that exposure to a combination of the pesticide Sivanto (flupyradifurone, as an active ingredient) and the fungicide Quadris top (azoxystrobin + difenoconazole) had sub-lethal impacts on the behavior and reproduction of female Hoary Squash bees. Interestingly, bumblebee queens hibernating in the ground might be exposed to pesticide residues in soil in agricultural environments (Rondeau et al. 2022), and preliminary data from another hoop-house based experiment suggested that bumblebee queens may prefer to hibernate in soil contaminated with pesticides, increasing their potential exposure risk. In combination, these data confirm that soil is an important route of pesticide exposure that should be considered in environmental risk assessment for insect pollinators.

Parasites and pathogens

Allyson Ray: evidence of decreased virulence of a major viral variant in isolated, mite-surviving honey bees

The arrival of the ectoparasitic mite *Varroa destructor* altered the disease ecology of the deformed wing virus (DWV) facilitating its virulence and increasing its distribution (Ray et al. 2021). *Varroa* transmitted DWV contributes to honey bee colony failure if not properly managed; however, some honey bee populations are able to survive despite high levels of mite infestation. Ray investigated if virulent strains of DWV may explain the ability of unmanaged colonies within the Arnot Forest (New York State, USA) to persist despite high mite levels. DWV isolates from Arnot Forest honey bee populations were compared against isolates sampled from managed apiaries. Viral load per individual bee was similar across field sites but viral isolates from the Arnot Forest samples exhibited significant genotypic differences. The underlying genotypic differences resulted in

variation in virulence as Arnot Forest DWV samples had reduced pupal and adult mortality, as well as reduced incidences of the deformed wing phenotype in laboratory assays. As these experiments were limited to a subset of isolates, a fascinating future research direction is to examine additional viral genotypes and the dynamics that underlie presence of less-virulent form of DWV in these feral bees.

Yves Le Conte: *Varroa* resistant honey bees: keys for the understanding of a balanced host-parasite relationship

Despite the devastating impact of *Varroa* mites on honey bee health, some populations have been able to mitigate the effects of mite infestation in the absence of management or treatment (Mondet et al. 2021; Moro et al. 2021; Oddie et al. 2021). Le Conte and Mondet examined *Varroa* resistant honey bee colonies in France to understand the underlying mechanisms by which some bee populations persist. *Varroa* resistance does not stem from a single factor but a combination of behavioral and physiological changes in honey bee hosts as well as physiological changes in mite pests. Honey bees in resistant colonies were observed to swarm with greater frequency and have a better ability to recognize *Varroa*-specific chemical compounds. Olfactory genes were overexpressed in resistant bees providing an underlying basis for the recognition of mite compounds. Resistant bees also engaged in elevated levels of hygienic behavior including the removal of infected brood and the collection of greater quantities of propolis. Le Conte also presented evidence for reduced reproductive capabilities and virulence for *Varroa* in resistant colonies. These specific markers for resistant colonies may provide beekeepers with resources to identify resistance for selective breeding.

Boris Baer: innate immune responses as effective parasite defenses in honey bees

A variety of pests and pathogens can negatively impact honey bee health resulting in colony losses; however, honey bees may combat various threats through innate immune responses (Fang et al. 2022; Holt et al. 2021). To better understand honey bee immune responses, Baer examined the horizontal transmission of the fungal pathogen *Nosema* between drones and queens. *Nosema* can occur in the ejaculate transferred to queens during mating; thus, drones are able to confer some degree of protection through the upregulation of antimicrobial molecules in seminal fluid. These protective factors also conferred protection to the drones themselves, helping to suppress *Nosema* prevalence. Further evidence of innate immune responses was presented in honey bee larval responses to *Varroa* mites, where the upregulation of proteins involved in immune responses

facilitated larval defense. The innate immune responses documented in both larval and adult honey bees may have implications for management practices for important pests and pathogens. In the case of antifungal chitinases or other proteins, the identification of antimicrobial molecules and their physiological functioning can be used for future bee breeding purposes to select for bees with increased levels of disease tolerance. The identification of individual antimicrobial metabolites can also be used for the development of novel medications that can be used in case of disease outbreaks. Given that these metabolites are naturally produced by honey bees as part of their innate immune systems, such medications are not expected to have any toxic effects on bees or pose additional contamination risks in bee products used from human consumption.

Marla Spivak: Honey bee social immunity and beekeeping

Spivak presented on the social immunity mechanisms by which honey bees collectively defend against various parasites and pathogens, such as the removal of infected brood through hygienic behavior, and the collection of antimicrobial plant resins, or propolis (Spivak and Danka 2021). Current beekeeping practices, particularly the large-scale, migratory movement of commercial operations for pollination and honey production facilitate increased transmission of parasites and pathogens, overburdening natural social immunity. Nevertheless, some commercial operations are allowing honey bees' natural defenses to evolve, resulting in increased resistance to *Varroa* mites. An example was provided of a commercial operation of 8000 colonies that selects 4% of their top honey producing colonies and does not treat those colonies for *Varroa* mites, but does treat the remaining 96% of the colonies. In March, the beekeepers select colonies from the untreated 4% that still have low mite levels and large colony populations as breeder colonies for a next generation of queens for the entire operation. This philosophical shift away from treating all colonies multiple times per year to leaving a portion untreated as potential breeders increases the effectiveness of natural social immunity by complementing rather than counteracting natural honey bee social immunity.

Land use and management

Briann Dorin: Wild bee conservation in vineyards— an interdisciplinary approach

Pollinator diversity is necessary for both natural and agricultural ecosystems (Garibaldi et al. 2013; Ollerton 2017). However, population declines are occurring for many bee

species, likely due to a variety of environmental stressors (Vanbergen and Insect Pollinators Initiative 2013). Cooperation with land managers may be a key factor in promoting the conservation of wild bees and addressing several of their threats including habitat loss and pesticide exposure. Dorin examined the effect of land management practices in a pollinator-independent crop, the European wine grape (*Vitis vinifera*), on bee species diversity and abundance in Canada. Floral abundance and vegetation height between the vine rows was positively correlated with bee diversity and abundance for certain taxa, suggesting that efforts to protect pollinators in agricultural systems should extend beyond the fields where they are required for crop pollination. Further, Dorin presented developments in improving dialog with growers and promoting the implementation of more effective land use practices for pollinator protection. This is especially important in pollinator-independent crops which lack the economic motivation of enhancing crop pollination services.

Gaurav Singh: spatial and temporal distribution of stingless bees in mango orchards and its effect on fruit set

In tropical habitats, various stingless bee species are managed for crop pollination (Meléndez Ramírez et al. 2018) but face challenges due to agricultural practices that disrupt habitat availability and facilitate exposure to pesticides. Singh and colleagues investigated changes in the spatio-temporal distribution of the stingless bee species *Tetragonula mellipes*, and other pollinators as well as the resulting agricultural outcomes in mango orchards. The proximity of natural habitat to mango orchards facilitated the pollination services of native bees in mango orchards, increasing fruit set. However, stingless bee distribution in a mango orchard was limited by distance from natural habitat; thus, the inclusion of natural habitats within orchards may promote greater crop productivity. Various fly species were also observed to visit mango flowers and were more evenly distributed in mango orchards; however, fruit set corresponded to stingless bee distribution. Understanding the importance of natural and semi-natural habitats for native pollinator behavior and efficiency may facilitate conservation and agricultural productivity.

Margarita López-Urbe: crop widespread cultivation facilitates rapid population growth and regional adaptation in an oligolectic bee pollinator

Agricultural practices including the domestication and cultivation of various plant species have dramatically altered ecological conditions for associated insect pollinators. To examine the effects of plant cultivation on a close insect associate, López-Urbe and colleagues examined the effects of *Curcubita* spp. cultivation on the *Curcubita* specialist

squash bee *Eucera (Peponapis) pruinosa*. Genomic analyses of various *E. pruinosa* populations across its modern range suggest that *E. pruinosa* geographic distribution and recent demographic history have been directly shaped by the human-mediated widespread cultivation of *Curcubita* spp. in North America. A high concentration of selective sweeps was detected in the population of eastern North America suggesting widespread positive selection that is likely linked to the colonization of areas where these bees exclusively rely on agricultural resources.

Climate change

Tereza Cristina Giannini: impact of climate change on Eastern Amazon native bees and possible consequences on food production

Climate change may affect natural and agricultural ecosystems, impacting native pollinator distribution and pollination services. Giannini analyzed the current and projected distribution of several native bee species using models that accounted for potential climate change induced scenarios (Giannini et al. 2020). The overwhelming majority of bee species may experience significant reductions in range due to the loss of suitable habitats. Habitat loss and range restriction were projected for both specialists and generalist bee species which may adversely affect agricultural production. Projected bee losses suggest that climate change may have a devastating impact on bee species diversity and abundances, as well as crop productivity. This is particularly concerning given the importance of bee diversity for buffering agriculture against other environmental stressors.

Kimberly Przybyla: effects of heat stress on mating behavior and colony development in bumblebees

The increased occurrence of extreme weather events associated with climate change may reduce agricultural production by adversely affecting pollinating insects. Heatwaves in particular may induce physiological disturbances and reduce fertility. To examine heatwave effects on the reproductive capacity of a pollinator, Przybyla and colleagues examined the effects of a static and constant exposure of 40 °C, until heat stupor is reached, on males of the bumble bee species *Bombus terrestris* (Przybyla et al. 2021). Heat stressed *B. terrestris* males exhibited resiliency as they did not experience a reduction in pheromone quality or copulatory behavior, and the heat exposure did not adversely affect nest development for queens mated with these males. These findings suggest that some pollinators may engage in adaptive responses that allow for the mitigation of heat stresses that are not too extreme.

The interactions between multiple anthropogenic stressors

Michael Garratt: pesticide and pathogen effects on pollinators: Implications for crop pollination and food production

Pollination services are delivered by a diversity of pollinator species, yet there are opportunities to improve the yields of several crop species by managing these pollination services (Dainese et al. 2019; Garratt et al. 2021; Lemanski et al. 2022). Pollinators are threatened by multiple different anthropogenic stressors (Vanbergen and Insect Pollinators Initiative 2013); however, the effects of these on the delivery of pollination services have rarely been directly studied. Garratt presented work on the potential impact of pesticides and parasites on the pollination services provided to crops by bumblebees (*Bombus terrestris*). In a semi-field experiment using pollination cages, it was found that the neonicotinoid thiamethoxam can impair the pollination of apples by bumblebees. Flower visitation was reduced when bees were exposed to the pesticide and the number of bees carrying pollen was also lower (Stanley et al. 2015a, b). This had downstream negative consequences for fruit seed set (Stanley et al. 2015a, b). Using examples with preliminary data, a methodology was then presented for exploring effects of different stressors (including parasites) on *Bombus terrestris* and its pollination services. Standardized methods are required for assessing interactions between stressors, including pesticides and parasites, in order to improve our understanding of the potential consequences for pollination.

Mark Brown: parasites, pathogens, and pesticides: impacts on bumblebee health

Bumblebees are exposed to a multitude of different natural and anthropogenic stressors, including pesticides and parasites, and understanding how they influence bumblebee health is complicated. Indeed, even determining how to measure bumblebee health is not a trivial task. Brown presented a framework for considering bumblebee health, that scaled from the individual to the guild, and summarized how his research group and others have been answering these questions at each level. At the level of individual bumblebees, pesticides and parasites can have direct impacts on bumblebee mortality (Brown et al. 2000; Fürst et al. 2014; Straw et al. 2021) and they can also have a range of sub-lethal effects (Brown et al. 2003; Linguadoca et al. 2021). At a colony level, both pesticides and parasites can have negative effects on colony development (Baron et al. 2017; Brown et al. 2003; Rundlöf et al. 2015; Siviter et al. 2018a, b), yet in certain contexts, parasite exposure might improve

colony fitness. For example, uncontrolled infections of the parasite *Crithidia bombi* led to a reduction in worker ovary development, which means it takes the colony longer to get to competition stage, and thus the queen has longer to lay eggs (Shykoff and Schmid-Hempel 1991). At the population level, mathematical models based on empirical data or historical data can be used to infer population level trends (Baron et al. 2017; Woodcock et al. 2016). In the case of parasites, the decline of some bumblebee species is correlated with a rise in the prevalence of *V. bombi* (Cameron et al. 2011, 2016). Brown concluded that we cannot determine the overall impact of pesticides and parasites on global bumblebee health due the nature of studies that we can, and cannot conduct (Straub et al. 2022). Thus, a precautionary principle, which aims to reduce bumblebee exposure to pesticides and parasites as a consequence of anthropogenic change, should be implemented.

Synthesis and future directions

Several generalizations for four types of threats emerge from integration of the material presented at this symposium:

Pesticides

First, there is overwhelming evidence that many pesticides have sub-lethal effects on both managed and wild insect pollinators, decreasing pollinator fitness and negatively impacting agricultural productivity (Fisher et al. 2021; Siviter et al. 2021a, b; Stanley et al. 2015a, b; Willis Chan and Raine 2021). A major goal for researchers and government regulators will be to find methods to control plant diseases and pests without adversely affecting the pollinators that are essential for both agricultural and natural ecosystem function. The evidence presented shows also that there is variation in the toxicity of pesticides to pollinators and clear evidence of dosage effects. The latter demonstrates that there may be possibilities to control plant diseases and pests with more targeted applications that do not adversely affect pollinators. Finally, a particular area of needed research is developing a better understanding of the impact of field-realistic pesticide exposure on wild bees (Franklin and Raine 2019; Siviter and Muth 2020).

Emerging pests and diseases

Invasive mites and viruses have had major negative effects on the populations of honey and bumble bees (Cameron et al. 2011; Fürst et al. 2014; Le Conte et al. 2010). Yet, there are exciting recent findings showing multiple mechanisms by which bees may evolve resistance to both mites and viruses, suggesting that careful selection of stocks and traits

may aid resistance of managed bees, and that natural selection may allow wild bees to evolve resistance to new invasive pathogens and parasites. As solitary species continue to increase in use for pollination, it will likely be necessary to consider how transmission dynamics and immune responses are altered in wild, non-managed pollinators.

Habitat loss

Habitat loss is very likely a major factor in declines of many wild pollinators, due to loss of specific plants, loss of nesting habitats, and a general decline in available food quality (Carvell et al. 2006, 2017). There are exciting new findings that show that land management practices that increase widespread patches of native flowering plants can conserve pollinator species diversity and abundance, particularly for species that need a high diversity of pollen resources. Practices that encourage patches of native flowering plants adjacent to, or within, agricultural fields can also improve fruit set and agricultural productivity (Blaauw and Isaacs 2014; Kremen et al. 2002; Morandin and Winston 2006). More information on the specific mechanisms by which habitat loss affects particular bee species is critical in order to develop land management practices that conserve pollinators and our natural and managed ecosystems. Future research should also include understanding farmer perspectives regarding various pollinator-friendly practices and mechanisms of support that would enhance their uptake.

Climate change

Climate change, in the form of heat waves or more variable rainfall, is predicted to have major negative effects on many pollinators (Giannini et al. 2017; Nicholson and Egan 2020). However, it is striking how few studies exist of how warmer temperatures will affect pollinator function and fitness. Moreover, there is extreme variation in the thermal tolerance and thermal range of managed and wild pollinators. For example, honey bee colonies experience all four seasons, but many wild pollinators spend their entire lifespan in just early spring or late summer. Additional information about how social and solitary bees deal with thermal stress as a function of their ecology will be useful to inform conservation solutions.

Conclusion

Pollinators and their pollination services are essential for food production and wild ecosystems. The 20 presentations given during the symposium 'Protecting pollinators and our food supply: Understanding and managing threats to pollinator health' demonstrate just some of the different ways that anthropogenic stressors threaten pollinators, how some

pollinators are adapting to these conditions, and provide refreshing suggestions on how they can be safeguarded in the future. However, there is clearly much to do. The complexity of the interactions between these anthropogenic stressors and pollinators provides a major challenge to scientists and regulators, and interdisciplinary and international collaborations will be essential to address these challenges.

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Declarations

Conflict of interest The authors declare they have no competing interests.

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