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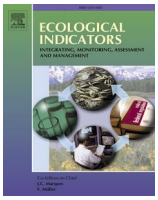

Review

Honey bees as biomonitors of environmental contaminants, pathogens, and climate change

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ABSTRACT

Monitoring the environment for pollution, pesticides, and pathogens is crucial for protecting human, agriculture, and overall ecosystem health. Diverse strategies ranging from physical sensors to sentinel species have been used for environmental monitoring. The European honey bee, *Apis mellifera*, is a globally managed pollinator that can serve as a continuous biomonitoring species. During foraging, honey bees are exposed to contaminants and pathogens and carry them to their hives where they can be detected and quantified. Although individual bees are vulnerable to environmental stressors, the honey bee colony as a whole is more resilient and can accumulate contaminants or respond to them without collapsing. This allows for long-term monitoring of the colony to map contaminants in a geographical area and study ecotoxicology gradients over space and time. In this paper, we review demonstrated and proposed uses of honey bees for environmental monitoring. We focus our discussion on heavy metals, air pollutants, pesticides, and plant pathogens that can be detected in bees and their hive materials including honey, wax, and stored pollen. We present the use of gene expression, microbiome profiling, and other high-throughput methodologies to study dose-dependent exposure and increase detection sensitivity; for example, stored pollen analysis with next generation sequencing can reveal the presence of plant viruses, fungi, and invasive species earlier than traditional detection methods. Finally, we discuss opportunities for using honey bees to monitor emerging threats such as climate change and antimicrobial resistance. This narrative review highlights the versatility and potential utility of the European honey bee as a biomonitoring species for ecosystem health.

1. Introduction

Environmental contaminants from agricultural, urban, and industrial activities, as well as emerging pathogens and climate fluctuations can negatively impact microbial, plant, and animal life. Contaminants of interest are heavy metals, environmentally persistent chemicals, and agrochemical pesticides. These contaminants can have drastic effects on the environment; they can deposit and move through soil, water, and air, accumulating in body tissues and causing reproductive failure, neurotoxic damage, and death (Moroń et al., 2014; Williams et al., 2015). These detrimental effects are not limited to the natural environment. In humans, contaminants can be linked to respiratory diseases and cancer, amongst other ailments (Briffa et al., 2020; Carpenter, 2006; Dockery et al., 1993; Lambert et al., 2012a). Real time monitoring of environmental quality has become increasingly critical to record fluctuations, and to help maintain landscape biodiversity, food security, and human health.

Environmental monitoring can be conducted using biotic or abiotic

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systems, and a combination of physical, chemical, and genomic analyses (Cordier et al., 2020; Kienzl et al., 2003). An environmental bioindicator is generally defined as a species that responds predictably to environmental change and indicates environment quality (Mcgeogh, 1998) while a biomonitor is often described as a species that can also indicate quantitative aspects of the environment (Markert and Wünschmann, 2011). In this paper, however, we use the terms bioindicator and biomonitor in a broad sense and often interchangeably. Plant, animal, and microbial species are used for biomonitoring specific environments. For example algae, amphibians, aquatic midges and caddisfly larvae are routinely used to monitor aquatic pollution (Gillis et al., 2002; Werner et al., 2000; Zhou et al., 2008; Awrahman et al., 2016). Land snails, cattle, and owls are examples of terrestrial species that are used to monitor contamination (Amadi et al., 2020). In addition, termites have been used to determine soil quality (Parikh et al., 2020), and butterflies can indicate the effects of climate change (An and Choi, 2021).

The European honey bee, *Apis mellifera*, has unique characteristics that can improve upon biomonitoring efforts using other insect species. As the main managed pollinator of agricultural systems, *A. mellifera* has diverse interactions with the environment and is a microlivestock of global distribution. In Canada, they pollinate a variety of crops ranging from canola to berries, and their pollination services are valued at up to $5.5 billion per year (Mukezangango and Page, 2017). Honey bees are long-range foragers that bring nectar, pollen, resin, and other materials back to the colony. While individual honey bees are vulnerable to environmental stressors, a honey bee colony is more resilient and can accumulate stressors or respond to them without collapsing. A colony contains tens of thousands of forager bees that act as sampling devices of the surrounding environment, where foragers can be exposed to contaminants at pollination sites or while flying to and from the hive. Honey bees interact with and create a variety of matrices that can be measured for contaminant accumulation, such as freshly collected pollen, honey, stored pollen, and beeswax. These characteristics, as well as their global distribution and widespread management by humans, makes *A. mellifera* an ideal candidate biomonitoring species.

In this review we present findings from various studies that have investigated honey bees and their products for environmental biomonitoring (Fig. 1). We focus on three main areas: honey bees as biomonitors of 1) environmental contaminants, including heavy metals, airborne particulate matter, persistent chemicals, and agrochemical pesticides, 2) plant and pollinator pathogens, and 3) emerging threats such as climate change and antimicrobial resistance. We conclude with a discussion on the prospect of using honey bees and bee products as widespread biomonitors. We show that honey bee biomonitoring has the potential to improve human, animal, and ecosystem health and to enhance the efficiency of agricultural systems and food security.

2. Honey bees and hive products; sample collection and analysis

Honey bees are eusocial insects generally managed as colonies of 10,000–80,000 individuals including several hundred males present during the spring and summer seasons, and one queen who is the only reproductive female of the colony. Most of the bees are infertile female workers with a general lifespan of six weeks, except in an overwintering colony when they can live for several months. Honey bee workers conduct a variety of tasks from nursing as young adults to foraging later in life. Foraging bees leave their hives to collect nectar and pollen from a variety of flowering plants and are able to thrive in diverse

Fig. 1. Map illustrating the location of several research groups in the Americas, Europe, and Oceania studying environmental pollutants (blue), pesticides (violet) and plant pathogens (red) in honey bees and their hive matrices. Groups studying emerging areas are in orange; these include bee microbiome profiling in response to environmental stressors, antimicrobial resistance genes, and climate change.

environments, including urban areas (Baldock, 2020). While foraging, bees are in contact with environmental matrices including plant, air, water, and soil. They can be exposed to contaminants and pathogens that adhere to their body or are ingested during nectar and pollen collection or water uptake. It is this accumulation of contaminants in or on honey bees and their hive matrices: pollen, honey, and beeswax, that facilitate their use as monitors of environmental quality (Sadeghi et al., 2012; Silici et al., 2016; Zarić et al., 2016).

Honey bees are sampled from the interior of the hive; foragers are most abundant on the outer frames of the hive while nurse bees are generally found on brood frames. Foragers can also be sampled at the hive entrance when they return from foraging flights. Stored pollen is sampled from the hive frames while pollen traps can be used to collect fresh pollen brought to the hive by active foragers. Bee-collected nectar, honey, and wax can be sampled from the hive frames as well. These can be analyzed using a variety of methods depending on the sample and the analyte of interest. Techniques used for the analysis of heavy metals in honey bees include atomic absorption spectrometry (Conti and Botrè, 2001; Perugini et al., 2011), inductively coupled plasma-atomic emission spectrometry (van der Steen et al., 2012), and inductively coupled plasma mass spectrometry (Smith et al., 2019; Zarić et al., 2018, 2021). Methods for the detection of particulate matter include scanning electron microscopy coupled with energy dispersive X-ray fluorescence (Negri et al., 2015; Papa et al., 2021); methods for pesticide detection include gas–liquid chromatography and gas chromatography-mass spectrometry (Ruschioni et al., 2013; de Oliveira et al., 2016) while pathogen detection methods include polymerase chain reaction (PCR) and high throughput sequencing (Roberts et al., 2018; Bilodeau et al., 2020).

3. Environmental contaminants

The following sub-sections: a) heavy metals, b) persistent chemicals and airborne particulate matter, and c) agrochemical pesticides, describe environmental contaminants that can be detected in bee-associated materials.

3.1. Heavy metals

Heavy metal contamination is a concern in densely populated areas, particularly in regions with heavy industrial activity. Major anthropogenic sources of heavy metals include vehicle exhaust, burning of fossil fuels, smelting, and agrochemical use. Trace metals such as lead (Pb), cadmium (Cd), mercury (Hg), and chromium (Cr) are highly toxic (Mahurpawar, 2015; Jyothi, 2021). In humans, heavy metals cause acute and chronic poisoning and are linked to malignancies, particularly of the upper gastrointestinal tract (Khan et al., 2008). Foraging bees pick up heavy metals from contaminated water, air particulates, and vegetation which adhere to the hairs on their bodies (Zarić et al., 2017; Negri et al., 2015). Once they return to their colonies, these metals can be found in stored pollen, often referred to as bee bread, as well as beeswax, honey, and propolis, the resin-like material collected from trees. In bees, elevated heavy metals can negatively impact brood production, navigation abilities, and survival rate (Burden et al., 2019; Di et al., 2016; Moroń et al., 2014). In most cases, however, metal accumulation in honey bees and their hives is non-lethal for the colony and presents an opportunity for environmental monitoring.

Conti and Botrè (2001) showed that honey bees and their hive products: pollen, propolis and wax, sampled in the center of Rome with high vehicle traffic contained higher levels of heavy metals compared to areas outside the city. In a 2006 study involving biweekly sampling of honey bees in three locations in the Netherlands over a 3-month period, van der Steen et al (2012) showed spatial and temporal variation of metal concentrations in adult honeybees using inductively coupled plasma–atomic emission spectrometry. Perugini et al. (2011) used atomic absorption spectrometry to compare the accumulation of metals in bees in urban areas and natural reserves and found the highest values of Pb in hives located in the Ciampino area (Rome), next to the airport. Ruschioni et al. (2013) measured the concentration of various heavy metals in honey and whole bees in Italy. They observed higher levels of metal contaminants in forager bees than in honey samples, likely due to exposure during foraging activities. A lower level of heavy metals observed in honey compared to other bee matrices is consistent with other studies (Álvarez-Ayuso and Abad-Valle, 2017; Formicki et al., 2013; Satta et al., 2012) and indicates that highly precise laboratory equipment is needed for analyzing honey as a monitoring matrix and to quantify differences between sites (Smith and Weis, 2020). Ruschioni et al. (2013) also showed that trends in metal contamination correlated with weather patterns and anthropogenic activities in the region where samples were obtained. Chromium was found to be the most prevalent metal, and the months in which Cr most often exceeded threshold levels correlated with a lack of rainfall in a period before sampling. This is supported by other studies that found wet weather reduced metal concentrations in honey bees (Lambert et al., 2012b; Satta et al., 2012; Zarić et al., 2017). Nickel (Ni) was the least prevalent metal, which is consistent with the limited combustion of coal and fuel oil in the region (Ruschioni et al., 2013).

Some heavy metals, such as Pb, have multiple isotopes that can be linked to the sources of pollution (Grousset et al., 1994). The utility of using honey to monitor trace metal concentrations and Pb isotopic composition at a local scale has been demonstrated in studies conducted in Serbia, Australia and Canada (Zarić et al., 2018, Zhou et al., 2018; Smith et al., 2019). Zarić et al. (2018) reported the use of stable isotopes and Kohonen self-organizing maps to study spatio-temporal variations and origins of Pb pollution. Smith et al (2019) also measured the concentrations of Pb, Cd, Cr, aluminum (Al), and copper (Cu), as well as determined Pb isotopic compositions in honey sampled from different sectors within the Greater Vancouver Regional District in British Columbia, Canada. Anthropogenically sourced trace elements were generally elevated in honey from downtown Vancouver, compared to suburban and rural areas. The one exception was manganese (Mn), which had the highest concentrations in honey from Delta. Manganese is commonly found in fertilizers and pesticides and Delta is an area with high agricultural activity (Smith et al., 2019). Honey sampled from hives located close to Vancouver's main shipping port had higher levels of trace Pb, higher $^{208}Pb/^{206}Pb$ and lower $^{207}Pb/^{206}Pb$ isotopic ratios compared to honey sampled from rural areas. Shipping emissions from the port were thought to contribute to increased trace Pb levels and the characteristic Pb isotopic composition of downtown honey. Honey sampled from rural and suburban areas had Pb isotopic ratios that were similar to the profile seen in other environmental proxies including oysters and lichens harvested from unpopulated areas on the west coast of B.C. (Smith et al., 2019). In a more recent report, Smith et al. (2021) presented data from honey sampled around the world which revealed local Pb gradients and Pb isotopic compositions in honey associated with human activities.

A comparison of different matrices in a follow up study examined variations in trace element levels and Pb isotopic compositions in honey, bee tissues, bee bread, and propolis (Smith and Weis, 2020). Bee tissues and bee bread followed the same pattern of accumulation previously reported for honey by Smith et al. (2019). However, propolis was less effective at mirroring spatial variations in trace metal contamination (Smith and Weis, 2020). Beeswax is another hive matrix that can be used for monitoring metal contamination, in particular long term exposures. Beeswax has a lipid based composition that allows for the accumulation of environmental contaminants (Buchwald et al., 2009; Calatayud-Vernich et al., 2017). Gajger et al. (2019) compared the levels of heavy metals in newly constructed hive combs and old reused combs. Pb levels were higher in reused combs compared to the new combs, and Cu and Pb levels were highest in combs from hives exposed to intensive agricultural or industrial activity (Gajger et al., 2019). Their findings support the biomonitoring capabilities of beeswax, although data from

reused combs may represent recent as well as past colony exposure to contaminants.

The use of molecular biomarkers to monitor heavy metal contamination in honey bees has also been explored. Metallothioneins are metal binding proteins that play an important role maintaining essential heavy metal homeostasis, and provide protection against toxic heavy metals (Coyle et al., 2002). Purać et al. (2019) showed that the expression of *AmMT*, a metallothionein encoding gene, increased in a dose-dependent manner when forager bees were fed sucrose solutions containing sublethal doses of Cd, Cu, and Pb. In field-based experiments they examined the expression profile of *AmMT* in forager bees from two locations in Serbia: the city of Belgrade and the industrial area of Zajača. Foragers from Zajača had increased *AmMT* expression compared to those from Belgrade, which corresponded to the elevated levels of heavy metals in the industrial environment. Thus, the expression profiles observed in the lab and in field-based experiments suggest that *AmMT* in *A. mellifera* could be used as a bioindicator of environmental Cd, Cu, and Pb contamination (Purać et al., 2019).

The studies presented in this subsection showed that heavy metal concentrations, Pb isotopes and molecular biomarkers like AmMT in honey bees and/or their hive matrices align with spatial variations in metal pollution sources. Monitoring heavy metals in the environment on a regular basis could offer insight into the degree and source of pollution with broad implications for protecting human and ecosystem health. Frequent monitoring can be implemented by measuring levels of metals, isotopic ratios and/or relevant biomarkers in honey bees, honey, and beeswax.

3.2. Persistent chemicals and airborne particulate matter

Air pollution due to environmentally persistent chemicals, particulate matter (PM), and other air contaminants are a serious global problem correlated with respiratory diseases and lung cancer (Dockery et al., 1993). Environmentally persistent chemicals, often referred to as persistent organic pollutants (POPs), are contaminants of global concern. These compounds can move long distances in air or water and resist degradation in the environment (Wania and MacKay, 1996). Furthermore, there is overwhelming evidence to suggest that these compounds bioaccumulate, biomagnify, and are biotransported by migratory species (Montory et al., 2020). Coupled with their toxicity, these properties make establishing reliable monitoring programs for POPs essential. Herein, we present reports supporting the use of honey bees and their hive matrices to measure two classes of POPs: polychlorinated biphenyls and polycyclic aromatic hydrocarbons (Tulini et al., 2020; Villalba et al., 2020).

Polychlorinated biphenyls (PCBs) are a class of environmentally persistent synthetic organochlorine chemicals released from landfills containing old electrical equipment, the incineration of municipal waste, and evaporation from contaminated lakes (Faroon et al., 2003). PCBs are of high concern as they accumulate in human tissues and are associated with immune system suppression, increased risk of cardiovascular disease, and cancer (Carpenter, 2006). Sari et al. (2020) assessed the feasibility of using honey bees and their products to monitor PCBs. Of the bee-associated matrices tested, honey bees were the most contaminated with PCBs followed by honey and then bee-collected pollen. PCBs have low solubility in water and are not easily absorbed into plant vascular systems, which explains their low levels in bee pollen. It is likely that the pollen measurements largely represent PCBs on the surface of pollen (Roszko et al., 2016; Sari et al., 2020). PCB concentrations were highest in forager bees during periods of hot dry weather, as increased evaporation of PCBs from contaminated soil resulted in their exposure to higher levels in the air (Sari et al., 2020). Recently, Sari et al. (2021), proposed using bees and honey samples as an alternative to passive air samplers (PASs) for the measurement of atmospheric pollutants, based on a correlation study of PCB values obtained with PASs and analysis of bee-associated materials.

Polycyclic aromatic hydrocarbons (PAHs) are another type of air pollutant that naturally occur in coal, crude oil, and gasoline. PAHs are released into the atmosphere from vehicle exhaust, cigarette smoke, wood burning, and fumes from asphalt roads (Center for Disease Control, 2017). Some PAHs irritate eyes and lungs and are considered to be carcinogenic (De La Torre-Roche et al., 2009). Perugini et al (2009) reported detection of diverse PAHs in worker honey bees and in honey collected from two different regions in Italy. Lambert et al. (2012a) examined PAH levels in French apiaries, measuring pollen, honey, and bees. They demonstrated that bees were the best indicators of environmental PAH contamination, and that the level of detected PAHs was influenced by the region the apiary was located. Al-Alam et al. (2019) measured PAHs in honey samples from across Lebanon and showed that PAH sources, such as petrol or diesel emissions, could be estimated from measurements in honey. Detections in honey aligned with anthropogenic activities prevalent in the different regions; population dense areas had higher levels of PAHs corresponding to fuel combustion and vehicle emissions, compared with less dense regions which were dominated by PAHs released from burning wood for heat.

The distribution of airborne PM on worker honey bees was examined by Negri et al. (2015) in a highly polluted post mining region in Italy. Using electron microscopy and X-ray spectroscopy (SEM-EDX), they found airborne PM to be heavily concentrated at the edges of the forewings, medial plane of the head, and inner surface of the hind legs; all areas containing secreted wax that trap airborne PM. The types of particles detected in soil and sediment samples from the region aligned with those on worker body parts, suggesting that honey bees are effective monitors of airborne PM (Negri et al., 2015). Metal-based ultrafine particulate matter (UFP), i.e., PM less than 0.1 μm in diameter, has been detected in honey bees, bee-collected pollen, and honey collected in an area of intense traffic in Northern Italy (Papa et al., 2021).

Another type of PM are microplastics, small pieces of plastic created for industrial purposes or degraded from larger materials (Zhang et al., 2020). Amato-Lourenço et al. (2020) discussed microplastics as an emerging class of air pollutants with potential effects to respiratory human health. They reviewed human exposure in urbanized areas, and discussed the physical and chemical characteristics of airborne plastic debris, as well as the presence of additives and polymer distributions. The particles are often carried long distances by wind and can be carcinogenic, or serve as a medium for other environmental contaminants (Zhang et al., 2020). Edo et al. (2021) demonstrated that microplastics can adhere to the honey bee body and can thus be measured. They found higher levels of microplastics in urban areas, though suburban and rural levels were comparable, likely due to distribution by wind.

The studies discussed in this subsection demonstrate the potential for using honey bees and bee-associated matrices to monitor different air pollutants that affect human and ecosystem health. Furthermore, particulate matter pollution has been shown to act as a catalyst for climate change (Kyotani and Iwatsuki, 2002; Seaton et al., 1995). Measuring air pollutants and persistent chemicals in honey bees and hive matrices can help identify target areas where reductions of emissions or remediation efforts are most critical.

3.3. Agrochemical pesticides

Agrochemical pesticides are environmentally persistent contaminants that may pose a risk to humans, pollinators, and surrounding ecosystems. Honey bees and their hives can be used as bioindicators of agrochemical pesticides due to the sensitivity of an individual bee, the resilience of the colony unit, and the number of bee-related testable matrices (Balayiannis and Balayiannis, 2008; Bargańska et al., 2016; de Oliveira et al., 2016; Ruschioni et al., 2013). In addition, honey bee foraging choices tend to overlap with other bee species and insect pollinators, thus measuring pesticide residues in bee matrices provides relevant information on the exposure of other pollinator species in an

ecosystem (Bishop et al., 2020; Paini, 2004; Quigley et al., 2019).

Neonicotinoids are the most widely used class of insecticide worldwide (Simon-Delso et al., 2015). Lab and field studies showed that neonicotinoids as well as other pesticides including fungicides and next-generation insecticides reduce colony survival, or have sub-lethal effects on bees such as impaired memory and foraging activity, as well as reduced immunity (DesJardins et al., 2021; Schneider et al., 2012; Tosi et al., 2021; Tsvetkov et al., 2017; Wu et al., 2011). When pesticides levels are lethal, bees are indicators of acute exposure. Often, however, the colony survives and the bees and their associated matrices can be used for short and long-term monitoring. A US study detected 120 agrochemical's active ingredients or metabolites in bee-collected pollen (Traynor et al., 2021). Although most detection levels were predicted to be of low risk to honey bee colonies, the study indicated the potential of using bee-collected pollen as a terrestrial bioindicator of environmental pesticide exposure. Quantification of pesticides in hive matrices depends on the chemical characteristics of the pesticide being measured and the hive matrix used. Niell et al. (2017) investigated how honey bee foragers transfer three neonicotinoids: acetamiprid, imidacloprid, and thiamethoxam from soybean crops to the colony, and measured the accumulation in three hive matrices: pollen, honey, and beeswax. All three neonicotinoids were detected in beeswax but acetamiprid had the lowest transfer ratio, thought to be due to its high volatility, while thiamethoxam had the highest transfer ratio (Niell et al., 2017). Calatayud-Vernich et al. (2018) measured the concentration of 63 pesticides in in-hive bees, freshly stored pollen, and beeswax. Beeswax was the matrix with the highest concentrations of agrochemicals while pollen contained the greatest diversity of pesticide types. This study found that the pesticide content in pollen was higher in intense agricultural settings compared to rural, or grassland settings, indicating that pesticides in stored pollen can mirror spatial differences in environmental pesticide contamination (Calatayud-Vernich et al., 2018). As an alternative to sampling bees and bee matrices, Murcia-Morales et al. (2020) proposed the use of a non-biological in-hive strip that acts as passive sampler of pesticides in honey bee colonies.

Sampling bees and their colony matrices can identify areas where pesticides may be negatively impacting pollinator health, or creating toxic conditions for human populations. Bee-based monitoring may also guide additional testing with environmental or human urine or blood samples, as used for the environmental chemical evaluation of the Canadian population (Pollock et al., 2021). In addition, data obtained from testing honey bees and bee-associated matrices after pesticide pollution incidents could be used as indicator of potential pesticide exposure affecting human, animal and ecosystem health, and integrated as part of the One Health approach (Martinello et al., 2021).

4. Plant and pollinator pathogens

Crop plants are affected by a large number of bacterial, viral, or fungal pathogens. These pathogens present a significant economic challenge as they typically decrease crop yields. Plant pathogens can be passed from one generation to the next via vertical transmission, or between individual plants via horizontal transmission facilitated by abiotic and biotic vectors, including insects. The body of honey bees indirectly transports plant pathogenic material during foraging flights, which include bacterial and fungal organisms (McArt et al., 2014; Pattemore et al., 2014). At least 45 viruses are known to be pollen transmitted, which belong to the genera *Tobamavirus, Ilarvirus*, *Nepovirus*, *Sobemovirus*, and *Idaevirus* (Bhat and Rao, 2020; Levitzky et al., 2019). Molecular techniques such as PCR or enzyme-linked immunosorbent assays (ELISA) have been used for large scale surveys that target plant pathogens (Beaver-Kanuya and Harper, 2019; Roberts et al., 2018). Since the cost of these techniques increases rapidly with the number of pathogens tested, today's screening methods are transitioning to high throughput sequencing (HTS) technologies which can sequence multiple DNA or RNA molecules in parallel (Churko et al., 2013; Roberts et al., 2018; Tremblay et al., 2019). HTS technologies are becoming more affordable, more advanced, and currently the most efficient option for analyzing complex environmental samples such as honey bee-collected pollen (Roberts et al., 2018; Tremblay et al., 2019).

Honey bee biosurveillance provides distinct advantages over conventional screening techniques in that forager bees can collect pollen from multiple plants over a large area more quickly and efficiently than humans. Mature *A. mellifera* colonies contain 20,000–50,000 foragers that act as sampling devices: flying and collecting pollen from floral species within a 4 km radius of their hives (Greenleaf et al., 2007; Michener, 1974). Sampling bees and bee-collected pollen can help reduce the number of samples usually needed to survey for plant pathogens and also allow for early detection (Roberts et al., 2018; Tremblay et al., 2019). Pathogens detected in bees can originate from plants they actively pollinate as well as other species they visit. For example, corn and rice are wind- and self-pollinated crops but they are commonly visited by honey bees, which makes the detection of corn and rice viruses possible (Malerbo-Souza, 2011; Pu et al., 2014; Roberts et al., 2018). Furthermore, the wide foraging range of bees can allow for identification of virus reservoirs and transmission pathways in both managed and non-managed plant species.

In a recent study from our laboratories, analysis of bee-collected pollen showed that metabarcoding, a type of HTS that mass amplifies and sequences variable genomic regions of target species, is effective for detecting fungi, oomycete, and plant species (Tremblay et al., 2019). Visual observations of the flora that surrounded the sampled hives throughout the pollen collection period showed that many of the species observed were also detected by quantitative PCR (qPCR) and HTS. Several genera pathogenic to forest or agricultural plants including *Alternaria* sp., *Colletotrichum* sp., *Fusarium* sp., and *Ophiostoma* sp. were detected in parallel with the plant species they infect. Since collecting pollen pellets from honey bee colonies is simple and inexpensive, this approach has the potential to become an effective tool for the surveillance of plant pathogens (Tremblay et al., 2019). In addition, we recently reported results from our evaluation of bee matrices using HTS as a tool for the identification of plant and bee pests. In this study, we found that more species could be identified from bee-collected pollen than bee samples. Multiple pathogens were identified from the material tested including plant pathogens as well as bee-associated fungi such as the hive fungus *Bettsia alvei*, and the bee fungal pathogen *Ascosphaera apis* (Bilodeau et al., 2020).

Roberts et al. (2018) used RNA sequencing (RNA-Seq), a type of HTS that examines the quantity and sequences of RNA, on pooled honey bee samples from commercial hives across Australia; an island continent with strict biosecurity systems. They detected two plant viruses that mainly infect cucurbits, cucumber green mottle mosaic virus (CGMMV) and Tomato ringspot virus (ToRSV), that had not been detected in the country at the time using conventional screening methods. Depending on the region, CGMMV was detected three months to three years earlier in bee samples than in diseased plant material using traditional screening approaches. The authors suggested that performing HTS on pooled honey bee samples is a promising method for the detection of exotic plant viruses in the region. Surveying for exotic viruses by visually identifying disease symptoms in the field is difficult, as endemic viruses can have similar symptoms and thus create background noise. Performing HTS on pooled honey bee samples can help detect exotic viruses whose disease symptoms have not yet been officially recognized in the field. Thus, honey bee assisted surveillance may improve plant biosecurity programs (Roberts et al., 2018).

The greenhouse vegetable production sector is one area with the potential to greatly benefit from bee-mediated pathogen detection. Greenhouses are enclosed environments that frequently have longer pollination windows due to continuous production, and employ bee pollinators for longer periods than other crops. Tomatoes and cucumbers are two common greenhouse vegetables frequently under threat from tobamovirus infection such as tomato brown rugose fruit virus

(ToBRFV), an emergent threat to tomato production. First detected in Jordan in 2014, this virus has since spread around the world and has effectively evaded all sources of genetic resistance to tobamoviruses (Salem et al., 2016). Infections caused by ToBRFV and CGMMV, which are both pollen transmitted (Levitzky et al., 2019; Liu et al., 2014), frequently result in complete destruction of the crop followed by extensive decontamination, causing serious losses to growers. Bee-based biosurveillance programs could be used to detect these viruses effectively within greenhouses.

Honey bees can also serve as monitors of pathogens affecting other bee species. Bee diseases can spread between species of wild and managed pollinators when healthy bees forage on flowers that have been visited by infected bees of the same or different species. This mechanism contributes to disease spillover between managed honey bees and wild bee populations (Di Prisco et al., 2016; Grassl et al., 2018). For example, de Sousa Pereira et al. (2019) identified viral and fungal parasites in honey bee pollen, including deformed wing virus (DWV) and *Ascosphaera apis*. They also found bumble bee (*Bombus* spp.) larvae infected with *A. apis* showing similar symptoms of Chalkbrood disease as observed in honey bees. In other studies, the prevalence of DWV in bumble bees has been correlated with its prevalence in honey bees (Fürst et al., 2014; Manley et al., 2019). Thus, honey bees can be used as bioindicators of bee pathogens in a local environment and indicate when further surveillance of wild pollinator species is needed.

The studies from our group and others provide strong evidence for using honey bees and the pollen they collect to monitor pollinator and plant pathogens based on the efficiency with which honey bees visit surrounding plants (Bilodeau et al., 2020; Roberts et al., 2018; Tremblay et al., 2019). Since plant diseases can present serious threats to food security, bee-based monitoring could be effective for the early detection of pathogens and for limiting their spread and negative impact. In addition to detecting plant and pollinator pathogens, HTS can identify foreign or invasive plant species that compete with native plants for space and resources and may require intervention.

5. Emerging threats: Climate change and antimicrobial resistance

Climate change, specifically variations in temperature and precipitation, threatens to affect many animal species, ranging from humans to honey bees (Luber and McGeehin, 2008; Switanek et al., 2017). Compared to solitary insects, honey bees are less vulnerable to temperature variations. They are able to closely regulate temperature in the hive to maintain growing conditions during temperate weather and ensure colony survival during winter (Fahrenholz et al., 1989). Increasing global temperatures may, however, negatively affect honey bee thermoregulation and disrupt honey bee colony homeostasis, growth, and survival. Honey bees, in particular honey bee queens in small colonies or nucleus colonies (nucs), may experience measurable effects as direct or indirect consequence of climate variations.

Extreme temperatures have been shown to compromise reproductive success across the animal kingdom by affecting spermatogenesis, sperm cell viability, and overall fertility which leads to reduced reproductive output (Hansen, 2009; Sales et al., 2018; Walsh et al., 2019; Zeh et al., 2012). Studies on honey bees in our laboratories and others have shown that when bee queens are exposed to both low and high temperature, they experience a reduction in fertility (McAfee et al., 2020; Pettis et al., 2016). Gene expression changes after exposure to high temperatures, in particular specific heat shock proteins (HSPs), have the potential to serve as biomarkers for heat stress and environmental bioindicators of heat waves. Measuring changes in queen fertility or quantifying specific proteins such as HSPs, as biomarkers of temperature fluctuations and the effects of climate change, may enable a biomonitoring program to study the prevalence of heat-induced loss of fertility in different landscapes (McAfee et al., 2020).

Extreme temperatures and weather variability may affect plant resources that bees and other animals depend on for food. For example, higher than normal summer temperatures and droughts can end flower blooms prematurely, reducing pollen and nectar for bees to forage on and thus affecting colony mortality (Flores et al., 2019; Switanek et al., 2017). Flores et al. (2019) found that adult populations, hive weights, and stores of honey and bee bread were affected by weather patterns. They observed lower increases of hive weight during the summer of 2017 than in 2016 as well as a decrease in adult population in the later half of the 2017. The results were attributed to the extreme heat in 2017 which reduced the flowering period by three weeks, and decreased the nectar and pollen available to bees (Flores et al., 2019). Monitoring colonies throughout the beekeeping season may provide insight into the environmental effect of extreme temperatures and reduced precipitation. Furthermore, using standardized nucs or small colonies have the potential for improved climate change monitoring as these are more sensitive to environmental changes.

Antimicrobial resistance (AMR) is an emerging global threat of increasing concern in medicine and agriculture (Canadian Food Inspection Agency, 2017). Antimicrobial-resistant bacteria are found in humans, other animals, and plants as well as in soil and water ecosystems. The presence and movement of antibiotics and AMR genes within and between ecosystems is of particular concern. Honey bees and their associated micro-organisms can acquire and carry AMR genes and may be useful as indicators of AMR genes in the environment. Cenci-Goga et al. (2020) analysed honey bees collected in 35 sites in Umbria, Italy and found resistance genes against antimicrobials commonly used in humans and in veterinary medicine. In another study Piva et al. (2020) detected AMR in Enterobacteriaceae from honey bee guts located in different environmental sites. Of particular interest was the finding of amoxicillin/clavulanic acid because it is not used in beekeeping but extensively used for veterinary applications and human medicine. These findings indicate that AMR genes found in honey bees can have an environmental origin which supports the potential utility of honey bees as indicators of environmental AMR (Piva et al., 2020).

Evaluation of honey bee queen fertility and colony parameters, as well as gene expression analyses and microbiome sequencing merit follow-up studies to confirm the utility of honey bees as biomonitors of climate change, antimicrobial resistance, and other emerging threats.

6. Conclusion and future prospects

This narrative review discusses proven and potential uses of honey bees and their hive products for monitoring environmental contaminants, plant and pollinator pathogens, as well as emerging threats such as climate change and antimicrobial resistance. Honey bee matrices mirror spatial variations in environmental agrochemicals, heavy metals, airborne particulate matter, and persistent synthetic chemicals. Using bee matrices to monitor contaminants has widespread implications and the results can guide changes in agricultural management practices as well as target remediation efforts to improve environmental quality and reduce human exposure to toxic or carcinogenic compounds. Analysis of bee colony matrices for the biosurveillance of plant and pollinator pathogens as well as invasive species can facilitate efforts to protect crop yields, food security, and beneficial species.

The use of genomic signatures to monitor stressors in honey bees has been recently reviewed (Grozinger and Zayed, 2020), and the expression of specific genes can be a biochemical fingerprint of environmental contamination or heat stress. This approach can be expanded to using multiple high-throughput ‘omics techniques, including bee gut microbiome profiling. The honey bee gut microbiome is a highly structured system that directly impacts the health and immunity of the bee host and can reflect their exposure to environmental variables (Engel et al., 2016; Kwong and Moran, 2016; Raymann and Moran, 2018). Studies with metals and agrochemicals demonstrated that sub-lethal doses alter the abundance and diversity of the bee gut microbiota (Alberoni et al., 2021; Motta and Moran, 2020; Motta et al., 2018; Rothman et al., 2019).

Microbial communities of other animals, including red-backed salamanders, Shaoxing ducks, and bioeroding sponges, are also affected by environmental stressors, specifically increasing temperatures (Fontaine et al., 2018; Ramsby et al., 2018; Tian et al., 2020). Future research will assess the utility of various bee 'omics and microbiome profile signatures for monitoring environmental health.

While a bee-based biomonitoring approach can be effective, it has limitations such as the preferential detection of contaminant or pathogen groups in bee-associated material, including pollen-transmitted pathogens (Bilodeau et al., 2020). In-hive and between-hive variation on the concentration of detected elements also needs to be considered (Zarić et al., 2021), as well as the differential efficiency with which diverse compounds, such as pesticides, are transferred by foraging bees (Niell et al., 2017). Additional research and implementation efforts are needed to better define the sensitivity of detection for different biotic and abiotic targets in diverse environments, as well as to confirm the utility and limitations of this bee-based monitoring approach for the spatial and temporal study of ecosystem health.

The implementation of local and national bee-monitoring systems could be initiated with the participation of beekeepers for longitudinal sampling of their hives within a citizen science program, and/or with the assistance of local technology transfer teams or professional apiculturists. Coordination with academic, industry, or government laboratories would be needed for sample analysis and data interpretation. To reach a global scale, participation of diverse research groups located in different regions of the world, such as the ones cited in this paper (Fig. 1) could help coordinate efforts. Adoption of this approach in agricultural and urban settings has the potential to provide powerful indicators of ecosystem health to inform policy at the local and global scale. Data collected through bee-related foraging activities can increase our understanding of a rapidly changing world, while promoting the security of food production systems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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