Title (and short running title)

Underlying mechanisms shaping wild bee decline

Journal

Biological Journal of the Linnean Society

DOI

10.1093/biolinnean/blaf043

Authors

Antoine Gekière[1]*, Maxence Gérard[1], Simon G. Potts[2], Denis Michez[1], Guillaume Ghisbain[1,3]

Corresponding author (*)

AG: 0000-0001-5337-1305 (ORCiD)

Postal address: Laboratory of Zoology, University of Mons, 20 Place du Parc, Mons, Belgium

Phone: +32489394002

Email address: antoine.gekiere@umons.ac.be

Affiliations

1. Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Mons, Belgium
2. Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, Reading, UK
3. Spatial Epidemiology Lab (SpELL), Free University of Brussels, Brussels, Belgium

Abstract

Within the Drivers-Pressures-States-Impacts-Responses (DPSIR) framework, anthropogenic activities such as environmental pollution and climate change have consistently been identified as major pressures contributing to the alarming decline of bee populations. While the DPSIR framework provides a valuable structure for assessing the broader context of bee decline, it lacks the resolution to capture the underlying mechanisms that mediate the link between anthropogenic pressures and changes in bee population states. In particular, it does not consider how these pressures disrupt key biological processes that ultimately compromise bee reproductive fitness. This substantial knowledge gap currently limits our ability to pinpoint the causal pathways linking anthropogenic pressures to population declines. To address this limitation, we propose an extension of the DPSIR framework by incorporating a missing yet central component, namely mechanisms, which delineates the biological processes mediating the relationship between pressures and the observed bee population states. We identify and discuss five key mechanisms intrinsically linked to critical phases of the life cycle of bees, each directly affecting reproductive fitness. The delineation of these mechanisms offers a structured and experimentally testable approach for hypothesis-driven research, facilitates the understanding of causal relationships, and fosters more effective communication within the scientific community working on bee conservation.

Keywords

DPSIR; Fitness; Mechanisms; Pollinators; Pressures; States

Introduction

Contemporary anthropogenic activities represent an unprecedented challenge to pollinators globally, threatening the sustainability of ecosystems and human welfare (Brunet & Fragoso 2024; Devkota *et al.* 2024; Dicks *et al.* 2021; Potts *et al.* 2010). Amongst the pollinators for which there is substantial evidence of drastic changes in populations are wild bees (Kerr *et al.* 2015; Zattara & Aizen 2021), a group of >20,000 described species globally that exhibit remarkable ecological, morphological and behavioural diversity (Michener 2007). Most bee species have a solitary lifestyle, with each female independently constructing and provisioning her nest without interacting with offspring or conspecifics. In contrast, social bees form organised colonies characterised by cooperative brood care, division of labour, and overlapping generations (Danforth *et al.* 2019; Rasmont *et al.* 2021). The overwhelming majority of wild bees depend on floral resources for nutrition, with nectar serving as their primary carbohydrate source and pollen providing essential proteins and lipids. While some species specialise in collecting pollen from specific plants, others display a broader diet, gathering resources from a wider range of plant species (Wood *et al.* 2023). Nesting strategies also vary widely, with most species nesting in the soil, constructing underground tunnels and brood cells (Antoine & Forrest 2021). Others nest above ground, utilising pre-existing cavities or constructing nests using plant materials, mud, or resins (Danforth *et al.* 2019). Anthropogenic pressures have been shown to severely impact bee populations, especially in Europe and North America where most studies have been conducted (Cameron *et al.* 2011; Dominique *et al.* 2023; Michez *et al.* 2019). The vast ecological diversity of bees means that species can respond to anthropogenic stressors in markedly different ways. Although a small fraction appears to currently benefit from some specific aspects of global changes (reviewed in Ghisbain *et al.* 2021), the populations of a significant minority of assessed species have been shown to plummet at an alarming rate (Nieto *et al.* 2014; Zattara & Aizen 2021).

In 2009, the Drivers-Pressures-States-Impacts-Responses (DPSIR) framework, widely applied to biodiversity in general (Maxim *et al.* 2009), was employed to decipher the cause-consequence pathways leading to pollinator decline, including bees (Kuldna *et al.* 2009). Building upon the DPSIR framework, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) later conducted a comprehensive global assessment of the health of bees in response to calls from international scientists and policy makers (IPBES 2016). Within their assessment, the IPBES identified both indirect and direct drivers of bee decline. Indirect drivers (referred to as ***drivers*** in the DPSIR framework) are distal processes encompassing social, economic, and institutional systems inherent to the functioning of modern human societies, that do not affect bees directly, but that ultimately lead to declines in their populations. Indirect drivers are the foundational causes for direct drivers (referred to as ***pressures*** in the DPSIR framework), that are processes such as habitat loss, environmental pollution, climate change, alien species invasion and pathogen spread, that operate directly on bee populations (Díaz *et al.* 2015). Such pressures are responsible for the observed extirpation of bee populations globally (referred to as ***states*** in the DPSIR framework) (Kerr *et al.* 2015; Zattara & Aizen 2021) and the associated reduction of ecosystem services (referred to as ***impacts*** in the DPSIR framework) (Brunet & Fragoso 2024; Devkota *et al.* 2024; Dicks *et al.* 2021; Potts *et al.* 2010). To address this issue, numerous initiatives have been implemented to support bee populations at local, national and continental scales (referred to as ***responses*** in the DPSIR framework) (IPBES 2016; Stout & Dicks 2022).

While the DPSIR framework provides a valuable structure for framing the broader context of bee decline, it lacks the resolution to capture the underlying mechanisms linking anthropogenic pressures to changes in bee population states. Specifically, the DPSIR framework does not consider how these pressures affect key biological processes that ultimately undermine reproductive success and the production of viable, fertile offspring (i.e., components of biological fitness). For instance, in the UK, elevated bee population extinction rates were observed in response to neonicotinoid seed treatments (Woodcock *et al.* 2016). However, the underlying mechanisms connecting neonicotinoid exposure to population extirpation were not investigated (e.g., reduced sperm quality; Minnameyer *et al.* 2021). This limitation represents a critical knowledge gap in the rapidly expanding field of bee research, potentially impeding scientists' ability to accurately characterise the mechanistic pathways through which anthropogenic pressures influence bee population states.

To address this limitation, we propose an extension of the DPSIR framework by incorporating a new component, namely mechanisms, which elucidates the biological processes mediating the relationship between well-characterised anthropogenic pressures and the observed states of bee populations (**Figure 1**). Specifically, we identify five key mechanisms that directly impact reproductive fitness, each intrinsically linked to critical phases of the life cycle of bees (**Figure 2**). First, adult individuals may perish, an especially critical outcome if they have not had the opportunity to mate (mechanism no. 1). Should individuals seek to mate, they may encounter challenges in either locating a partner or mating (mechanism no. 2). Even if mating occurs, the gametes may fail to fertilise the partner’s gametes (mechanism no. 3). Subsequently, egg-bearing individuals may fail to lay eggs (mechanism no. 4). Finally, if eggs are successfully laid, offspring may succumb before reaching adulthood (mechanism no. 5). In addition to better connecting the anthropogenic pressures to the current states of bee populations, these mechanisms offer the advantage of being systematically experimentally testable through hypothesis-driven protocols. These mechanisms therefore pave the way for future rigorous studies and are key to underpin more effective communication within the scientific community.

The purpose of this extension of the DPSIR framework is not to exhaustively list all the ways pressures shape mechanisms (**Table 1**), nor to tackle all the potential interactions between these mechanisms (e.g., synergies). Instead, it aims to clearly delineate the mechanisms underlying bee population declines and exemplify how well-characterised pressures impact these mechanisms. Through *ad-hoc* knowledge and iterative data collection, this paper illustrates each mechanism and proposes outstanding questions based on the knowledge gaps found in the literature. These outstanding questions may help academic scientists identify novel experimentally testable avenues to better understand the observed declining states of bee populations.

Although the present framework is designed to formally structure and enhance our limited understanding of the decline of 'all' threatened bees, we mainly reference results from studies on social or domesticated species, including bumble bees (*Bombus* spp.), mason bees (*Osmia* spp.), stingless bees (Meliponini spp.) or the Western honey bee (*Apis mellifera*). Currently, these organisms are the most extensively studied due to their long-standing use as model species, their suitability for laboratory rearing, and their well-documented life cycles (Cameron & Sadd 2020; Medrzycki *et al.* 2013). While not all patterns observed in these species can be directly extrapolated to other bees with contrasting ecologies (e.g., with restricted diet breadths, or reduced tolerance to xenobiotics and extreme climatic events; Ghisbain 2021; Wood *et al.* 2020), many mechanisms have been first demonstrated in these models under standardised conditions (e.g., Gekière *et al.* 2024; Martinet *et al.* 2021b). These findings can subsequently be tested and validated on lesser studied, non-model species (Raine & Rundlöf 2024; Siviter *et al.* 2021).

Mechanism No. 1: Impeding adult survival

A chief factor constraining the reproductive success of bees is the mortality of adults. Prior to the Anthropocene, death was primarily attributed to natural events, predation, disease transmission and parasitism. Although these pressures persist, human enterprises have significantly altered their temporal and spatial dynamics, increasing the scale, severity and probability of effects, particularly after the beginning of the industrial era (Pelletier & Coltman 2018). The international transport of goods and infrastructures has, for instance, led to the introduction of non-native predators (Requier *et al.* 2019) and microsporidian parasites (Brown 2017), posing novel direct threats to local native bee populations (Ghisbain *et al.* 2021; Willcox *et al.* 2023). Concurrently, anthropogenic pressures can exacerbate the vulnerability of adults to these new and elevated patterns of competition, predation, parasitism, and other threats. Human activities resulting in habitat loss, degradation and fragmentation, in conjunction with pesticide use, altering floral resource availability have, for instance, diminished the resilience of bee populations against their historical predators and parasites by compromising their size, cognitive abilities and immunocompetence (Aguiar *et al.* 2023; Anderson & Harmon-Threatt 2019; Brandt *et al.* 2016; Gray *et al.* 2024; Kaakinen *et al.* 2024; McNeil *et al.* 2020; Al Naggar *et al.* 2022; Tan *et al.* 2014).

In addition to modulating resilience towards predation and parasitism, xenobiotics (e.g., ‘active’ and 'inert' components in pesticides) are also directly involved in bee mortality (Raine & Rundlöf 2024; Shannon *et al.* 2023). Insecticides, considered as the most toxic class of pesticides for bees, typically disrupt neurotransmission and cellular respiration (Sparks & Nauen 2015). Other pesticide classes such as fungicides and herbicides may also exhibit acute toxicity on bee individuals, as demonstrated by the adverse impact of globally used glyphosate-based formulations in common herbicides (Belsky & Joshi 2020; Straw *et al.* 2021). Similarly, the fungicide pyraclostrobin has been demonstrated to cause midgut damage leading to subsequent mortality in the stingless bee *Melipona scutellaris* (da Costa Domingues *et al.* 2020). Compounding this issue, pesticides can act synergistically, for instance with fungicides impeding a crucial enzyme involved in insecticide detoxification (Schuhmann *et al.* 2022). Beyond pesticides, environmental pollutants including heavy metals and microplastics can also directly contribute to bee mortality through physiological dysfunctions involving oxidative stress, enzyme inhibition and DNA damage (Gekière *et al.* 2023; Al Naggar *et al.* 2021).

Bee individuals and populations progressively face pressures from climatic factors, particularly from the increased frequency, length and intensity of extreme climatic events. Prolonged periods of heat, especially in arid lands, induced by climate change, elevate metabolic rates, leading to increased free radical production as well as protein unfolding, DNA damage, and lipid peroxidation, ultimately resulting in death (Kuo *et al.* 2023). Heatwaves have also been shown to perturb bumble bee immunity and survival in the face of infection (Tobin *et al.* 2024). However, the resilience of bees to heat stress is highly species-specific. For example, while most 'large' bees (e.g., the bumble bee *Bombus lucorum* and the carpenter bee *Xylocopa pubescens*) from Mediterranean regions can withstand temperatures of 40 °C for 10 hours (Boustani *et al.* 2024; Martinet *et al.* 2015), the majority of bumble bees from colder regions (e.g., *B. alpinus*, *B. hyperboreus*, *B. neoboreus*) die within an hour under similar conditions (Martinet *et al.* 2021a).

Finally, a lack of food resources (i.e., pollen and nectar) through landscape alteration and managed beekeeping activities, and their associated competition for food, threaten bee populations (Iwasaki & Hogendoorn 2022; Phillips *et al.* 2018). Insufficient resource quality and quantity can potentially cause death by starvation (Kyrkjebø Vinnes *et al.* 2022; Schenk *et al.* 2018) (**Box 1**). Death by starvation arises when bees rely on protein breakdown to fuel energy demand, ultimately leading to organ damages and the complete cessation of vital activities. Starvation mainly occurs when bees lack carbohydrates to support their foraging activity (Carnell *et al.* 2020; Tew *et al.* 2023). Starvation also occurs when bees fail to collect sufficient amounts and specific profiles of other macromolecules, such as amino acids and sterols (Carnell *et al.* 2020).

Outstanding questions

- What combinations of chemical pollutants are most responsible for the direct killing of adult bees?
- To what extent do environmental pressures and sublethal effects interact synergistically to cause mortality in adult bees?

Mechanism No. 2: Preventing mate searching and mating

Numerous anthropogenic pressures can influence the likelihood of adult bees encountering suitable mating partners, thereby affecting the probability of offspring production. Even minor alterations in pheromone mixtures have been shown to disrupt conspecific recognition, potentially impeding mate detection (Gomez Ramirez *et al.* 2023). Temperature extremes, of which occurrence and intensity are exacerbated by climate change, have emerged as a noteworthy factor in modifying sex pheromone profiles, affecting the chemical signature of various bee species including solitary bees and bumble bees (Conrad *et al.* 2017; Martinet *et al.* 2021b). Interestingly however, queens of the bumble bee *Bombus terrestris* exhibited equal attraction to the cephalic labial gland secretions of males exposed to heat stress compared to males from the control group (Przybyla *et al.* 2021). Thus, changes in the chemical signature of sexual secretions do not necessarily imply lower mate attractivity. Exposure to miticides during honey bee development has been observed to reduce the attractiveness of queen mandibular gland contents and alter the relative composition of chemical compounds within the glands (Walsh *et al.* 2020). Likewise, sublethal concentrations of an insecticide shaped precopulatory behaviour and mate quality assessment in the megachilid bee bee *Heriades truncorum* (Boff & Ayasse 2024). In the stingless bee *Scaptotrigona bipunctata*, exposure to a fungicide during larval development has been shown to result in reduced male genitalia size in adults, potentially impairing their mating ability (Ramos *et al.* 2023).

Anthropogenic pressures leading to lower population growth rates, such as decreased food quality and quantity as well as pesticide exposure, can also reduce mate encounter rates

(Oliveira & Schlindwein 2010; Whitehorn *et al.* 2012). These factors can diminish overall population size and thus decrease the pool of potential mating partners available to bee individuals. Parasitism, urbanisation and limited resource availability have been identified as pressures capable of altering bee sex ratios, often resulting in a male bias (Fitch *et al.* 2019; Seidelmann *et al.* 2010). Reducing flower availability may also result in a lack of mating sites, as male bees are known to attract females by releasing pheromones on flowers (Oliveira & Schlindwein 2010). A sex-dependent impact of developmental temperature has also been suggested for bumble bees. Indeed, while temperature variations significantly increased queen production in colonies of *Bombus terrestris* maintained at high temperatures when compared to colonies maintained at lower temperatures, male production was not affected (Guiraud *et al.* 2021; Nasir *et al.* 2019). Chronic exposure to neonicotinoid insecticides has been associated with a drastic reduction in queen production, with treated colonies producing up to 85% fewer queens compared to control colonies (Whitehorn *et al.* 2012). Colonies exposed to pesticide-treated pollen also exhibit diminished capacity for viable queen production (Milone & Tarpy 2021), while colonies treated with a fungicide had delayed male emergence and reduced male body size (Runnion *et al.* 2024).

Outstanding questions

- To what extent can pathogens alter the sex ratio of the mother bee’s offspring?
- Is mating success influenced by the availability of floral resources during the mating season?

Mechanism No. 3: Disrupting gamete development and performance

Another non-lethal mechanism constraining the production of viable and fertile offspring in bee populations is linked to a decline in bee fecundity, namely a diminished ability for gametes to fuse and form a viable zygote. For instance, various pesticides, such as the widely studied neonicotinoids, have been demonstrated to have deleterious effects on the fecundity of pollinators. Negative impacts of neonicotinoid exposure have been demonstrated in the bumble bee *Bombus terrestris*, affecting their reproductive anatomy (Barbosa *et al.* 2015; Baron *et al.* 2017b; Laycock *et al.* 2012). In males of the bumble bee *Bombus terrestris* and the mason bee *Osmia cornuta*, exposure to neonicotinoids was shown to negatively affect overall sperm quality (Minnameyer *et al.* 2021; Strobl *et al.* 2021), a trend also observed in honey bee drones (Ciereszko *et al.* 2017). Interestingly, honey bee queens exposed to an insecticide as larvae had reduced sperm viability in their spermatheca after mating (Kozii *et al.* 2021). Queens of the honey bee *Apis mellifera* and the bumble bee *Bombus terrestris* exposed to an insecticide harboured degenerated and resorbed ovarioles, affecting fertilisation and colony development (Baron *et al.* 2017a; Moreira *et al.* 2022). Likewise, females of the mason bee *Osmia bicornis* exposed to a mixture of insecticide and fungicide had reduced oocyte length (Sgolastra *et al.* 2018).

In a variety of animals, including bees, fecundity can deteriorate at temperatures less severe than the lethal thermal limits of the individuals themselves. In a recent experiment, the viability of male bumble bee spermatozoa was reduced (both *in vivo* and *in vitro*) when exposed to non-lethal, heatwave-like temperatures. Increased oxidative stress or denatured seminal fluid proteins lead to damaged cell membranes and are suggested as possible processes underlying sperm viability decline (Avila *et al.* 2011; Bisconti *et al.* 2021). Hence exposure to short-term heatwaves could make males particularly vulnerable to reductions in fecundity, especially given that most male bees spend their whole adult life outside of thermoregulated nests (Martinet *et al.* 2021a). Decline in sperm viability can be further exacerbated in bee species in which males tend to be produced in late spring or summer, when the likelihood of heatwaves is the highest (Rasmont *et al.* 2021). This issue is even more worrying given that, in bumble bees, it was shown that sperm production only occurs during male ontogeny and mature males no longer produce new sperm even in case of significant degradation (Baer 2003). Alternatively, mated females storing initially undamaged sperm in their spermatheca can be exposed to sperm-killing temperature spikes, with colony failure as a possible consequence (Pettis *et al.* 2016). Abnormal temperature also impacts female gametes, although evidence remains limited. In the Western honey bee *Apis mellifera*, workers reared at 38 °C had reduced oocyte length compared to workers reared at 34 °C (Khedidji *et al.* 2024).

Declines in spermatozoa cell viability only constitute, however, one of many possible proxies of overall sperm quality. Recent evidence demonstrated, for instance, a detrimental impact of simulated heatwaves on sperm DNA integrity in two cold-adapted bumblebee species (Martinet *et al.* 2021a). Other key proxies of overall sperm quality, including alterations in cell concentration, morphology, motility and mitochondrial function, are increasingly explored in a myriad of other taxonomic groups at various life stages (Sales *et al.* 2021; Walsh *et al.* 2019) and are yet to be fully explored in wild bees, especially after exposure to stressors. Declines in bee fecundity are particularly challenging for monandrous species, in which a female mating with a single sterile, sperm-damaged male would be unable to produce offspring (White & Dillon 2023).

Outstanding questions

- Do sperm and ovaries harbour similar resistance in the face of the same anthropogenic pressures?
- How do pollen and nectar diets affect the development of sperm and ovaries?

Mechanism No. 4: Altering nesting and egg laying

Numerous social bee species enter diapause as adults after mating (Santos *et al.* 2019), which represents a pivotal stage in their bee life cycles before seeking a nest to lay eggs. Most of the literature on mortality during hibernation has focused on social species, especially bumble bees and honey bees (e.g., Shi *et al.* 2023). Apart from inherent individual characteristics such as genetic diversity, age and body size, adverse environmental conditions can lead to high mortality rates when compared to background mortality under optimal conditions (Shi *et al.* 2023; Straub *et al.* 2015). Resource scarcity can amplify mortality during diapause. For instance, limited access to pollen and nectar disrupts diapause survival, primarily due to reduced pre-diapause body weight and diminished reserves of lipids and carbohydrates (Treanore & Amsalem 2020; Woodard *et al.* 2019). Overwintering temperature represents another critical determinant of diapause success: cold stress diminishes diapause survival (Yoon *et al.* 2013), whereas warmer temperatures trigger diapause termination and force activity in the winter season, posing phenological mismatches in the absence of sufficient blooming floral resources (Dos Santos *et al.* 2016). Moreover, exposure to pesticides and parasites prior to diapause has been shown to escalate mortality during this phase (Fauser *et al.* 2017). The mechanisms underlying these observations likely entail indirect pathways, such as induced weight loss and compromised immune function, rather than direct mortality following stressor exposure (Brown *et al.* 2003; Costa *et al.* 2020; Fauser *et al.* 2017).

Intensive agricultural practices, including grazing and tillage, affect the availability of nesting sites for below solitary ground-nesting bees (which comprise ~70% of bee species; Michez *et al.* 2019; Kimoto *et al.* 2012; McHugh *et al.* 2022; Murray *et al.* 2012; Sjödin *et al.* 2008) as well as the availability of rodent nests which are crucial for bumble bees (McFrederick & LeBuhn 2006; Wan *et al.* 2022). Decrease in nesting site availability due to grazing can also affect above-ground nesting bees, as observed for different species of solitary osmiine bees (e.g., *Osmia aurulenta*), for which the decrease of snail shells (a key nesting resources on semi-natural grassland) directly affects their populations (Hopfenmüller *et al.* 2020).

Climate change exacerbates the challenge of finding suitable nesting sites, with extreme precipitation and flooding potentially compromising nesting site quality. In the absence of suitable nesting localities around flooded sites, extreme precipitation can be devastating, as evidenced by a >50% reduction of the solitary bee *Andrena vaga* population in Germany

(Fellendorf *et al.* 2004; Neumüller *et al.* 2018). For above-ground nesting bees, the loss of standing dead wood poses a significant threat (Westerfelt *et al.* 2018). Such nesting substrates also represent resources subject to competition, as shown from the literature on the highly invasive *Megachile sculpturalis*. This species, indigenous to Asia and invasive in both Europe and North America, exhibits aggressive behaviour to 'evict' native individuals from pre-existing nesting sites (Lanner *et al.* 2020; Straffon-Díaz *et al.* 2021).

Once a female finds a nesting site, its probability of successful egg laying, and the laying rate, vary depending on different factors (Baron *et al.* 2017a). Anthropogenic pressures, like chronic exposure to insecticides or low diet quality, can result in bumble bee colony initiation being delayed (Baron *et al.* 2017a; Dance *et al.* 2017; Leza *et al.* 2018; Straub *et al.* 2023). Laying rate can also decrease subsequent to miticide (Walsh *et al.* 2020) or insecticide exposure (Williams *et al.* 2015; Wu-Smart & Spivak 2018), both in social and solitary species (Stuligross & Williams 2020). Pesticides are not the only stressors decreasing the laying rate, as poor-quality diet and elevated temperature also result in fewer eggs laid by bumble bees colonies (Becher *et al.* 2024; Gérard *et al.* 2022; Vanderplanck *et al.* 2019).

Outstanding questions

- To what extent do invasive species prevent endemic bees from finding a nest and laying eggs?
- Do impaired cognitive abilities prevent bees from returning to their nest?

Mechanism No. 5: Impeding juvenile development and survival

Ultimately, bee reproductive fitness may be compromised if their offspring perish during a juvenile stage (i.e., larval or pupal development) preceding adulthood. As for adult bees, larvae may perish due to exposure to xenobiotics (Schwarz *et al.* 2024) as well as heatwaves (Melone *et al.* 2024), lack of high-quality resources (McAulay *et al.* 2021), and parasite infection (Anderson *et al.* 2023).

Exposure to xenobiotics constitutes a major driver of juvenile mortality, despite inherent detoxification capabilities in these life stages (Yu *et al.* 2021). For instance, in honey bee larvae, neonicotinoid insecticides trigger histo-physiological damages in various organs (Carneiro *et al.* 2023; Favaro *et al.* 2023). Fungicides and herbicides also pose a significant threat to juvenile survival, with herbicides and fungicides impeding larval ontogeny and defecation, respectively, ultimately leading to death (Phan *et al.* 2024; Vázquez *et al.* 2023). In addition to pesticides, pollutants such as trace metals in contaminated areas jeopardise juvenile survival, with increased mortality after exposure to copper, cadmium, and their combination in honey bees (Di *et al.* 2016, 2020). Abiotic conditions beyond xenobiotics, such as environmental temperature, also strongly influence the viability of bee juveniles. Exposure of juveniles to suboptimal temperature regimes resembling heatwaves can substantially increase their mortality (Melone *et al.* 2024).

A significant biotic factor contributing to juvenile mortality is the insufficient availability of high-quality food resources. Bee juveniles require balanced proportions of macro- and micro-nutrients (Austin & Gilbert 2021; Crone *et al.* 2022; Filipiak *et al.* 2021). Juveniles also have to deal with toxic, specialised metabolites present in certain pollen sources (Trunz *et al.* 2020), as well as some harmful pollen exines (Rivest *et al.* 2024). Issues may therefore arise when juveniles are fed by adults with inappropriate pollen diets, although it remains unclear whether adult bees do forage on such inappropriate resources in the field (Bukovinszky *et al.* 2017). For instance, juveniles of two phylogenetically close generalist bee species (i.e., *Osmia cornuta* and *O. bicornis*) showed striking differences in their ability to develop on pollen of the same plant species, highlighting that even generalist bees need physiological adaptations to cope with the unfavourable chemical properties of certain pollen (Sedivy *et al.* 2011). This phenomenon was also demonstrated for Asteraceae flowers, with juveniles of non-Asteraceae specialist species (e.g., *O. iridis*) failing to develop on Asteraceae pollen (McAulay *et al.* 2021; Vanderplanck *et al.* 2018).

Finally, parasites and pathogens constitute significant biotic factors that profoundly influence juvenile survival in bee populations. Parasitoids (e.g., *Melittobia* spp.; Anderson *et al.* 2023), fungi (e.g. *Ascosphaera* spp., *Aspergillus* spp. and *Vairimorpha* spp.; Bramke *et al.* 2019; Evison & Jensen 2018), bacteria (e.g., *Paenibacillus* spp. and *Melissococcus* spp.; Fünfhaus *et al.* 2018) and viruses (e.g., black queen cell virus; Yañez *et al.* 2020) are all known to cause significant mortality in juveniles. Although parasites and pathogens are inherent, even to healthy networks (Brown 2022), many have been documented in high abundance in commercial honey bee and bumble bee populations, raising concerns regarding potential spillover events from managed to wild bee populations (Fürst *et al.* 2014). This issue is even more concerning in a context of anthropogenic pollution and lack of sufficient food resources, with both stressors impeding the resistance of juveniles against antagonist organisms (Wilfert *et al.* 2021).

Outstanding questions

- Do bee larvae harbour species-specific resistance towards xenobiotics?
- To what extent do nest-usurping alien bee species increase larval mortality in native bee populations?

Discussion

For decades, growing evidence has highlighted the detrimental effects of anthropogenic pressures, such as pollution and climate change, on the states of bee populations. While these studies have been instrumental in demonstrating the risks posed by these pressures, they have largely fallen short of elucidating the underlying mechanisms that translate these pressures into population declines. This emphasis on pressures rather than on underlying mechanisms constrains our understanding of the causal relationships leading to bee population decline.

Moreover, the continued focus on pressures without sufficient attention to mechanisms has impeded the establishment of a clear hierarchy of risks among these pressures in the scientific community, limiting our ability to prioritise and mitigate their consequences effectively.

By introducing an extension of the DPSIR framework that incorporates a mechanistic link, we aim at better elucidating how anthropogenic pressures shape the observed states of bee populations. Because these mechanisms are experimentally testable, our extension provides a more comprehensive framework designed to guide both empirical research and modelling efforts within the scientific community. By delving deeper into the individual-level mechanisms driving population-level declines, this framework disentangles the multiple interacting mechanisms influencing bee populations. Consequently, it underscores the importance of considering sublethal individual effects when evaluating the effects of anthropogenic pressures on bee populations. As an example, pesticides are often approved if they do not significantly affect bee mortality in the first tier of risk assessment (Sgolastra *et al.* 2020). However, pesticides with negligible acute lethality can still impair reproductive fitness and have follow-up effects on bee populations (Barascou *et al.* 2021). Using the present framework thus highlights the need for a more holistic approach to pesticide risk assessment in bees (Siviter *et al.* 2023).

A remaining critical gap is around the challenge of quantifying the relative proportion of bee population decline attributable to each of the five mechanisms. Adopting the present framework can help the design and implementation of experimental approaches to investigate this issue. The framework also contributes to rapidly identifying some of the outstanding knowledge gaps around the biological mechanisms of bee decline. For example, there is no knowledge around the effects of parasites on the ability of bees to find partners and mate, and no studies addressing the effects of poor-quality resources on the bees' gametes (**Table 1**).

Later, another critical avenue of research will be exploring how bees' gut microbial symbionts contribute to their resilience against the mechanisms underlying their decline (**Box 2**).

In addition to guiding scientists, the presently refined framework may be used as an additional tool for practitioners and policymakers engaged in bee conservation, and in biodiversity conservation in general. Better characterisation of the underpinning mechanisms may help tailor responses towards the main pressures and most sensitive life history stages of threatened organisms, thereby potentially increasing the effectiveness and relevance of both empirical approaches and mitigation actions. For instance, preserving and restoring suitable habitats for bee nesting may be more immediately actionable at local scales than mitigating the broader impacts of climate change on bee mating behaviours. Likewise, developing pesticides that do not impede larval development may be more directly actionable than eradicating invasive alien species usurping nesting sites.

References

Aguiar, J.M.R.B.V., Nocelli, R.C.F., Giurfa, M. & Nascimento, F.S. (2023) Neonicotinoid effects on tropical bees: imidacloprid impairs innate appetitive responsiveness, learning and memory in the stingless bee *Melipona quadrifasciata*. *Science of The Total Environment* 877, 162859. https://doi.org/10.1016/j.scitotenv.2023.162859

Anderson, A.R., Ramirez, R.A., Earl Creech, J. & Pitts-Singer, T.L. (2023) *Melittobia acasta* (Hymenoptera: Eulophidae) female longevity and life stage-dependent parasitism using commercially managed *Megachile rotundata* (Hymenoptera: Megachilidae) as hosts N. Leppla (Ed). *Journal of Insect Science* 23. https://doi.org/10.1093/jisesa/iead031

Anderson, N.L. & Harmon-Threatt, A.N. (2019) Chronic contact with realistic soil concentrations of imidacloprid affects the mass, immature development speed, and adult longevity of solitary bees. *Scientific Reports* 9, 3724. https://doi.org/10.1038/s41598-019-40031-9

Antoine, C.M. & Forrest, J.R. (2021) Nesting habitat of ground-nesting bees: a review. *Ecological Entomology* 46, 143–159. https://doi.org/10.1111/een.12986

Austin, A.J. & Gilbert, J.D.J. (2021) Solitary bee larvae prioritize carbohydrate over protein in parentally provided pollen. *Functional Ecology* 35, 1069–1080. https://doi.org/10.1111/1365-2435.13746

Avila, F.W., Sirot, L.K., LaFlamme, B.A., Rubinstein, C.D. & Wolfner, M.F. (2011) Insect seminal fluid proteins: identification and function. *Annual Review of Entomology* 56, 21–40. https://doi.org/10.1146/annurev-ento-120709-144823

Baer, B. (2003) Bumblebees as model organisms to study male sexual selection in social insects. *Behavioral Ecology and Sociobiology* 54, 521–533. https://doi.org/10.1007/s00265-003-0673-5

Barascou, L., Brunet, J.-L., Belzunces, L., Decourtye, A., Henry, M., Fourrier, J., Le Conte, Y. & Alaux, C. (2021) Pesticide risk assessment in honeybees: toward the use of behavioral and reproductive performances as assessment endpoints. *Chemosphere* 276, 130134. https://doi.org/10.1016/j.chemosphere.2021.130134

Barbosa, W.F., De Meyer, L., Guedes, R.N.C. & Smagghe, G. (2015) Lethal and sublethal effects of azadirachtin on the bumblebee *Bombus terrestris* (Hymenoptera: Apidae). *Ecotoxicology* 24, 130–142. https://doi.org/10.1007/s10646-014-1365-9

Baron, G.L., Jansen, V.A.A., Brown, M.J.F. & Raine, N.E. (2017a) Pesticide reduces bumblebee colony initiation and increases probability of population extinction. *Nature Ecology & Evolution* 1, 1308–1316. https://doi.org/10.1038/s41559-017-0260-1

Baron, G.L., Raine, N.E. & Brown, M.J.F. (2017b) General and species-specific impacts of a neonicotinoid insecticide on the ovary development and feeding of wild bumblebee queens. *Proceedings of the Royal Society B: Biological Sciences* 284, 20170123. https://doi.org/10.1098/rspb.2017.0123

Becher, M.A., Twiston-Davies, G., Osborne, J.L. & Lander, T.A. (2024) Resource gaps pose the greatest threat for bumblebees during the colony establishment phase. *Insect Conservation and Diversity*, 1–14. https://doi.org/10.1111/icad.12736

Belsky, J. & Joshi, N.K. (2020) Effects of fungicide and herbicide chemical exposure on Apis and non-Apis bees in agricultural landscape. *Frontiers in Environmental Science* 8, 81. https://doi.org/10.3389/fenvs.2020.00081

Bisconti, M., Simon, J.-F., Grassi, S., Leroy, B., Martinet, B., Arcolia, V., Isachenko, V. & Hennebert, E. (2021) Influence of risk factors for male infertility on sperm protein composition. *International Journal of Molecular Sciences* 22, 13164. https://doi.org/10.3390/ijms222313164

Boff, S. & Ayasse, M. (2024) Exposure to sublethal concentration of flupyradifurone alters sexual behavior and cuticular hydrocarbon profile in *Heriades truncorum*, an oligolectic solitary bee. *Insect Science* 31, 859–869. https://doi.org/10.1111/1744-7917.13268

Bonilla-Rosso, G. & Engel, P. (2018) Functional roles and metabolic niches in the honey bee gut microbiota. *Current Opinion in Microbiology* 43, 69–76. https://doi.org/10.1016/j.mib.2017.12.009

Borghi, M., Perez de Souza, L., Yoshida, T. & Fernie, A.R. (2019) Flowers and climate change: a metabolic perspective. *New Phytologist* 224, 1425–1441. https://doi.org/10.1111/nph.16031

Boustani, M., Martinet, B., Michez, D., Nemer, N. & Rasmont, P. (2024) Heat resistance variability in the Lebanese bee fauna. *Apidologie* 55, 29. https://doi.org/10.1007/s13592-024-01070-y

Bramke, K., Müller, U., McMahon, D.P. & Rolff, J. (2019) Exposure of larvae of the solitary bee Osmia bicornis to the honey bee pathogen Nosema ceranae affects life history. *Insects* 10, 380. https://doi.org/10.3390/insects10110380

Brandt, A., Gorenflo, A., Siede, R., Meixner, M. & Büchler, R. (2016) The neonicotinoids thiacloprid, imidacloprid, and clothianidin affect the immunocompetence of honey bees (*Apis mellifera* L.). *Journal of Insect Physiology* 86, 40–47. https://doi.org/10.1016/j.jinsphys.2016.01.001

Brown, M.J.F. (2017) Microsporidia : An emerging threat to bumblebees ? *Trends in Parasitology* 33, 754–762. https://doi.org/10.1016/j.pt.2017.06.001

Brown, M.J.F. (2022) Complex networks of parasites and pollinators: moving towards a healthy balance. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377. https://doi.org/10.1098/rstb.2021.0161

Brown, M.J.F., Schmid-Hempel, R. & Schmid-Hempel, P. (2003) Strong context-dependent virulence in a host-parasite system: reconciling genetic evidence with theory. *Journal of Animal Ecology* 72, 994–1002. https://doi.org/10.1046/j.1365-2656.2003.00770.x

Brunet, J. & Fragoso, F.P. (2024) What are the main reasons for the worldwide decline in pollinator populations? *CABI Reviews*, 0016. https://doi.org/10.1079/cabireviews.2024.0016

Bukovinszky, T., Rikken, I., Evers, S., Wäckers, F.L., Biesmeijer, J.C., Prins, H.H.T. & Kleijn, D. (2017) Effects of pollen species composition on the foraging behaviour and offspring performance of the mason bee *Osmia bicornis* (L.). *Basic and Applied Ecology* 18, 21–30. https://doi.org/10.1016/j.baae.2016.11.001

Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F. & Griswold, T.L. (2011) Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America* 108, 662–667. https://doi.org/10.1073/pnas.1014743108

Cameron, S.A. & Sadd, B.M. (2020) Global trends in bumble bee health. *Annual Review of Entomology* 65, 209–232. https://doi.org/10.1146/annurev-ento-011118-111847

Campbell, D.R., Sosenski, P. & Raguso, R.A. (2019) Phenotypic plasticity of floral volatiles in response to increasing drought stress. *Annals of Botany* 123, 601–610. https://doi.org/10.1093/aob/mcy193

Carneiro, L.S., Santos, C.G., Resende, M.T.C.S. de, Souza, D.L.L. de, Souza, D. dos S., Souza, A.M. da C., Motta, J.V. de O., Nere, P.H.A., Oliveira, A.H. de & Serrão, J.E. (2023) Effects of the insecticide imidacloprid on the post-embryonic development of the honey bee *Apis mellifera* (Hymenoptera: Apidae). *Science of The Total Environment* 905, 167278. https://doi.org/10.1016/j.scitotenv.2023.167278

Carnell, J.D., Hulse, R.A. & Hughes, W.O.H. (2020) A review of nutrition in bumblebees: the effect of caste, life-stage and life history traits. In: *Advances in Insect Physiology*. Elsevier Ltd., Sydney, New South Wales, Australia, pp. 71–129.

Ciereszko, A., Wilde, J., Dietrich, G.J., Siuda, M., Bąk, B., Judycka, S. & Karol, H. (2017) Sperm parameters of honeybee drones exposed to imidacloprid. *Apidologie* 48, 211–222. https://doi.org/10.1007/s13592-016-0466-2

Conrad, T., Stöcker, C. & Ayasse, M. (2017) The effect of temperature on male mating signals and female choice in the red mason bee, *Osmia bicornis* (L.). *Ecology and Evolution* 7, 8966–8975. https://doi.org/10.1002/ece3.3331

Costa, C.P., Duennes, M.A., Fisher, K., Der, J.P., Watrous, K.M., Okamoto, N., Yamanaka, N. & Woodard, S.H. (2020) Transcriptome analysis reveals nutrition- and age-related patterns of gene expression in the fat body of pre-overwintering bumble bee queens. *Molecular Ecology* 29, 720–737. https://doi.org/10.1111/mec.15361

da Costa Domingues, C.E., Bello Inoue, L.V., da Silva-Zacarin, E.C.M. & Malaspina, O. (2020) Fungicide pyraclostrobin affects midgut morphophysiology and reduces survival of Brazilian native stingless bee *Melipona scutellaris*. *Ecotoxicology and Environmental Safety* 206, 111395. https://doi.org/10.1016/j.ecoenv.2020.111395

Crone, M.K., Biddinger, D.J. & Grozinger, C.M. (2022) Wild bee nutritional ecology: integrative strategies to assess foraging preferences and nutritional requirements. *Frontiers in Sustainable Food Systems* 6. https://doi.org/10.3389/fsufs.2022.847003

Dance, C., Botías, C. & Goulson, D. (2017) The combined effects of a monotonous diet and exposure to thiamethoxam on the performance of bumblebee micro-colonies. *Ecotoxicology and Environmental Safety* 139, 194–201. https://doi.org/10.1016/j.ecoenv.2017.01.041

Danforth, B.N., Minckley, R.L. & Neff, J.L. (2019) *The solitary bees*. Princeton University Press. Available from: http://www.jstor.org/stable/10.2307/j.ctvd1c929

Descamps, C., Quinet, M. & Jacquemart, A.-L. (2021) The effects of drought on plant–pollinator interactions: what to expect? *Environmental and Experimental Botany* 182, 104297. https://doi.org/10.1016/j.envexpbot.2020.104297

Devkota, K., Ferreira, A.B., Timberlake, T.P. & dos Santos, C.F. (2024) The impact of pollinator decline on global protein production: Implications for livestock and plant-based products. *Global Ecology and Conservation* 50, e02815. https://doi.org/10.1016/j.gecco.2024.e02815

Dharampal, P.S., Danforth, B.N. & Steffan, S.A. (2022) Exosymbiotic microbes within fermented pollen provisions are as important for the development of solitary bees as the pollen itself. *Ecology and Evolution* 12, 1–13. https://doi.org/10.1002/ece3.8788

Di, N., Hladun, K.R., Zhang, K., Liu, T.-X. & Trumble, J.T. (2016) Laboratory bioassays on the impact of cadmium, copper and lead on the development and survival of honeybee (*Apis mellifera* L.) larvae and foragers. *Chemosphere* 152, 530–538. https://doi.org/10.1016/j.chemosphere.2016.03.033

Di, N., Zhang, K., Hladun, K.R., Rust, M., Chen, Y.-F., Zhu, Z.-Y., Liu, T.-X. & Trumble, J.T. (2020) Joint effects of cadmium and copper on *Apis mellifera* foragers and larvae. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology* 237, 108839. https://doi.org/10.1016/j.cbpc.2020.108839

Díaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N., Larigauderie, A., Adhikari, J.R., Arico, S., Báldi, A., Bartuska, A., Baste, I.A., Bilgin, A., Brondizio, E., Chan, K.M.A., Figueroa, V.E., Duraiappah, A., Fischer, M., Hill, R., Koetz, T., Leadley, P., Lyver, P., Mace, G.M., Martin-Lopez, B., Okumura, M., Pacheco, D., Pascual, U., Pérez, E.S., Reyers, B., Roth, E., Saito, O., Scholes, R.J., Sharma, N., Tallis, H., Thaman, R., Watson, R., Yahara, T., Hamid, Z.A., Akosim, C., Al-Hafedh, Y., Allahverdiyev, R., Amankwah, E., Asah, T.S., Asfaw, Z., Bartus, G., Brooks, A.L., Caillaux, J., Dalle, G., Darnaedi, D., Driver, A., Erpul, G., Escobar-Eyzaguirre, P., Failler, P., Fouda, A.M.M., Fu, B., Gundimeda, H., Hashimoto, S., Homer, F., Lavorel, S., Lichtenstein, G., Mala, W.A., Mandivenyi, W., Matczak, P., Mbizvo, C., Mehrdadi, M., Metzger, J.P., Mikissa, J.B., Moller, H., Mooney, H.A., Mumby, P., Nagendra, H., Nesshover, C., Oteng-Yeboah, A.A., Pataki, G., Roué, M., Rubis, J., Schultz, M., Smith, P., Sumaila, R., Takeuchi, K., Thomas, S., Verma, M., Yeo-Chang, Y. & Zlatanova, D. (2015) The IPBES Conceptual Framework - connecting nature and people. *Current Opinion in Environmental Sustainability* 14, 1–16. https://doi.org/10.1016/j.cosust.2014.11.002

Dicks, L. V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmill-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, Y.J., Lattorff, H.M.G., Lungharwo, T., Seymour, C.L., Vanbergen, A.J. & Potts, S.G. (2021) A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature Ecology & Evolution* 5, 1453–1461. https://doi.org/10.1038/s41559-021-01534-9

Dominique, Z., Sabine, S., Herbert, Z., Christa, H.-R. & Sophie, K. (2023) Changes in the wild bee community (Hymenoptera: Apoidea) over 100 years in relation to land use: a case study in a protected steppe habitat in Eastern Austria. *Journal of Insect Conservation* 27, 625–641. https://doi.org/10.1007/s10841-023-00486-8

Dong, Z.-X., Tang, Q.-H., Li, W.-L., Wang, Z.-W., Li, X.-J., Fu, C.-M., Li, D., Qian, K., Tian, W.-L. & Guo, J. (2022) Honeybee (*Apis mellifera*) resistance to deltamethrin exposure by Modulating the gut microbiota and improving immunity. *Environmental Pollution* 314, 120340. https://doi.org/10.1016/j.envpol.2022.120340

Engel, P., Martinson, V.G. & Moran, N.A. (2012) Functional diversity within the simple gut microbiota of the honey bee. *Proceedings of the National Academy of Sciences* 109, 11002–11007. https://doi.org/10.1073/pnas.1202970109

Evison, S.E. & Jensen, A.B. (2018) The biology and prevalence of fungal diseases in managed and wild bees. *Current Opinion in Insect Science* 26, 105–113. https://doi.org/10.1016/j.cois.2018.02.010

Fauser, A., Sandrock, C., Neumann, P. & Sadd, B.M. (2017) Neonicotinoids override a parasite exposure impact on hibernation success of a key bumblebee pollinator. *Ecological Entomology* 42, 306–314. https://doi.org/10.1111/een.12385

Favaro, R., Garrido, P.M., Bruno, D., Braglia, C., Alberoni, D., Baffoni, L., Tettamanti, G., Porrini, M.P., Di Gioia, D. & Angeli, S. (2023) Combined effect of a neonicotinoid insecticide and a fungicide on honeybee gut epithelium and microbiota, adult survival, colony strength and foraging preferences. *Science of The Total Environment* 905, 167277. https://doi.org/10.1016/j.scitotenv.2023.167277

Fellendorf, M., Mohra, C. & Paxton, R.J. (2004) Devasting effects of river flooding to the ground-nesting bee, *Andrena vaga* (Hymenoptera: Andrenidae), and its associated fauna. *Journal of Insect Conservation* 8, 311–312. https://doi.org/10.1007/s10841-004-0514-5

Filipiak, M., Woyciechowski, M. & Czarnoleski, M. (2021) Stoichiometric niche, nutrient partitioning and resource allocation in a solitary bee are sex-specific and phosphorous is allocated mainly to the cocoon. *Scientific Reports* 11, 1–12. https://doi.org/10.1038/s41598-020-79647-7

Fitch, G., Wilson, C.J., Glaum, P., Vaidya, C., Simao, M.-C. & Jamieson, M.A. (2019) Does urbanization favour exotic bee species? Implications for the conservation of native bees in cities. *Biology Letters* 15, 20190574. https://doi.org/10.1098/rsbl.2019.0574

Fünfhaus, A., Ebeling, J. & Genersch, E. (2018) Bacterial pathogens of bees. *Current Opinion in Insect Science* 26, 89–96. https://doi.org/10.1016/j.cois.2018.02.008

Fürst, M.A., McMahon, D.P., Osborne, J.L., Paxton, R.J. & Brown, M.J.F. (2014) Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature* 506, 364–366. https://doi.org/10.1038/nature12977

Gekière, A., Breuer, L., Dorio, L., Evrard, D., Vanderplanck, M. & Michez, D. (2024) Bumble bees do not avoid field-realistic but innocuous concentrations of cadmium and copper. *Ecotoxicology* 33, 1123–1134. https://doi.org/10.1007/s10646-024-02802-7

Gekière, A., Vanderplanck, M. & Michez, D. (2023) Trace metals with heavy consequences on bees: A comprehensive review. *Science of The Total Environment* 895, 165084. https://doi.org/10.1016/j.scitotenv.2023.165084

Gérard, M., Cariou, B., Henrion, M., Descamps, C. & Baird, E. (2022) Exposure to elevated temperature during development affects bumblebee foraging behavior. *Behavioral Ecology* 33, 816–824. https://doi.org/10.1093/beheco/arac045

Gérard, M., Vanderplanck, M., Wood, T. & Michez, D. (2020) Global warming and plant – pollinator mismatches. *Emerging Topics in Life Sciences* 4, 77–86.

Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., Ropars, L., Rollin, O., Thébault, E. & Vereecken, N.J. (2017) Massively introduced managed species and their consequences for plant–pollinator interactions. In: , pp. 147–199.

Ghisbain, G. (2021) Are bumblebees relevant models for understanding wild bee decline? *Frontiers in Conservation Science* 2, 752213. https://doi.org/10.3389/fcosc.2021.752213

Ghisbain, G., Gérard, M., Wood, T.J., Hines, H.M. & Michez, D. (2021) Expanding insect pollinators in the Anthropocene. *Biological Reviews* 8, brv.12777. https://doi.org/10.1111/brv.12777

Glenny, W.R., Runyon, J.B. & Burkle, L.A. (2018) Drought and increased CO2 alter floral visual and olfactory traits with context-dependent effects on pollinator visitation. *New Phytologist* 220, 785–798. https://doi.org/10.1111/nph.15081

Gomez Ramirez, W.C., Thomas, N.K., Muktar, I.J. & Riabinina, O. (2023) The neuroecology of olfaction in bees. *Current Opinion in Insect Science* 56, 101018. https://doi.org/10.1016/j.cois.2023.101018

Gray, L.K., Hulsey, M. & Siviter, H. (2024) A novel insecticide impairs bumblebee memory and sucrose responsiveness across high and low nutrition. *Royal Society Open Science* 11. https://doi.org/10.1098/rsos.231798

Guiraud, M., Cariou, B., Henrion, M., Baird, E. & Gérard, M. (2021) Higher developmental temperature increases queen production and decreases worker body size in the bumblebee *Bombus terrestris*. *Journal of Hymenoptera Research* 88, 39–49. https://doi.org/10.3897/jhr.88.73532

Hammer, T.J., Easton-Calabria, A. & Moran, N.A. (2023) Microbiome assembly and maintenance across the lifespan of bumble bee workers. *Molecular Ecology* 32, 724–740. https://doi.org/10.1111/mec.16769

Hammer, T.J., Le, E., Martin, A.N. & Moran, N.A. (2021) The gut microbiota of bumblebees. *Insectes Sociaux* 68, 287–301. https://doi.org/10.1007/s00040-021-00837-1

Heys, C., Lizé, A., Lewis, Z. & Price, T.A.R. (2020) Drosophila sexual attractiveness in older males is mediated by their microbiota. *Microorganisms* 8, 168. https://doi.org/10.3390/microorganisms8020168

Hopfenmüller, S., Holzschuh, A. & Steffan-Dewenter, I. (2020) Effects of grazing intensity, habitat area and connectivity on snail-shell nesting bees. *Biological Conservation* 242, 108406. https://doi.org/10.1016/j.biocon.2020.108406

IPBES (2016) *The assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services on pollinators, pollination and food production*. S. G. Potts, V. L. Imperatriz-Fonseca, and H. T. Ngo (Eds). Bonn, Germany, 827 pp.

Iwasaki, J.M. & Hogendoorn, K. (2022) Mounting evidence that managed and introduced bees have negative impacts on wild bees: an updated review. *Current Research in Insect Science* 2, 100043. https://doi.org/10.1016/j.cris.2022.100043

Jaworski, C.C., Geslin, B., Zakardjian, M., Lecareux, C., Caillault, P., Nève, G., Meunier, J., Dupouyet, S., Sweeney, A.C.T., Lewis, O.T., Dicks, L. V. & Fernandez, C. (2022) Long-term experimental drought alters floral scent and pollinator visits in a Mediterranean plant community despite overall limited impacts on plant phenotype and reproduction. *Journal of Ecology* 110, 2628–2648. https://doi.org/10.1111/1365-2745.13974

Kaakinen, K., Ramula, S., Loukola, O.J. & Helander, M. (2024) Effects of glyphosate and glyphosate-based herbicide on learning and memory of the buff-tailed bumblebee (*Bombus terrestris*). *Entomologia Experimentalis et Applicata* 172, 324–333. https://doi.org/10.1111/eea.13418

Kerr, J.T., Pindar, A., Galpern, P., Packer, L., Potts, S.G., Roberts, S.M., Rasmont, P., Schweiger, O., Colla, S.R., Richardson, L.L., Wagner, D.L., Gall, L.F., Sikes, D.S. & Pantoja, A. (2015) Climate change impacts on bumblebees converge across continents. *Science* 349, 177–180. https://doi.org/10.1126/science.aaa7031

Khedidji, H., Chellali, M., Cherrered, N., Ghaffar, I., Ladjali-Mohammedi, K. & Mohammedi, A. (2024) Effect of heat stress on *Apis mellifera intermissa* and *Apis mellifera sahariensis* in laboratory controlled conditions: a physiological approach. *Journal of Apicultural Research*, 1–9. https://doi.org/10.1080/00218839.2024.2398903

Kimoto, C., DeBano, S.J., Thorp, R.W., Taylor, R. V., Schmalz, H., DelCurto, T., Johnson, T., Kennedy, P.L. & Rao, S. (2012) Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere* 3, 1–19. https://doi.org/10.1890/ES12-00118.1

Koch, H. & Schmid-Hempel, P. (2011) Socially transmitted gut microbiota protect bumble bees against an intestinal parasite. *Proceedings of the National Academy of Sciences* 108, 19288–19292. https://doi.org/10.1073/pnas.1110474108

Kozii, I. V., Barnsley, S., Silva, M.C.B. da, Wood, S.C., Klein, C.D., de Mattos, I.M., Zabrodski, M.W., Silva, R. de C.M., Fabela, C.I.O., Guillemin, L., Dvylyuk, I., Ferrari, M.C.O. & Simko, E. (2021) Reproductive fitness of honey bee queens exposed to thiamethoxam during development. *Veterinary Pathology* 58, 1107–1118. https://doi.org/10.1177/03009858211031845

Kuldna, P., Peterson, K., Poltimäe, H. & Luig, J. (2009) An application of DPSIR framework to identify issues of pollinator loss. *Ecological Economics* 69, 32–42. https://doi.org/10.1016/j.ecolecon.2009.01.005

Kuo, Y., Lu, Y.H., Lin, Y.H., Lin, Y.C. & Wu, Y.L. (2023) Elevated temperature affects energy metabolism and behavior of bumblebees. *Insect Biochemistry and Molecular Biology* 155, 103932. https://doi.org/10.1016/j.ibmb.2023.103932

Kwong, W.K. & Moran, N.A. (2016) Gut microbial communities of social bees. *Nature Reviews Microbiology* 14, 374–384. https://doi.org/10.1038/nrmicro.2016.43

Kyrkjebø Vinnes, M., Aalberg Haugen, I.M., Diserud, O., Ødegaard, F. & Gjershaug, J.O. (2022) Why do we find dead bumblebees under linden trees? *Ecological Entomology* 47, 855–863. https://doi.org/10.1111/een.13175

Lanner, J., Huchler, K., Pachinger, B., Sedivy, C. & Meimberg, H. (2020) Dispersal patterns of an introduced wild bee, *Megachile sculpturalis* Smith, 1853 (Hymenoptera: Megachilidae) in European alpine countries C.-P. Lin (Ed). *PLOS ONE* 15, e0236042. https://doi.org/10.1371/journal.pone.0236042

Laycock, I., Lenthall, K.M., Barratt, A.T. & Cresswell, J.E. (2012) Effects of imidacloprid, a neonicotinoid pesticide, on reproduction in worker bumble bees (*Bombus terrestris*). *Ecotoxicology* 21, 1937–1945. https://doi.org/10.1007/s10646-012-0927-y

Leger, L. & McFrederick, Q.S. (2020) The gut–brain–microbiome axis in bumble bees. *Insects* 11, 1–9. https://doi.org/10.3390/insects11080517

Leza, M., Watrous, K.M., Bratu, J. & Woodard, S.H. (2018) Effects of neonicotinoid insecticide exposure and monofloral diet on nest-founding bumblebee queens. *Proceedings of the Royal Society B: Biological Sciences* 285, 20180761.

https://doi.org/10.1098/rspb.2018.0761

Li, W.-L., Huang, Q., Li, J.-L., Wu, P., Wei, B., Li, X.-J., Tang, Q.-H., Dong, Z.-X., Xiong, J., Tang, H., Zhang, J., Zhao, C.-H., Cao, Z., Chen, Y., Zhao, W., Wang, K. & Guo, J. (2023) Gut microbiota-driven regulation of queen bee ovarian metabolism B. Gao (Ed). *Microbiology Spectrum* 11. https://doi.org/10.1128/spectrum.02145-23

Liberti, J. & Engel, P. (2020) The gut microbiota — brain axis of insects. *Current Opinion in Insect Science* 39, 6–13. https://doi.org/10.1016/j.cois.2020.01.004

Magill, R.G. & MacDonald, S.M. (2023) Male infertility and the human microbiome. *Frontiers in Reproductive Health* 5. https://doi.org/10.3389/frph.2023.1166201

de Manincor, N., Fisogni, A. & Rafferty, N.E. (2023) Warming of experimental plant–pollinator communities advances phenologies, alters traits, reduces interactions and depresses reproduction. *Ecology Letters* 26, 323–334. https://doi.org/10.1111/ele.14158

Martinet, B., Dellicour, S., Ghisbain, G., Przybyla, K., Zambra, E., Lecocq, T., Boustani, M., Baghirov, R., Michez, D. & Rasmont, P. (2021a) Global effects of extreme temperatures on wild bumblebees. *Conservation Biology* 35, 1507–1518. https://doi.org/10.1111/cobi.13685

Martinet, B., Lecocq, T., Smet, J. & Rasmont, P. (2015) A protocol to assess insect resistance to heat waves, applied to bumblebees (*Bombus* latreille, 1802). *PLoS ONE* 10, 1–9. https://doi.org/10.1371/journal.pone.0118591

Martinet, B., Zambra, E., Przybyla, K., Lecocq, T., Anselmo, A., Nonclercq, D., Rasmont, P., Michez, D. & Hennebert, E. (2021b) Mating under climate change: impact of simulated heatwaves on the reproduction of model pollinators. *Functional Ecology* 35, 739–752. https://doi.org/10.1111/1365-2435.13738

Maxim, L., Spangenberg, J.H. & O'Connor, M. (2009) An analysis of risks for biodiversity under the DPSIR framework. *Ecological Economics* 69, 12–23. https://doi.org/10.1016/j.ecolecon.2009.03.017

McAulay, M.K., Killingsworth, S.Z. & Forrest, J.R.K. (2021) Understanding pollen specialization in mason bees: a case study of six species. *Oecologia* 195, 559–574. https://doi.org/10.1007/s00442-020-04786-7

McFrederick, Q.S. & LeBuhn, G. (2006) Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? *Biological Conservation* 129, 372–382. https://doi.org/10.1016/j.biocon.2005.11.004

McHugh, N.M., Bown, B., McVeigh, A., Powell, R., Swan, E., Szczur, J., Wilson, P. & Holland, J. (2022) The value of two agri-environment scheme habitats for pollinators: annually cultivated margins for arable plants and floristically enhanced grass margins. *Agriculture, Ecosystems & Environment* 326, 107773. https://doi.org/10.1016/j.agee.2021.107773

McNeil, D.J., McCormick, E., Heimann, A.C., Kammerer, M., Douglas, M.R., Goslee, S.C., Grozinger, C.M. & Hines, H.M. (2020) Bumble bees in landscapes with abundant floral resources have lower pathogen loads. *Scientific Reports* 10, 22306. https://doi.org/10.1038/s41598-020-78119-2

Medrzycki, P., Giffard, H., Aupinel, P., Belzunces, L.P., Chauzat, M.-P., Claßen, C., Colin, M.E., Dupont, T., Girolami, V., Johnson, R., Le Conte, Y., Lückmann, J., Marzaro, M., Pistorius, J., Porrini, C., Schur, A., Sgolastra, F., Delso, N.S., van der Steen, J.J.M., Wallner, K., Alaux, C., Biron, D.G., Blot, N., Bogo, G., Brunet, J.-L., Delbac, F., Diogon, M., El Alaoui, H., Provost, B., Tosi, S. & Vidau, C. (2013) Standard methods for toxicology research in *Apis mellifera*. *Journal of Apicultural Research* 52, 1–60. https://doi.org/10.3896/IBRA.1.52.4.14

Melone, G.G., Stuligross, C. & Williams, N.M. (2024) Heatwaves increase larval mortality and delay development of a solitary bee. *Ecological Entomology* 49, 433–444.

https://doi.org/10.1111/een.13317

Michener, C.D. (2007) *The bees of the world*. John Hopkins University Press, Baltimore.

Michez, D., Rasmont, P., Terzo, M. & Vereecken, N.J. (2019) *Bees of Europe (Hymenoptera of Europe Volume 1)*. N.A.P. Edi. Paris, France, 552 pp.

Milone, J.P. & Tarpy, D.R. (2021) Effects of developmental exposure to pesticides in wax and pollen on honey bee (*Apis mellifera*) queen reproductive phenotypes. *Scientific Reports* 11, 1020. https://doi.org/10.1038/s41598-020-80446-3

Minnameyer, A., Strobl, V., Bruckner, S., Camenzind, D.W., Van Oystaeyen, A., Wäckers, F., Williams, G.R., Yañez, O., Neumann, P. & Straub, L. (2021) Eusocial insect declines: insecticide impairs sperm and feeding glands in bumblebees. *Science of the Total Environment* 785, 146955. https://doi.org/10.1016/j.scitotenv.2021.146955

Moreira, D.R., de Souza, T.H.S., Galhardo, D., Puentes, S.M.D., Figueira, C.L., Silva, B.G. da, Chagas, F. das, Gigliolli, A.A.S., de Toledo, V. de A.A. & Ruvolo-Takasusuki, M.C.C. (2022) Imidacloprid induces histopathological damage in the midgut, ovary, and spermathecal stored spermatozoa of queens after chronic colony exposure. *Environmental Toxicology and Chemistry* 41, 1637–1648. https://doi.org/10.1002/etc.5332

Murray, T.E., Fitzpatrick, Ú., Byrne, A., Fealy, R., Brown, M.J.F. & Paxton, R.J. (2012) Local-scale factors structure wild bee communities in protected areas I. Dteffan-Dewenter (Ed). *Journal of Applied Ecology* 49, 998–1008. https://doi.org/10.1111/j.1365-2664.2012.02175.x

Al Naggar, Y., Brinkmann, M., Sayes, C.M., AL-Kahtani, S.N., Dar, S.A., El-Seedi, H.R., Grünewald, B. & Giesy, J.P. (2021) Are honey bees at risk from microplastics? *Toxics* 9, 109. https://doi.org/10.3390/toxics9050109

Al Naggar, Y., Estrella-Maldonado, H., Paxton, R.J., Solís, T. & Quezada-Euán, J.J.G. (2022) The insecticide imidacloprid decreases *Nannotrigona* stingless bee survival and food consumption and modulates the expression of detoxification and immune-related genes. *Insects* 13, 972. https://doi.org/10.3390/insects13110972

Nasir, M., Mohsan, A., Ahmad, M., Saeed, S., Aziz, M.A., Imran, M. & Sheikh, U.A.A. (2019) Effect of different temperatures on colony characteristics of *Bombus terrestris* (Hymenoptera: Apidae). *Pakistan Journal of Zoology* 51. https://doi.org/10.17582/journal.pjz/2019.51.4.1315.1322

Neumüller, U., Pachinger, B. & Fiedler, K. (2018) Impact of inundation regime on wild bee assemblages and associated bee–flower networks. *Apidologie* 49, 817–826. https://doi.org/10.1007/s13592-018-0604-0

Nieto, A., Roberts, S.P.M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P., De Meulemeester, T., Dehon, M., Dewulf, A., Ortiz-Sánchez, F.J., Lhomme, P., Pauly, A., Potts, S.G., Praz, C., Q., Window, J. & Michez, D. (2014) IUCN Global Species Programm *European Red List of Bees*.

Oliveira, R. & Schlindwein, C. (2010) Experimental demonstration of alternative mating tactics of male *Ptilothrix fructifera* (Hymenoptera, Apidae). *Animal Behaviour* 80, 241–247. https://doi.org/10.1016/j.anbehav.2010.04.024

Paludo, C.R., Menezes, C., Silva-Junior, E.A., Vollet-Neto, A., Andrade-Dominguez, A., Pishchany, G., Khadempour, L., do Nascimento, F.S., Currie, C.R., Kolter, R., Clardy, J. & Pupo, M.T. (2018) Stingless bee larvae require fungal steroid to pupate. *Scientific Reports* 8, 1122. https://doi.org/10.1038/s41598-018-19583-9

Pelletier, F. & Coltman, D.W. (2018) Will human influences on evolutionary dynamics in the wild pervade the Anthropocene? *BMC Biology* 16, 7. https://doi.org/10.1186/s12915-017-0476-1

Pettis, J.S., Rice, N., Joselow, K., VanEngelsdorp, D. & Chaimanee, V. (2016) Colony failure linked to low sperm viability in honey bee (Apis mellifera) queens and an exploration of potential causative factors J. C. Nieh (Ed). *PLOS ONE* 11, e0147220. https://doi.org/10.1371/journal.pone.0147220

Phan, N.T., Joshi, N.K., Rajotte, E.G., Zhu, F., Peter, K.A., López-Uribe, M.M. & Biddinger, D.J. (2024) Systemic pesticides in a solitary bee pollen food store affect larval development and increase pupal mortality. *Science of The Total Environment* 915, 170048. https://doi.org/10.1016/j.scitotenv.2024.170048

Phillips, B.B., Shaw, R.F., Holland, M.J., Fry, E.L., Bardgett, R.D., Bullock, J.M. & Osborne, J.L. (2018) Drought reduces floral resources for pollinators. *Global Change Biology* 24, 3226–3235. https://doi.org/10.1111/gcb.14130

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines : trends, impacts and drivers. *Trends in Ecology & Evolution* 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Pozo, M.I., Mariën, T., van Kemenade, G., Wäckers, F. & Jacquemyn, H. (2021) Effects of pollen and nectar inoculation by yeasts, bacteria or both on bumblebee colony development. *Oecologia* 195, 689–703. https://doi.org/10.1007/s00442-021-04872-4

Przybyla, K., Michez, D., Zambra, E., Anselmo, A. & Hennebert, E. (2021) Effects of heat stress on mating behavior and colony development in *Bombus terrestris* (Hymenoptera : Apidae). *Frontiers in Ecology and Evolution* 9, 1–8. https://doi.org/10.3389/fevo.2021.748405

Qiao, H., Keesey, I.W., Hansson, B.S. & Knaden, M. (2019) Gut microbiota affects development and olfactory behavior in *Drosophila melanogaster*. *Journal of Experimental Biology*. https://doi.org/10.1242/jeb.192500

Raine, N.E. & Rundlöf, M. (2024) Pesticide exposure and effects on non-*Apis* bees. *Annual Review of Entomology* 69, 551–576. https://doi.org/10.1146/annurev-ento-040323-020625

Ramos, J.D., Santos, C.F., Cristmann, L. & Blochtein, B. (2023) A systemic fungicide might reduce the male genitalia of a stingless bee species by one-third. *Entomological Communications* 5, ec05043. https://doi.org/10.37486/2675-1305.ec05043

Rasmont, P., Ghisbain, G. & Terzo, M. (2021) *Bumble bees of Europe and neighbouring regions (Hymenoptera of Europe Volume 3)*. NAP Editio. Verrières-le-Buisson, France, 632 pp.

Requier, F., Rome, Q., Chiron, G., Decante, D., Marion, S., Menard, M., Muller, F., Villemant, C. & Henry, M. (2019) Predation of the invasive Asian hornet affects foraging activity and survival probability of honey bees in Western Europe. *Journal of Pest Science* 92, 567–578. https://doi.org/10.1007/s10340-018-1063-0

Rivest, S., Muralidhar, M. & Forrest, J.R.K. (2024) Pollen chemical and mechanical defences restrict host-plant use by bees. *Proceedings of the Royal Society B: Biological Sciences* 291. https://doi.org/10.1098/rspb.2023.2298

Rollin, O. & Garibaldi, L.A. (2019) Impacts of honeybee density on crop yield: a meta-analysis T. Diekötter (Ed). *Journal of Applied Ecology* 56, 1152–1163. https://doi.org/10.1111/1365-2664.13355

Runnion, E.N., Strange, J.P. & Sivakoff, F.S. (2024) Consumption of pollen contaminated with field-realistic concentrations of fungicide causes sublethal effects in *Bombus impatiens* (Hymenoptera: Apidae) microcolonies S. DeBano (Ed). *Environmental Entomology*, nvae049. https://doi.org/10.1093/ee/nvae049

Rutrecht T., S. & Brown J. F., M. (2008) Within colony dynamics of *Nosema bombi* infections: disease establishment, epidemiology and potential vertical transmission. *Apidologie* 39, 504–514.

Sáez, A., Morales, J.M., Morales, C.L., Harder, L.D. & Aizen, M.A. (2018) The costs and benefits of pollinator dependence: empirically based simulations predict raspberry fruit quality. *Ecological Applications* 28, 1215–1222. https://doi.org/10.1002/eap.1720

Sales, K., Vasudeva, R. & Gage, M.J.G. (2021) Fertility and mortality impacts of thermal stress from experimental heatwaves on different life stages and their recovery in a model insect. *Royal Society Open Science* 8, rsos.201717. https://doi.org/10.1098/rsos.201717

Dos Santos, C.F., Nunes-Silva, P. & Blochtein, B. (2016) Temperature rise and its influence on the cessation of diapause in *Plebeia droryana*, a eusocial bee (Hymenoptera: Apidae). *Annals of the Entomological Society of America* 109, 29–34. https://doi.org/10.1093/aesa/sav096

Santos, P.K.F., Arias, M.C. & Kapheim, K.M. (2019) Loss of developmental diapause as prerequisite for social evolution in bees. *Biology Letters* 15, 20190398. https://doi.org/10.1098/rsbl.2019.0398

Schenk, M., Krauss, J. & Holzschuh, A. (2018) Desynchronizations in bee–plant interactions cause severe fitness losses in solitary bees R. Morris (Ed). *Journal of Animal Ecology* 87, 139–149. https://doi.org/10.1111/1365-2656.12694

Schuhmann, A., Schmid, A.P., Manzer, S., Schulte, J. & Scheiner, R. (2022) Interaction of insecticides and fungicides in bees. *Frontiers in Insect Science* 1, 1–14. https://doi.org/10.3389/finsc.2021.808335

Schwarz, J.M., Knauer, A.C., Alaux, C., Barascou, L., Barraud, A., Dievart, V., Ghazoul, J., Michez, D. & Albrecht, M. (2024) Diverse pollen nutrition can improve the development of solitary bees but does not mitigate negative pesticide impacts. *Science of The Total Environment* 912, 169494. https://doi.org/10.1016/j.scitotenv.2023.169494

Sedivy, C., Müller, A. & Dorn, S. (2011) Closely related pollen generalist bees differ in their ability to develop on the same pollen diet : evidence for physiological adaptations to digest pollen. *Functional Ecology* 25, 718–725. https://doi.org/10.1111/j.1365-2435.2010.01828.x

Seidelmann, K., Ulbrich, K. & Mielenz, N. (2010) Conditional sex allocation in the Red Mason bee, *Osmia rufa*. *Behavioral Ecology and Sociobiology* 64, 337–347. https://doi.org/10.1007/s00265-009-0850-2

Sgolastra, F., Arnan, X., Cabbri, R., Isani, G., Medrzycki, P., Teper, D., Bosch, J. & Mediche, S. (2018) Combined exposure to sublethal concentrations of an insecticide and a fungicide affect feeding , ovary development and longevity in a solitary bee. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 285, 20180887.

Sgolastra, F., Medrzycki, P., Bortolotti, L., Maini, S., Porrini, C., Simon-Delso, N. & Bosch, J. (2020) Bees and pesticide regulation: lessons from the neonicotinoid experience. *Biological Conservation* 241, 108356. https://doi.org/10.1016/j.biocon.2019.108356

Shannon, B., Jeon, H. & Johnson, R.M. (2023) Review: the risks of spray adjuvants to honey bees E. Walsh (Ed). *Journal of Insect Science* 23. https://doi.org/10.1093/jisesa/iead100

Sharon, G., Segal, D., Ringo, J.M., Hefetz, A., Zilber-Rosenberg, I. & Rosenberg, E. (2010) Commensal bacteria play a role in mating preference of *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences* 107, 20051–20056. https://doi.org/10.1073/pnas.1009906107

Shi, M., Guo, Y., Dong, K., Wu, J. & Huang, J. (2023) A review of factors influencing diapause in bumble bee queens. *Insectes Sociaux* 70, 157–165. https://doi.org/10.1007/s00040-023-00903-w

Siviter, H., Linguadoca, A., Ippolito, A. & Muth, F. (2023) Pesticide licensing in the EU and protecting pollinators. *Current Biology* 33, R44–R48. https://doi.org/10.1016/j.cub.2022.12.002

Siviter, H., Richman, S.K. & Muth, F. (2021) Field-realistic neonicotinoid exposure has sub-lethal effects on non-Apis bees: A meta-analysis. *Ecology Letters*, 1–12.

https://doi.org/10.1111/ele.13873

Sjödin, N.E., Bengtsson, J. & Ekbom, B. (2008) The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology* 45, 763–772. https://doi.org/10.1111/j.1365-2664.2007.01443.x

Sparks, T.C. & Nauen, R. (2015) IRAC: Mode of action classification and insecticide resistance management. *Pesticide Biochemistry and Physiology* 121, 122–128. https://doi.org/10.1016/j.pestbp.2014.11.014

Steffan, S.A., Dharampal, P.S., Danforth, B.N., Gaines-Day, H.R., Takizawa, Y. & Chikaraishi, Y. (2019) Omnivory in bees: elevated trophic positions among all major bee families. *American Naturalist* 194, 414–421. https://doi.org/10.1086/704281

Stout, J.C. & Dicks, L. V (2022) From science to society: implementing effective strategies to improve wild pollinator health. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377. https://doi.org/10.1098/rstb.2021.0165

Straffon-Díaz, S., Carisio, L., Manino, A., Biella, P. & Porporato, M. (2021) Nesting, sex ratio and natural enemies of the giant resin bee in relation to native species in Europe. *Insects* 12, 545. https://doi.org/10.3390/insects12060545

Straub, F., Birkenbach, M., Leonhardt, S.D., Ruedenauer, F.A., Kuppler, J., Wilfert, L. & Ayasse, M. (2023) Land-use-associated stressors interact to reduce bumblebee health at the individual and colony level. *Proceedings of the Royal Society B: Biological Sciences* 290. https://doi.org/10.1098/rspb.2023.1322

Straub, L., Williams, G.R., Pettis, J., Fries, I. & Neumann, P. (2015) Superorganism resilience: Eusociality and susceptibility of ecosystem service providing insects to stressors. *Current Opinion in Insect Science* 12, 109–112. https://doi.org/10.1016/j.cois.2015.10.010

Straw, E.A. & Brown, M.J.F. (2021) Co-formulant in a commercial fungicide product causes lethal and sub-lethal effects in bumble bees. *Scientific Reports* 11, 21653. https://doi.org/10.1038/s41598-021-00919-x

Straw, E.A., Carpentier, E.N. & Brown, M.J.F. (2021) Roundup causes high levels of mortality following contact exposure in bumble bees. *Journal of Applied Ecology* 58, 1167–1176. https://doi.org/10.1111/1365-2664.13867

Strobl, V., Albrecht, M., Villamar-Bouza, L., Tosi, S., Neumann, P. & Straub, L. (2021) The neonicotinoid thiamethoxam impairs male fertility in solitary bees, *Osmia cornuta*. *Environmental Pollution* 284, 117106. https://doi.org/10.1016/j.envpol.2021.117106

Stuligross, C. & Williams, N.M. (2020) Pesticide and resource stressors additively impair wild bee reproduction. *Proceedings of the Royal Society B: Biological Sciences* 287, 20201390. https://doi.org/10.1098/rspb.2020.1390

Tan, K., Chen, W., Dong, S., Liu, X., Wang, Y. & Nieh, J.C. (2014) Imidacloprid alters foraging and decreases bee avoidance of predators N. Desneux (Ed). *PLoS ONE* 9, e102725. https://doi.org/10.1371/journal.pone.0102725

Tew, N.E., Baldock, K.C.R., Morten, J.M., Bird, S., Vaughan, I.P. & Memmott, J. (2023) A dataset of nectar sugar production for flowering plants found in urban green spaces. *Ecological Solutions and Evidence* 4. https://doi.org/10.1002/2688-8319.12248

Tobin, K.B., Mandes, R., Martinez, A. & Sadd, B.M. (2024) A simulated natural heatwave perturbs bumblebee immunity and resistance to infection. *Journal of Animal Ecology* 93, 171–182. https://doi.org/10.1111/1365-2656.14041

Treanore, E. & Amsalem, E. (2020) The effect of intrinsic physiological traits on diapause survival and their underlying mechanisms in an annual bee species *Bombus impatiens* S. Cooke (Ed). *Conservation Physiology* 8. https://doi.org/10.1093/conphys/coaa103

Trunz, V., Lucchetti, M.A., Bénon, D., Dorchin, A., Desurmont, G.A., Kast, C., Rasmann, S., Glauser, G. & Praz, C.J. (2020) To bee or not to bee: The "raison d'être" of toxic secondary compounds in the pollen of Boraginaceae. *Functional Ecology* 34, 1345–1357.

https://doi.org/10.1111/1365-2435.13581

Vanderplanck, M., Decleves, S., Roger, N., Decroo, C., Caulier, G., Glauser, G., Gerbaux, P., Lognay, G., Richel, A., Escaravage, N. & Michez, D. (2018) Is non-host pollen suitable for generalist bumblebees? *Insect Science* 25, 259–272. https://doi.org/10.1111/1744-7917.12410

Vanderplanck, M., Martinet, B., Carvalheiro, L.G., Rasmont, P., Barraud, A., Renaudeau, C. & Michez, D. (2019) Ensuring access to high-quality resources reduces the impacts of heat stress on bees. *Scientific Reports* 9, 12596. https://doi.org/10.1038/s41598-019-49025-z

Vaudo, A.D., Dyer, L.A. & Leonard, A.S. (2024) Pollen nutrition structures bee and plant community interactions. *Proceedings of the National Academy of Sciences* 121, 2017. https://doi.org/10.1073/pnas.2317228120

Vázquez, D.E., Villegas Martínez, L.E., Medina, V., Latorre-Estivalis, J.M., Zavala, J.A. & Farina, W.M. (2023) Glyphosate affects larval gut microbiota and metamorphosis of honey bees with differences between rearing procedures. *Environmental Pollution* 334, 122200. https://doi.org/10.1016/j.envpol.2023.122200

Voulgari-Kokota, A., McFrederick, Q.S., Steffan-Dewenter, I. & Keller, A. (2019) Drivers, diversity, and functions of the solitary bee microbiota. *Trends in Microbiology* 27, 1034–1044. https://doi.org/10.1016/j.tim.2019.07.011

de Vries, E.J., Jacobs, G., Sabelis, M.W., Menken, S.B.J. & Breeuwer, J.A.J. (2004) Diet–dependent effects of gut bacteria on their insect host: the symbiosis of *Erwinia* sp. and western flower thrips. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271, 2171–2178. https://doi.org/10.1098/rspb.2004.2817

Walsh, B.S., Parratt, S.R., Hoffmann, A.A., Atkinson, D., Snook, R.R., Bretman, A. & Price, T.A.R. (2019) The impact of climate change on fertility. *Trends in Ecology & Evolution* 34, 249–259. https://doi.org/10.1016/j.tree.2018.12.002

Walsh, E.M., Sweet, S., Knap, A., Ing, N. & Rangel, J. (2020) Queen honey bee (*Apis mellifera*) pheromone and reproductive behavior are affected by pesticide exposure during development. *Behavioral Ecology and Sociobiology* 74, 33. https://doi.org/10.1007/s00265-020-2810-9

Wan, X., Yan, C., Wang, Z. & Zhang, Z. (2022) Sustained population decline of rodents is linked to accelerated climate warming and human disturbance. *BMC Ecology and Evolution* 22, 102. https://doi.org/10.1186/s12862-022-02056-z

Wang, K., Li, J., Zhao, L., Mu, X., Wang, C., Wang, M., Xue, X., Qi, S. & Wu, L. (2021) Gut microbiota protects honey bees (*Apis mellifera* L.) against polystyrene microplastics exposure risks. *Journal of Hazardous Materials* 402, 123828. https://doi.org/10.1016/j.jhazmat.2020.123828

Wang, L., Wu, J., Li, K., Sadd, B.M., Guo, Y., Zhuang, D., Zhang, Z., Chen, Y., Evans, J.D., Guo, J., Zhang, Z. & Li, J. (2019) Dynamic changes of gut microbial communities of bumble bee queens through important life stages. *mSystems* 4, 1–15. https://doi.org/10.1128/msystems.00631-19

Westerfelt, P., Weslien, J. & Widenfalk, O. (2018) Population patterns in relation to food and nesting resource for two cavity-nesting bee species in young boreal forest stands. *Forest Ecology and Management* 430, 629–638. https://doi.org/10.1016/j.foreco.2018.08.053

White, S.A. & Dillon, M.E. (2023) Climate warming and bumble bee declines: the need to consider sub-lethal heat, carry-over effects, and colony compensation. *Frontiers in Physiology* 14, 1–8. https://doi.org/10.3389/fphys.2023.1251235

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

Wilfert, L., Brown, M.J.F. & Doublet, V. (2021) OneHealth implications of infectious diseases of wild and managed bees. *Journal of Invertebrate Pathology* 186, 107506. https://doi.org/10.1016/j.jip.2020.107506

Willcox, B.K., Potts, S.G., Brown, M.J.F., Alix, A., Al Naggar, Y., Chauzat, M.-P., Costa, C., Gekière, A., Hartfield, C., Hatjina, F., Knapp, J.L., Martínez-López, V., Maus, C., Metodiev, T., Nazzi, F., Osterman, J., Raimets, R., Strobl, V., Van Oystaeyen, A., Wintermantel, D., Yovcheva, N. & Senapathi, D. (2023) Emerging threats and opportunities to managed bee species in European agricultural systems: a horizon scan. *Scientific Reports* 13, 18099. https://doi.org/10.1038/s41598-023-45279-w

Williams, G.R., Troxler, A., Retschnig, G., Roth, K., Yañez, O., Shutler, D., Neumann, P. & Gauthier, L. (2015) Neonicotinoid pesticides severely affect honey bee queens. *Scientific Reports* 5, 14621. https://doi.org/10.1038/srep14621

Wood, T.J., Michez, D., Paxton, R.J., Drossart, M., Neumann, P., Gérard, M., Vanderplanck, M., Barraud, A., Martinet, B., Leclercq, N. & Vereecken, N.J. (2020) Managed honey bees as a radar for wild bee decline? *Apidologie* 51, 1100–1116. https://doi.org/10.1007/s13592-020-00788-9

Wood, T.J., Müller, A., Praz, C. & Michez, D. (2023) Elevated rates of dietary generalization in eusocial lineages of the secondarily herbivorous bees. *BMC Ecology and Evolution* 23, 67. https://doi.org/10.1186/s12862-023-02175-1

Woodard, S.H., Duennes, M.A., Watrous, K.M. & Jha, S. (2019) Diet and nutritional status during early adult life have immediate and persistent effects on queen bumble bees H. MacMillan (Ed). *Conservation Physiology* 7, 1–10. https://doi.org/10.1093/conphys/coz048

Woodcock, B.A., Isaac, N.J.B., Bullock, J.M., Roy, D.B., Garthwaite, D.G., Crowe, A. & Pywell, R.F. (2016) Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nature Communications* 7, 12459. https://doi.org/10.1038/ncomms12459

Wu-Smart, J. & Spivak, M. (2018) Effects of neonicotinoid imidacloprid exposure on bumble bee (Hymenoptera: Apidae) queen survival and nest initiation. *Environmental Entomology* 47, 55–62. https://doi.org/10.1093/ee/nvx175

Yañez, O., Piot, N., Dalmon, A., de Miranda, J.R., Chantawannakul, P., Panziera, D., Amiri, E., Smagghe, G., Schroeder, D. & Chejanovsky, N. (2020) Bee viruses: routes of infection in Hymenoptera. *Frontiers in Microbiology* 11, 1–22. https://doi.org/10.3389/fmicb.2020.00943

Yoon, H.J., Lee, K.Y., Kim, M.A., Ahn, M.Y. & Park, I.G. (2013) Optimal cold temperature for the artificial hibernation of *Bombus ignitus* queen bumblebees. *International Journal of Industrial Entomology* 26, 124–130. https://doi.org/10.7852/ijie.2013.26.2.124

Yu, L., Yang, H., Cheng, F., Wu, Z., Huang, Q., He, X., Yan, W., Zhang, L. & Wu, X. (2021) Honey bee *Apis mellifera* larvae gut microbial and immune, detoxication responses towards flumethrin stress. *Environmental Pollution* 290, 118107. https://doi.org/10.1016/j.envpol.2021.118107

Zattara, E.E. & Aizen, M.A. (2021) Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* 4, 114–123. https://doi.org/10.1016/j.oneear.2020.12.005

Acknowledgments

The authors would like to thank David L. Wagner for his comments on a preliminary draft of this manuscript.

Funding

A.G. is supported by a F.R.S.-FNRS (Fonds National de la Recherche Scientifique) PhD grant "Aspirant". M.G. is supported by a F.R.S.-FNRS postdoctoral grant "Chargé de recherches".

Author Contributions Statement

AG: Conceptualization, Investigation, Visualization, Writing – Original draft, Writing – Review & Editing. **MG**: Conceptualization, Investigation, Writing – Original draft, Writing – Review & Editing. **SGP**: Writing – Original draft, Writing – Review & Editing. **DM**: Writing – Review & Editing. **GG**: Conceptualization, Investigation, Supervision, Writing – Original draft, Writing – Review & Editing.

Competing interests

No conflict of interest to declare

List of supplementary materials

None.

Box 1 - Mechanisms modulated through plants

While the presently refined framework focuses on mechanisms impacting bees directly, a wide range of mechanisms also affect flowering plants, the main food resources for bees. The life cycles of flowering plants and bees have coevolved with the temporal, spatial, and physio-chemical interconnections between the communities (Vaudo *et al.* 2024). However, the literature on bee population decline to date has often overlooked the growing frequency of extreme climatic and other environmental events shaping plant-bee interactions. Such events have demonstrated a myriad of negative impacts on both the interaction between the two parties, and on plant populations themselves (de Manincor *et al.* 2023).

Heatwaves, often combined with droughts, usually lead to reductions in plant size, floral resources, flower or inflorescence numbers, and floral longevity as well as to increased flower abortion (Descamps *et al.* 2021; Phillips *et al.* 2018). In addition to affecting floral morphogenesis or causing floral deformities, extreme weather conditions can also alter key parameters involved in pollinator attraction, such as the quantity and quality of volatile organic compounds (VOC) (Campbell *et al.* 2019). Although these changes often lead to negative impacts on visitation rates of various bee species, the fitness of several Mediterranean plant species can remain unaffected by heat and drought (Glenny *et al.* 2018). This resilience is attributed to the stability of their floral traits and the minor effect that alterations in VOCs have on their floral visitors (Jaworski *et al.* 2022). Beyond the impact on bee-plant interactions, abiotic stress can directly affect the reproductive success of flowering plants by reducing pollen viability and stigmatic receptivity to pollen grains, affecting pollen tube growth, altering the number of produced ovules, inducing ovary abortion, or modifying seed development, with implications for the reproductive success of the plants (Borghi *et al.* 2019).

Climate change can drive spatial and temporal mismatches resulting both from the redistribution of plant species and variations in their phenology (Gérard *et al.* 2020), and this may be further compounded by additional risks through the arrival of a growing number of domesticated, expanding, or invasive plants and pollinators (Ghisbain *et al.* 2021). Massively introduced managed species (MIMS), can readily integrate local communities and native plant-pollinator interaction networks (Geslin *et al.* 2017) with extremely high visitation rates leading to further costs for plants (Sáez *et al.* 2018), such as an oversaturation of pollination which in turn can impede fruit production and may even diminish yields of entomophilous plants (Rollin & Garibaldi 2019). Further research is needed to assess to what extent these phenomena can affect wild plants inside or outside agroecosystems, where MIMS are purposely implanted.

Box 2 - The emerging importance of the holobiont in bee conservation

Symbiotic gut microbiomes are being extensively characterised in social bees (Kwong & Moran 2016) and to a lesser extent in solitary bees (Voulgari-Kokota *et al.* 2019). Despite recent advancements in qualitatively and functionally describing these communities (Bonilla-Rosso & Engel 2018; Hammer *et al.* 2021), investigations often fall short in quantifying how gut symbionts contribute to the reproductive success of the holobiont, i.e. the association of the host and its associated symbionts. Here we highlight that gut symbionts can shape bee reproductive fitness through the five mechanisms considered in the present framework.

The capacity of gut symbionts to enhance bee survival has been robustly demonstrated, particularly under conditions of environmental stress (Koch & Schmid-Hempel 2011). In honey bees, mortality rates increased in microbiota-depleted individuals following exposure to polystyrene microplastics (Wang *et al.* 2021). Furthermore, gut symbionts are involved in mitigating the adverse effects of pesticides, as evidenced by microbiota-depleted honey bees provided with bacterial strains and subsequently exposed to the insecticide deltamethrin (Dong *et al.* 2022).

Given the importance of the gut-brain axis in insects, it is likely that the bee gut microbiota plays a significant role in partner selection and mating behaviour (Liberti & Engel 2020; but see Leger & McFrederick 2020). In non-bee insects, individuals harbouring similar gut bacterial communities exhibited a greater propensity to mate, whereas microbiota-depleted individuals showed no mating preference (Sharon *et al.* 2010). Subsequently, microbiota have been shown to serve as an honest signal used by females to assess male age (Heys *et al.* 2020). A potential role of healthy microbial communities in bee mating is further underscored by the dynamic shifts in microbial symbiont communities observed in the gut of bumble bee queens across key life stages (Wang *et al.* 2019).

The influence of gut symbionts on gamete production in insects remains poorly understood, yet warrants attention given the documented roles of gut bacteria in human sperm production (Magill & MacDonald 2023). Severe alterations in gut microbial communities were observed in honey bee queens and prevented them from laying eggs, with certain bacteria positively associated with ovarian development (Li *et al.* 2023).

Bumble bee queens provided with a combination of flower- and insect-associated bacteria and yeasts displayed enhanced egg laying and greater brood development (Pozo *et al.* 2021). In fruit flies, supplementation with additional native gut microbes led to an increase in oviposition (Qiao *et al.* 2019), a physiological modification that was also observed in thrips (de Vries *et al.* 2004).

The gut microbiota composition of bee larvae markedly differs from that of adults, particularly in social species (Engel *et al.* 2012; Hammer *et al.* 2023). Despite the growing understanding of gut symbionts in adult bees, their roles in larvae remain poorly characterised. Evidence suggests that gut symbionts originating from larval food sources may serve as a crucial trophic component for larval development, to such an extent that bees could be classified as 'omnivores' (Steffan *et al.* 2019). Subsequently, it was shown that pollen-associated microbes were vital for the development of solitary bee larvae (Dharampal *et al.* 2022). Notably, exposure to microbiota-impeding herbicides were shown to affect metamorphosis in honey bee larvae (Vázquez *et al.* 2023), while specific fungi serve as a source of ergosterol for larval pupation in stingless bee larvae (Paludo *et al.* 2018).

Figure 1. Extension of the Drivers-Pressures-States-Impacts-Responses (DPSIR) framework to include the underlying biological mechanisms linking the anthropogenic pressures to changes in bee population states. While anthropogenic pressures and bee population states have been considered in the DPSIR framework, the underlying mechanisms, namely the biological processes immediately responsible for a reduction in bee reproductive fitness, have not been systematically addressed.

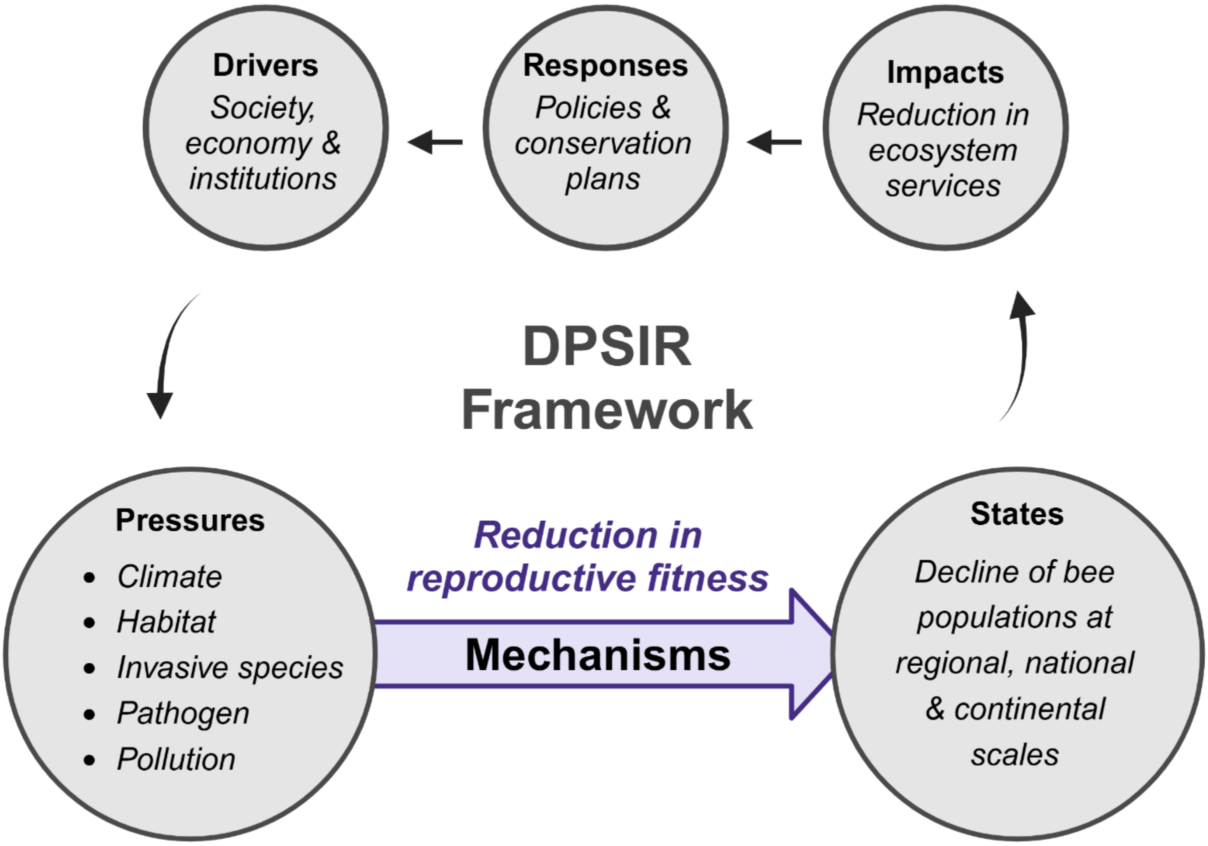

Figure 2. Decrease in the reproductive fitness of bees along their life cycle. As bees proceed through their life cycle, they encounter many anthropogenic pressures (e.g., pesticide exposure) that can reduce their reproductive fitness (i.e., ability to produce viable and fertile offspring) through five biological mechanisms.

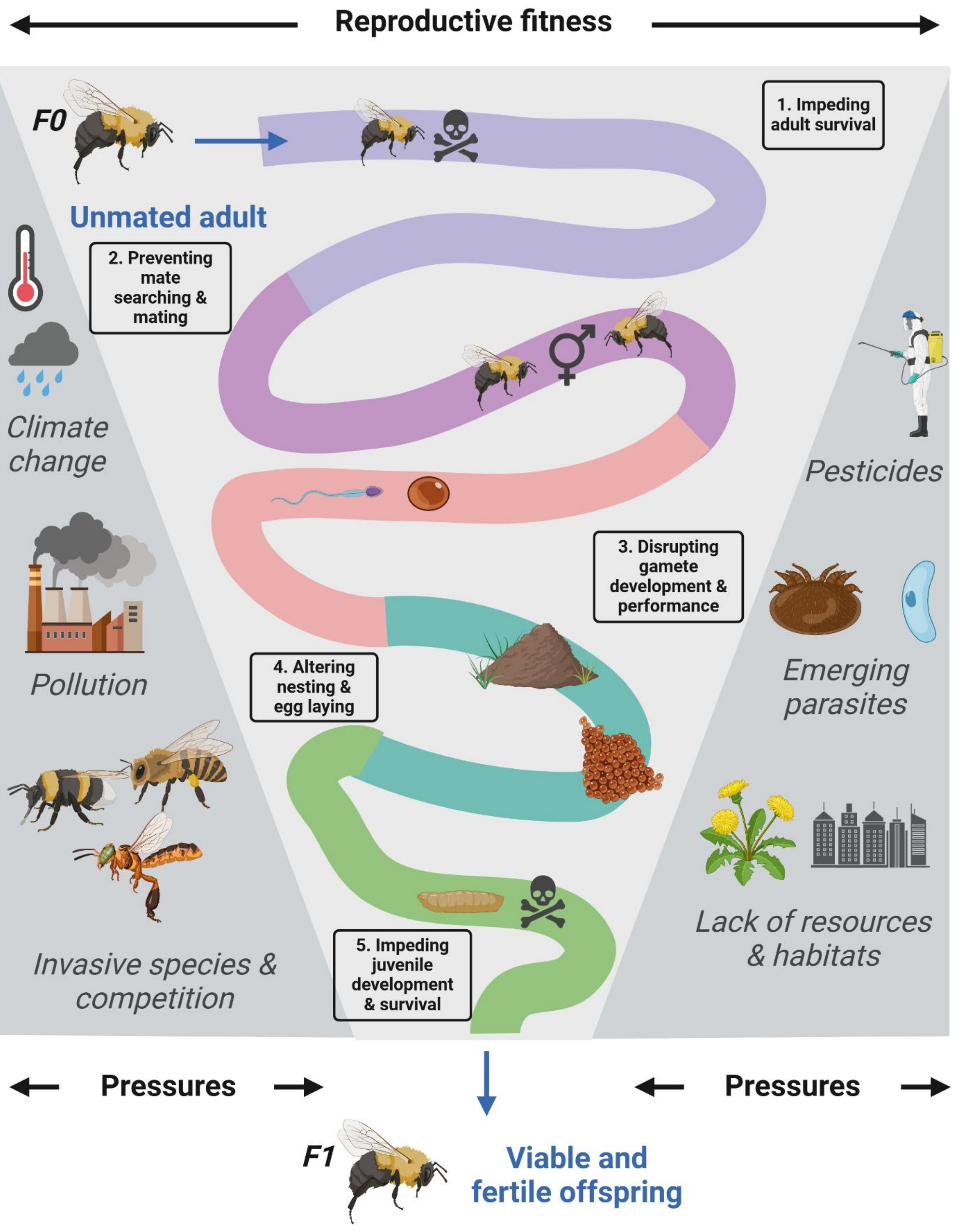

Table 1. Current evidence of the interplay between the anthropogenic pressures and the mechanisms underlying the states of declining bee populations. Areas with significant knowledge gaps are highlighted in light grey. Examples are illustrative and non-exhaustive.

	Habitat	**Pollution**	**Climate**	**Alien invasive species**	**Pathogen**
Impeding adult survival	Increased bumble bee death by starvation, ageing and predation around linden trees (*Bombus hypnorum*, *B. pratorum*, *B. pascuorum*, *B. lapidarius*) (Kyrkjebø Vinnes *et al.* 2022)	Increased mortality in a bumble bee (*B. terrestris*) exposed to alcohol ethoxylate adjuvants (Straw & Brown 2021)	Rapid heat stupor in several bee genera exposed to heatwaves (including *Anthidium*, *Anthophora*, *Bombus* and *Eucera*) (Boustani *et al.* 2024)	Predation of managed honey bees (*Apis mellifera*) by invasive Asian hornets in France (Requier *et al.* 2019)	Higher prevalence of microsporidian parasites in wild bumble bee populations after bumble bee commercialisation (Brown 2017)
Preventing mate searching and mating	Reduced number of mating sites when reduced flower availability (Oliveira & Schlindwein 2010)	Reduced production of queens in colonies of a bumble bee (*B. terrestris*) exposed to insecticides (Whitehorn *et al.* 2012)	Alteration of pheromone profiles in males of a bumble bee (*B. jonellus*) exposed to heatwaves (Martinet *et al.* 2021a)	Key knowledge gap	Key knowledge gap
Disrupting gamete development and performance	Key knowledge gap	Reduced sperm viability in males of a bumble bee (*B. terrestris*) exposed to pesticides (Minnameyer *et al.* 2021)	Reduced sperm viability in males of bumble bees (*B. jonellus*, *B. magnus*) exposed to heat waves (Martinet *et al.* 2021a)	Key knowledge gap	Castration of queens of a bumble bee (*B. pratorum*) by a nematode (Rutrecht T. & Brown J. F. 2008)

Altering nesting and egg laying	Delayed nest initiation in queens of a bumble bee (*B. impatiens*) fed monofloral diet (Leza *et al.* 2018)	Reduced diapause survival in queens of a bumble bee (*B. terrestris*) exposed to pesticides (Fauser *et al.* 2017)	Reduced brood production in heat stressed colonies of a bumble bee (*B. terrestris*) (Vanderplanck *et al.* 2019)	Mason bees (*Osmia cornuta*) evicted from their nests by invasive giant resin bees (*Megachile sculpturalis*) (Lanner *et al.* 2020)	Key knowledge gap
Impeding juvenile development and survival	Reduced survival in larvae of non-Asteraceae specialist mason bees (*Osmia iridis*, *O.tersula*, *O. tristella*) (bred on Asteraceae pollen (McAulay *et al.* 2021)	Reduced survival in larvae of a mason bee (*Osmia bicornis*) exposed to pesticides (Schwarz *et al.* 2024)	Reduced survival in larvae of a mason bee (*Osmia lignaria*) exposed to heatwaves (Melone *et al.* 2024)	Key knowledge gap	Larvae of a leafcutter bee (*Megachile rotundata*) killed by a Hymenopteran parasitoid (*Melittobia acasta*) (Anderson *et al.* 2023)