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Underlying mechanisms shaping wild bee decline

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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

289 mortality rates when compared to background mortality under optimal conditions (Shi *et al.*
290 2023; Straub *et al.* 2015). Resource scarcity can amplify mortality during diapause. For
291 instance, limited access to pollen and nectar disrupts diapause survival, primarily due to reduced
292 pre-diapause body weight and diminished reserves of lipids and carbohydrates (Treanore &
293 Amsalem 2020; Woodard *et al.* 2019). Overwintering temperature represents another critical
294 determinant of diapause success: cold stress diminishes diapause survival (Yoon *et al.* 2013),
295 whereas warmer temperatures trigger diapause termination and force activity in the winter
296 season, posing phenological mismatches in the absence of sufficient blooming floral resources
297 (Dos Santos *et al.* 2016). Moreover, exposure to pesticides and parasites prior to diapause has
298 been shown to escalate mortality during this phase (Fauser *et al.* 2017). The mechanisms
299 underlying these observations likely entail indirect pathways, such as induced weight loss and
300 compromised immune function, rather than direct mortality following stressor exposure (Brown
301 *et al.* 2003; Costa *et al.* 2020; Fauser *et al.* 2017).

302 Intensive agricultural practices, including grazing and tillage, affect the availability of
303 nesting sites for below solitary ground-nesting bees (which comprise ~70% of bee species;
304 Michez *et al.* 2019; Kimoto *et al.* 2012; McHugh *et al.* 2022; Murray *et al.* 2012; Sjödin *et al.*
305 2008) as well as the availability of rodent nests which are crucial for bumble bees (McFrederick
306 & LeBuhn 2006; Wan *et al.* 2022). Decrease in nesting site availability due to grazing can also
307 affect above-ground nesting bees, as observed for different species of solitary osmiine bees
308 (e.g., *Osmia aurulenta*), for which the decrease of snail shells (a key nesting resources on semi-
309 natural grassland) directly affects their populations (Hopfenmüller *et al.* 2020).

310 Climate change exacerbates the challenge of finding suitable nesting sites, with extreme
311 precipitation and flooding potentially compromising nesting site quality. In the absence of
312 suitable nesting localities around flooded sites, extreme precipitation can be devastating, as
313 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

363 juveniles of non-Asteraceae specialist species (e.g., *O. iridis*) failing to develop on Asteraceae
364 pollen (McAulay *et al.* 2021; Vanderplanck *et al.* 2018).

365 Finally, parasites and pathogens constitute significant biotic factors that profoundly
366 influence juvenile survival in bee populations. Parasitoids (e.g., *Melittobia* spp.; Anderson *et*
367 *al.* 2023), fungi (e.g. *Ascosphaera* spp., *Aspergillus* spp. and *Vairimorpha* spp.; Bramke *et al.*
368 2019; Evison & Jensen 2018), bacteria (e.g., *Paenibacillus* spp. and *Melissococcus* spp.;
369 Fünfhaus *et al.* 2018) and viruses (e.g., black queen cell virus; Yañez *et al.* 2020) are all known
370 to cause significant mortality in juveniles. Although parasites and pathogens are inherent, even
371 to healthy networks (Brown 2022), many have been documented in high abundance in
372 commercial honey bee and bumble bee populations, raising concerns regarding potential
373 spillover events from managed to wild bee populations (Fürst *et al.* 2014). This issue is even
374 more concerning in a context of anthropogenic pollution and lack of sufficient food resources,
375 with both stressors impeding the resistance of juveniles against antagonist organisms (Wilfert
376 *et al.* 2021).

377 Outstanding questions

378 • Do bee larvae harbour species-specific resistance towards xenobiotics?

379 • To what extent do nest-usurping alien bee species increase larval mortality in native bee
380 populations?

381 ***Discussion***

382 For decades, growing evidence has highlighted the detrimental effects of anthropogenic
383 pressures, such as pollution and climate change, on the states of bee populations. While these
384 studies have been instrumental in demonstrating the risks posed by these pressures, they have
385 largely fallen short of elucidating the underlying mechanisms that translate these pressures into
386 population declines. This emphasis on pressures rather than on underlying mechanisms
387 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**).

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

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

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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.

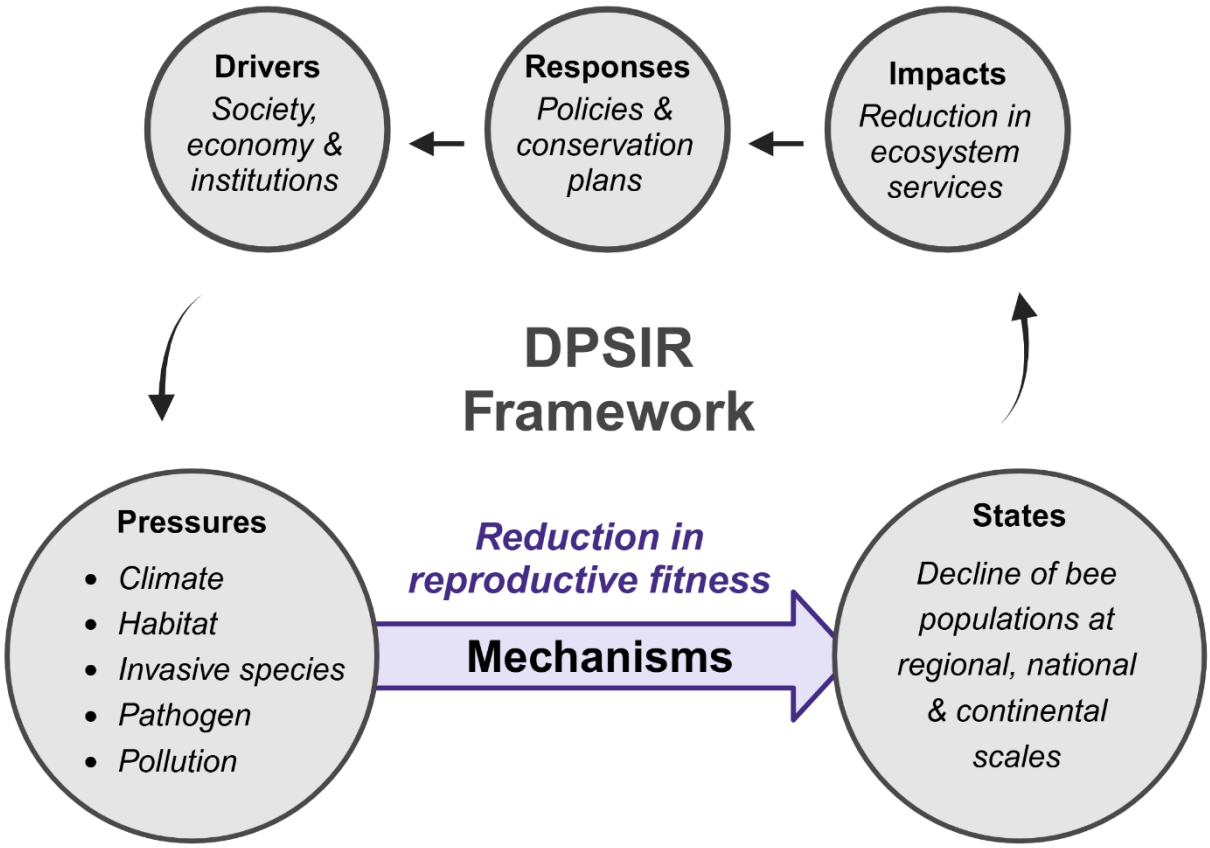

Figure 2. Decrease in the reproductive fitness of bees along their life cycle. As bees proceed through their life cycle, they encounter many anthropogenic pressures (e.g., pesticide exposure) that can reduce their reproductive fitness (i.e., ability to produce viable and fertile offspring) through five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

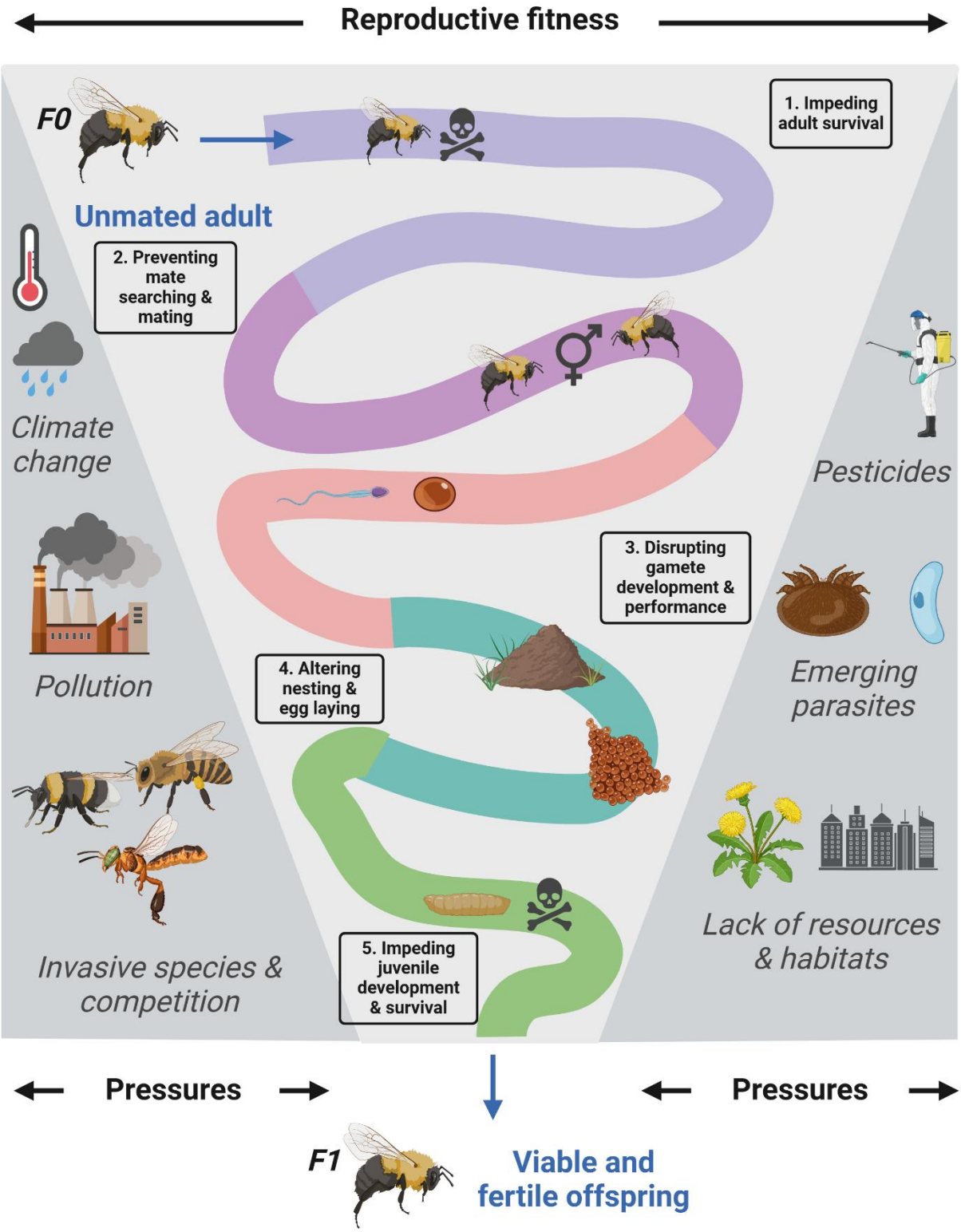

Table 1. Current evidence of the interplay between the anthropogenic pressures and the mechanisms underlying the states of declining bee populations. Areas with significant knowledge gaps are highlighted in light grey. Examples are illustrative and non-exhaustive.

	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)

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