



## POLLINATOR HEALTH UNDER MULTIPLE ENVIRONMENTAL STRESSORS: PESTICIDE EXPOSURE, NUTRITIONAL LIMITATION, MICROBIOME DYSBIOSIS, AND IMMUNE RESPONSES

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Received: 28/03/2026, Revised: 25/06/2026, Accepted: 16/08/2026, Published: 28/08/2026

### ABSTRACT

Pollinator health is increasingly being affected by several environmental stressors acting at various molecular, physiological, behavioral, and ecological levels simultaneously. Of these stresses, pesticide exposure, nutritional limitation, microbiome dysbiosis, and altered immune function are especially noteworthy because they interact through shared biological pathways. Pesticides can affect neural signaling, oxidative balance, detoxification, metabolism and behavior, and food deprivation can decrease resources for development, reproduction, immune system function and chemical tolerance. The stability of microbial communities is also a crucial part of pollinator resilience as it plays a role in nutrient processing, xenobiotic metabolism, pathogen resistance and immune regulation. These systems can be stressed, leading to biological cascades, where one stressor modifies or amplifies the effects of another. These interactions can ultimately shape the survival of individuals, cognition, foraging efficiency, reproductive fitness, colony performance, population persistence, plant–pollinator networks, and ecosystem functioning. There is also evidence to show that there is significant variation in the response of the different categories of honey bees, bumblebees, solitary bees and other pollinating insects, which limits the value of using managed honey bees as the primary source for ecological risk assessment. Future research should incorporate realistic pesticide mixtures, nutritional environments, microbiome responses, pathogens, climate-related pressures, and species-specific traits within standardized multi-stressor frameworks. To enhance pollinator conservation and the maintenance of pollination-dependent biodiversity and food production, it is critical to integrate ecological management and biologically informed risk assessment.

**Keyword:** pollinator health; pesticide exposure; nutritional stress; gut microbiome; immune responses; multi-stressor interactions

## Introduction

Pollinator services are critical to the ecology of terrestrial ecosystems and include supporting plant reproduction, maintaining floral diversity, and directly improving the productivity of many crops grown by humans. They are not only important for their role in increasing the yield of crops but also for their role in enhancing the functioning and stability of plant–pollinator networks. The impact of pollination on agricultural production globally illustrates how biodiversity-mediated pollination can play an important role in crop production, especially when species complement each other in space and time (Dainese et al., 2019). In parallel, modern agriculture has increasingly relied on pollinator-mediated crops with little parallel increase in crop diversity, raising the risk of losses due to declines in pollinator abundance and performance (Aizen et al., 2019). Pollination deficits have already been associated with measurable production constraints in several major crops, demonstrating that insufficient pollinator activity can have direct consequences for agricultural output (Reilly et al., 2020).

Multiple environmental stressors are increasingly affecting pollinator health. Survival, reproduction, behaviour and physiological condition may be impacted by habitat change, intensification, reduction in floral resources, climate variability, pathogens, and landscape fragmentation. Solitary bees are especially useful in this regard as they are highly informative with respect to the very aspects of habitat quality, resource availability, pesticide exposure and species-specific life history traits that impact vulnerability (LeBuhn & Luna, 2021). On a broader scale, pollinator diversity is vital not just to crop production, but also to environmental health, ecosystem resilience and the sustainability of wild plant communities (Katumo et al., 2022). More recently, syntheses also suggest that land use and climate change can influence pollinator distribution and community composition, but not in a consistent way across regions and taxa (Whipple & Bowser, 2023).

Such explanations as single stressors are limited in use because of the complexity of these pressures. Pollinators are seldom exposed to pesticides, nutritional limitation, pathogens or climatic stress alone. These are more likely to happen at the same time, and to affect each other in some way via common biological mechanisms. Both poor nutrition and pesticide exposure can deplete the body's metabolic resources for detoxification and immune defence, and disrupt the gut microbial communities that help digest food, process nutrients, and defend against pathogens. Microbiome dysbiosis has the capacity to further alter immune homeostasis and host susceptibility, thus enabling feedback loops to further amplify or alter effects of external stress. Under changing environments, interactions are particularly crucial when reduced floral resources and plant–pollinator interactions shift, which can increase pollinator physiological vulnerability. Many examples have occurred where climate and land-use change have been shown to compromise the provision of pollination services, with consequences cascading from the individual pollinator to the agricultural and ecological outcomes (Millard et al., 2023).

Thus, a multi-stressor biological framework is needed for the realistic understanding of pollinator health. This should then tie external exposure to internal physiological response and these responses to behavioural, reproductive, population and ecosystem impacts. Importantly, anthropogenic land use does not impact all pollinators in the same way, so differences in species, ecological traits, and environmental contexts must be taken into account rather than assumed to be the same (Williams et al., 2024).

**The objectives of this review are to:**

- Synthesize current evidence on pesticide exposure and nutritional limitation as major environmental pressures affecting pollinator health.
- Examine how these stressors influence microbiome composition, detoxification, metabolism, and immune responses.
- Integrate their combined effects across molecular, individual, colony, population, and ecosystem levels to identify key biological mechanisms, knowledge gaps, and priorities for pollinator protection.

## **2. Environmental Drivers of Pollinator Stress**

Pollinator habitat loss, habitat alteration, and landscape simplification are all caused by agricultural intensification. Depleted semi-natural habitat may create a reliance on floral resources that are available for shorter periods of time, while native habitat may help mitigate times of floral resource scarcity and promote forage continuity for honey bees (Dolezal, St. Clair, et al., 2019). In addition, prairie strips can be established within croplands to sustain native bee communities by supplying forage and refuge in simplified croplands (Kordbacheh et al., 2020).

A decrease in floral diversity also impacts pollinators through reduced availability and quality of nectar and pollen and a loss in seasonal availability. Some extensive farming techniques such as increasing vegetation heterogeneity and increasing the length of time for flowering can contribute to the provision of floral resources (Langlois et al., 2020). Pollinator communities can also shift in response to land-use intensification, as it can benefit generalist pollinators that are able to access wider-ranging diets, and reduce the availability of more specialized pollinators (Peters et al., 2022).

In addition to being in an agricultural environment, there is chemical contamination pressure. Pesticides and other agrochemicals can be encountered by pollinators in nectar, pollen, water, vegetation contact, and in residues of foraging habitats. This exposure is frequently in conjunction with nutritional and habitat limits, and not as a singular challenge.

This can be further altered by climate variability. Temporal mismatches between pollinators and floral resources may arise as a result of changes in flowering phenology, floral traits, reproductive success, and the timing of pollinator activity in response to rising temperatures, altered rainfall, drought, and extreme events (Martén-Rodríguez et al., 2025).

These environmental pressures frequently overlap. Pollinator foraging activity and exposure may be equally affected by land use change, as it can also change floral availability and foraging distances, which in turn changes resource selection, pollinator behavior and pollinator-exposure (Birkenbach et al., 2024). Pollinator stress is better considered as the result of the interaction between habitat, nutritional, chemical and climatic factors than a reaction to a single environmental factor.

Figure 1 illustrates how landscape modification, resource limitation, chemical exposure, climatic stress, and pathogens converge through multiple exposure pathways to influence pollinator physiology.

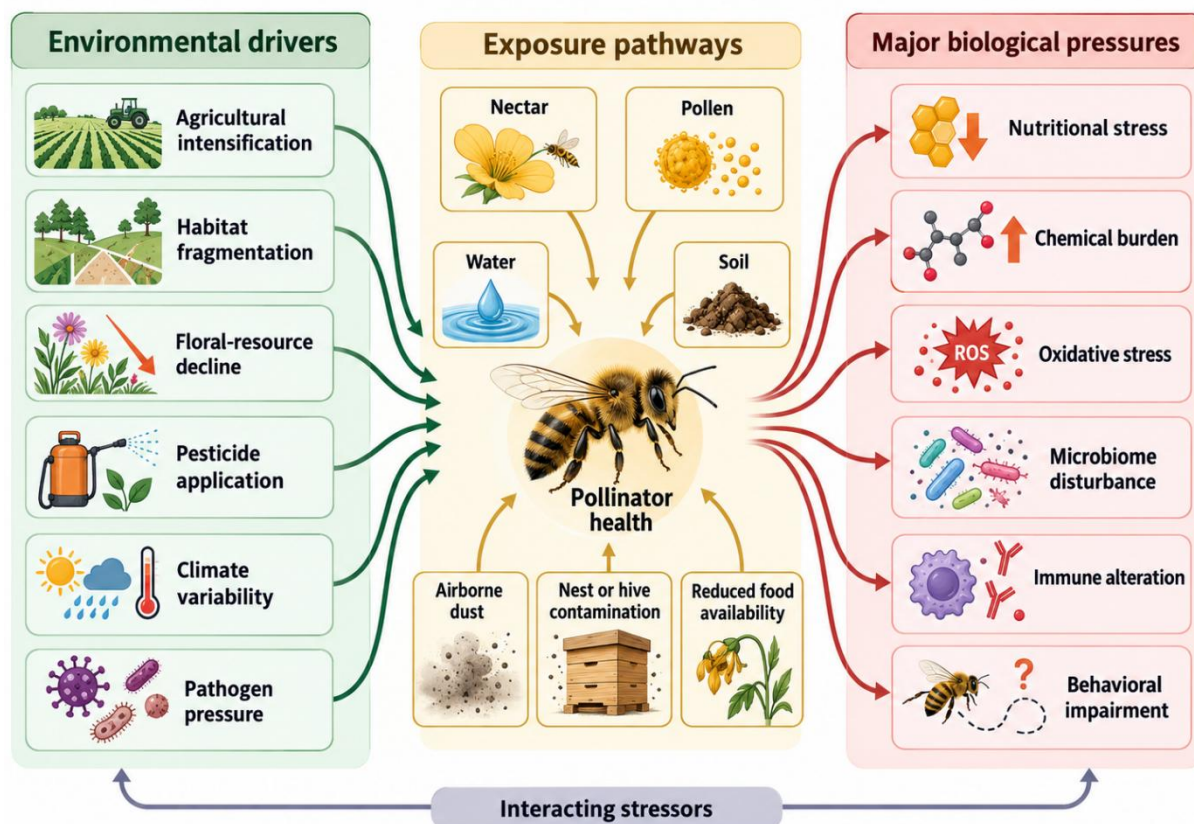


Figure 1. Environmental drivers, exposure pathways, and major biological pressures influencing pollinator health

Table 1 presents the major environmental pressures affecting pollinators and summarizes their principal biological pathways and potential consequences.

Table 1. Major Environmental Stressors and Their Biological Effects on Pollinators

| Environmental stressor | Main exposure or pressure                 | Primary biological effects              | Potential consequence         |
|------------------------|-------------------------------------------|-----------------------------------------|-------------------------------|
| Habitat modification   | Loss and fragmentation of natural habitat | Reduced nesting and forage availability | Lower abundance and diversity |

|                            |                                                              |                                                            |                                         |
|----------------------------|--------------------------------------------------------------|------------------------------------------------------------|-----------------------------------------|
| Floral-resource limitation | Reduced pollen and nectar quantity or diversity              | Nutritional imbalance and metabolic stress                 | Reduced development and resilience      |
| Pesticide exposure         | Nectar, pollen, water, soil, and plant residues              | Neurotoxicity, oxidative stress, and detoxification burden | Impaired survival and behavior          |
| Climate variability        | Heat, drought, altered rainfall, phenological shifts         | Physiological stress and resource mismatch                 | Disrupted plant–pollinator interactions |
| Pathogen pressure          | Viruses, fungi, parasites, and other pathogens               | Immune activation or dysregulation                         | Increased disease susceptibility        |
| Multiple stressors         | Simultaneous chemical, nutritional, and biological pressures | Interacting physiological disturbances                     | Cumulative or context-dependent effects |

### 3. Pesticide Exposure and Biological Effects in Pollinators

#### 3.1 Major Pesticide Classes and Routes of Exposure

Farmers use a variety of pesticides such as neonicotinoids, pyrethroids, organophosphates, fungicides, herbicides and combinations of these in agriculture, with which pollinators come into contact. Exposure may occur through contaminated nectar, pollen, water, soil, dust, treated plant surfaces, and residues carried into nests or colonies. While insecticides are toxic to insect nervous and/or physiological systems, fungicides and herbicides can also directly or indirectly affect pollinator health in combination with other chemicals (Cullen et al., 2019). Pollinators often come into contact with multiple compounds in the field, making field exposure often complicated. For instance, bumblebees can come in contact with glyphosate when foraging in landscapes treated with these products (Thompson et al., 2022). Combined exposure is especially important as toxicity may be influenced by the interaction between insecticides and fungicides (Schuhmann et al., 2022).

#### 3.2 Acute, Chronic, and Sublethal Toxicity

Pesticide effects vary from immediate death after high dose exposure, to chronic and sublethal effects after repeated or low level exposure. If survival is not affected, sublethal exposure can still affect colony or population survival processes. These include changes in activity, sensory function, feeding, development and reproductive function (Di Noi et al., 2021). Exposure to treated vegetation may also last

beyond the period of treatment, as well as not always be captured by the protection interval (PI) found on the label (Swanson et al., 2024).

### 3.3 Molecular and Cellular Mechanisms

Pesticides, at the cellular level, can disrupt neural communication, oxidative balance, energy use and detoxification. Neonicotinoids target the nicotinic acetylcholine receptor as their target site of action, and interference with neural transmission may have an impact on sensory processing, learning and behaviour (Cabirol & Haase, 2019). However, there can also be changes in the transcription response to pesticides, which differ by caste and pesticide type in bumblebees (Colgan et al., 2019). The alterations in antioxidant and metabolic parameters after pesticide and pesticide mixture exposure also suggest the disruption of cellular stress regulation and detoxification mechanisms (Murawska et al., 2025).

### 3.4 Physiological and Behavioral Consequences

The resulting molecular changes manifest themselves as stunted development, reproductive failure, cognitive and navigational deficits, declines in foraging success, and shorter life spans. Low dose exposure has been shown to negatively affect honey bee conditioning and biosensory function (Bartling et al., 2019), which represents a decrease in performance that is necessary to acquire essential resources for the honey bee. When repeated, these effects can build up over developmental and/or adult exposure.

### 3.5 Differences Among Pollinator Groups

This is because there are differences in body size, physiology, nesting habits, diet, and exposure routes among pollinator taxa, which leads to variation in sensitivity to pesticides. Honey bees are not necessarily representative of other groups, as toxicological studies in stingless bees indicate that responses cannot automatically be extrapolated across pollinator taxa (Botina et al., 2020). This is also the case for solitary bees, where data on pesticides is still relatively scarce and inconsistent (Lehmann & Camp, 2021). Moreover, the findings from contact-toxicity testing of *Megachile rotundata* highlights the need for species-specific testing of pesticide risk (Ansell et al., 2021).

Table 2 summarizes the major pesticide groups encountered by pollinators and their principal biological targets and associated responses.

Table 2. Major Pesticide Groups and Biological Responses in Pollinators

| Pesticide group | Major biological target or effect | Representative pollinator response                |
|-----------------|-----------------------------------|---------------------------------------------------|
| Neonicotinoids  | Nicotinic acetylcholine receptors | Impaired learning, sensory function, and foraging |
| Pyrethroids     | Voltage-gated sodium channels     | Neural disturbance and reduced motor              |

|                    |                                         |                                                           |
|--------------------|-----------------------------------------|-----------------------------------------------------------|
|                    |                                         | performance                                               |
| Organophosphates   | Acetylcholinesterase inhibition         | Neurotoxicity and altered behavior                        |
| Fungicides         | Metabolic and detoxification pathways   | Sublethal physiological effects and chemical interactions |
| Herbicides         | Direct and indirect biological pathways | Microbiome changes and reduced forage availability        |
| Pesticide mixtures | Multiple interacting targets            | Additive, synergistic, or antagonistic effects            |

## 4. Nutritional Limitation and Pollinator Physiological Resilience

### 4.1 Floral-Resource Loss and Dietary Simplification

Floral abundance, diversity and seasonality are all of critical importance to pollinator nutrition. Intensive agriculture and habitat simplification may lead to periods of dietary imbalance and nutritional scarcity due to less access to varied pollen sources. In the case of honey bees (*Apis mellifera* L.), limited pollen diversity has been linked to decreased nutritional flexibility and changes in susceptibility to viral infections in highly cultivated scenarios (Zhang et al., 2020). Additionally, there is also variation in pollen diet diversity across bee lineages based on their ecological lifestyle, suggesting that the ability to deal with simplified floral environments may differ significantly among the different groups of pollinators (Devkota et al., 2024).

### 4.2 Nutritional Requirements of Pollinators

Carbohydrates are the main source of energy for pollinators and pollen is a source of protein, amino acids, lipids, vitamins, minerals, and many bioactive plant compounds. Pollen's nutritional value thus not only relies on quantities but also on its biochemical composition and essential nutrient balance (Lau et al., 2022). Plant secondary metabolites may also affect feeding behaviour, metabolic processes, microbial communities and physiological responses. This nutritionally diverse pollen can therefore offer benefits beyond the simple energy and protein needs (Vanderplanck et al., 2023).

### 4.3 Effects of Poor Nutrition on Development, Metabolism, Reproduction, and Longevity

Nutritional deficiency may reduce larval development, body condition of adults, metabolism, reproductive capacity and longevity. Pollen substitutes can be used partially to compensate for the shortage of resources, but their nutritional value and biological effect are quite different (Paray et al.,

2021). Diet composition can also alter host gene expression and gut microbial structure, showing that nutrition affects multiple physiological systems simultaneously (Powell et al., 2023).

#### **4.4 Nutrition and Detoxification Capacity**

Appropriate nutrition promotes metabolic processes necessary for antioxidant protection and xenobiotic detoxification. Protein, lipids, micronutrients and phytochemicals can affect enzyme activity and cell defense mechanisms, while nutrient deficits can limit the cellular ability to handle environmental contaminants.

#### **4.5 Nutrition-Mediated Modulation of Pesticide Susceptibility**

Nutritional status may significantly influence pesticide effects. It is also known that pesticide toxicity is related to the pollen diet of the honey bees (Barascou et al., 2021), with some diets leading to greater tolerance. But sometimes dietary compensation is not enough, as a varied pollen mix improved development for solitary bees, but failed to cancel out negative impacts from pesticides (Schwarz et al., 2024).

#### **4.6 Nutritional Status and Immune Competence**

Nutrition also influences immune function by influencing the ability of cells to defend themselves, fight infectious agents, maintain tissues, and repair tissues after an infection. Nutritional limitation can be a source of vulnerability to pathogens and other environmental pressures due to its impact on the physiology of individuals and communities (Vaudo et al., 2024). Pollinator nutrition should therefore be viewed as an important modifier of biological resilience, which may amplify or buffer effects from pesticides, pathogens and other stressors.

### **5. Pollinator Microbiome: Homeostasis, Dysbiosis, and Environmental Sensitivity**

Pollinator-associated microbial communities are an intrinsic component of the host's physiology, especially its gut flora. Core gut bacteria are involved in digestion, metabolic regulation, immunity and protective against opportunistic microorganisms in the honey bees, and lactic acid bacteria might have a role in pathogen suppression and gut homeostasis (Nowak et al., 2021). However, the microbial makeup does differ between pollinator taxa, developmental stages, pollinator diet and environmental exposure. Microorganisms are responsible for carbohydrate metabolism, fermentation, production of organic acids and conversion of pollen nutrients. Microbial shifts with restricted pollen use suggest that nutritional availability can alter the diet–microbiota–host axis, resulting in changes to host physiological resilience (Ricigliano & Anderson, 2020).

The microbiome is also involved in the metabolism of environmental chemicals. There are some natural gut micro-organisms which may break down pesticide residues in the body, which can affect the effective dose and persistence of xenobiotics in the host. The discovery that resident microbes in the gut of honey

bees can mediate pesticide biotransformation is direct evidence for the role of gut microbiota in biotransforming pesticides (El Khoury et al., 2022). Pesticide use, however, may also affect microbial abundance and community structure directly, as the effects of pesticide depend on the pesticide class, dosage, formulation and host species. The exposure to glyphosate was linked to modifications in the microbiota of honey bees, while the exposure to the glyphosate metabolite aminomethylphosphonic acid was not (Blot et al., 2019). Long-term exposure to other groups of insecticides has also been associated with microbial alteration, especially when combined with *Nosema ceranae* infection (Rouzé et al., 2019). The effects of oral and topical exposure to formulations containing glyphosate may also impact on the composition of the microbiota and on the outcomes of survival (Motta et al., 2020).

Another significant influence on the microbial stability is provided by nutrition. Restriction of diet can change the amount of available substrate for beneficial microorganisms and change the microbial metabolic activity. Nutritional simplification might result in a decrease of functional stability, as it can favor some microbial groups, and disadvantage other groups, depending on the diversity of the flower. Dysbiosis can therefore reduce the ability to resist colonization, process nutrients and maintain homeostasis, and make the host more vulnerable to other stressors. However, because of the different sensitivity of individual bacterial taxa, microbial responses cannot be extrapolated from one to another (Cuesta-Maté et al., 2021). Furthermore, physiological health indicators can be altered by low-level chronic pesticide exposure without measurable disruption of the core gut microbiota, indicating that microbiome stability and host health do not always respond in parallel (Almasri et al., 2022).

When thinking about how to measure environmental stress through microbiome alterations, these complexities come to the fore. In some studies, glyphosate exposure changed bumblebee's gut microbiome (Helander et al., 2023), while in others, there was no detectable effect of glyphosate, *Crithidia bombi*, or their combination on the bumblebee microbiome (Straw et al., 2023). Such contrasting findings indicate that microbiome responses are strongly context dependent. Therefore, when evaluating the health of pollinators, it is important to take microbial changes into account in conjunction with a physiological, ecological, nutritional, and exposure-based assessment.

## **6. Immune Responses and Stress-Induced Immune Dysregulation**

Pollinators rely mainly on innate immunity involving Toll, immune deficiency (Imd), Janus kinase/signal transducer and activator of transcription (JAK/STAT), RNA interference, antimicrobial peptides, and cellular defenses such as phagocytosis, nodulation, and encapsulation. These mechanisms work together to control pathogen recognition and antiviral and antimicrobial responses. Their activity varies with developmental stage, pathogen exposure, and physiological condition, while seasonal and age-related changes in immune markers are associated with physiological status and longevity (Zhao & Liu, 2022; Kunc et al., 2019).

Exposure to pesticides at sublethal doses may affect immune regulation but not necessarily result in death. Short-term exposure to flupyradifurone has been shown to alter survival and immune function, suggesting that brief pesticide exposure can have prolonged physiological effects (Al Naggar & Baer, 2019). Exposure to chlorothalonil also has the potential to change immune-related markers that can relate to susceptibility to viral infection, thus connecting pesticide stress with disease vulnerability (O’Neal et al., 2019). There is also the possibility for chemical stressors to alter immune-gene expression and affect the outcome of viral infection even when the concentration of chemical is not acutely lethal (Parekh et al., 2021).

Nutritional status also plays a significant role in immune activity as immune defense systems can utilize a significant amount of metabolic resources. Protein, amino acids, lipids, micronutrients and bioactive compounds, which are essential for immune signaling and cellular maintenance, are provided by adequate pollen intake. The results indicate that the quality of the pollen source directly affects the physiological resilience by causing measurable differences in digestion, antioxidant capacity, immune function and gut microbial composition, highlighting the impact of diet on physiological resilience (Li et al., 2025). Nutrition can have a significant impact on microbiome function, which has a clear relationship to the regulation of immune homeostasis through interactions with epithelial barriers, modulation of immune-gene expression and regulation of pathogen establishment. These microbial communities may, therefore, have a secondary impact on host defense if they are disrupted. In the case of honey bees, immune dysregulation has been linked to exposure to glyphosate, a chemical present in the environment that may connect microbiome disturbance with altered immune functioning (Motta et al., 2022).

There are also common physiological mechanisms involved in detoxification, antioxidant protection and immunity. This could lead to tissue damage from the increased oxidative stress, and shifts in metabolic priorities to deal with the detox of xenobiotics could further increase energetic costs. The ability to maintain effective defense may be diminished in such a trade-off when faced with long-term environmental exposure. Immune disruption can lead to susceptibility to other pathogens, viruses and parasites. For instance, flupyradifurone has been demonstrated to affect antiviral immunity and decrease worker survival (Harwood et al., 2022). Therefore, the susceptibility of pollinators to infection should be considered as a result of their exposure to pesticide, nutritional status, stability of microflora, oxidative balance, and immune competence, not a single impact of pathogen pressure.

## **7. Multi-Stressor Interactions and Biological Cascades**

### **7.1 Pesticide × Nutritional Limitation**

Pollinators commonly encounter pesticide exposure alongside nutritional limitation. Lowered resources for detoxification, repair, immunity and behavior are likely from reduced floral diversity and poor diet quality. The impacts of pesticide exposure and decreased floral resources on reproduction were additive in

wild bees, indicating that resource limitation can amplify chemical stress (Stuligross & Williams, 2020). Among the bees, exposure to insecticide also led to memory impairment and a lack of sucrose responsiveness in both high and low nutrition situations (Gray et al., 2024). Thus, nutrition is an important modifier of pesticide susceptibility.

## 7.2 Microbiome-Centered Multi-Stressor Interactions

Chemical exposure, nutrition, and infection are linked via the gut microbiome. Pesticides can alter microbial composition or activity, which can impact nutrient processing, xenobiotic metabolism and pathogen resistance. The disturbance of microbial homeostasis makes it harder for the host to supply the necessary metabolic support, microbial resistance to colonization, and barrier function and can simultaneously disrupt microbial communities and reduce host energy and nutrient availability via poor-quality diets.

Diet quality also modifies biological responses to infection. Honey bees exposed to nutritional stress and viral challenge can show outcomes that differ from those produced by either stressor independently, demonstrating that nutritional condition can influence disease-related physiological responses (Dolezal, Carrillo-Tripp, et al., 2019). The microbiome further interacts with immunity by supporting epithelial integrity, regulating immune signaling, and limiting pathogen establishment. Pathogen pressure can go beyond localized infection and cause general metabolic changes, as in the case of *Nosema ceranae* infection which has been linked to general metabolic changes (Broadrup et al., 2019). Microbiome-mediated effects should therefore be understood as part of a reciprocal network linking diet, chemical exposure, metabolism, and host defense.

## 7.3 Pesticide–Immune–Pathogen Interactions

Immune signaling and pathogen susceptibility can be altered in the absence of obvious changes in survival or overall condition caused by exposure to pesticides. The impact of chlorothalonil on transmission potential of a pathogen of bumblebees, for instance, did not result in an obvious change in the health of individual bumblebees, suggesting that ecological effects can occur before organism-level effects are obvious (Calhoun et al., 2021). Pesticide–pathogen interactions are an emerging concern for both managed and wild bees, as sublethal exposure to pesticides can affect how pathogens spread and disease develops (Straub et al., 2022).

These interactions can become more complex when nutrition is simultaneously constrained. Larval stages might be particularly susceptible due to the simultaneous exposure to pesticides and diseases in the phases of rapid growth and high nutrient requirements (Yordanova et al., 2022). In these instances, nutritional limitation may limit the resources available for detoxification and immunity, and pesticide exposure may cause host defence to be changed in response to pathogens. The interactions among pesticides, nutrition

and pathogens, however, may create results that can not necessarily be predicted from the individual stressor experiments.

#### 7.4 Context-Dependent Responses and Environmental Stressor Multipliers

The multiple stressor effects are not necessarily additive/synergistic. Responses can be additive or synergistic, antagonistic or negligible, and can be positive or negative depending on the combination of stressors and can be dose dependent, life stage dependent, caste and species dependent, and environmentally dependent. Even when considering co-occurring pesticides, the semi-field results may differ from those of individual laboratory exposures, further highlighting the need for “realistic” mixtures and exposures (Shepherd et al., 2024). A system approach is therefore more suitable than a combination of effects following only as the sum of effects (EFSA Scientific Committee, 2021).

Stress factors can also be compounded by environmental factors. Chemical and physiological pressures could be enhanced by temperature extremes, habitat loss, lack of food, and high pathogen levels. Some of these effects can be mitigated through social organization mechanisms, such as collective defenses, grooming, and resources sharing, as well as regulating individuals' behavior when two or more threats are present at the same time (Gaubert et al., 2023). Nutrition, microbiome stability, detoxification, immunity, pathogens, pesticides and environmental conditions thus constantly affect each other and make them interconnected, making pollinator health reflect a biological cascade.

Table 3 integrates the principal interactions among pesticide exposure, nutrition, microbiome stability, immunity, and pathogen pressure that shape multi-stressor responses in pollinators.

Table 3. Interactions Among Nutrition, Microbiome, Immunity, and Pesticide Exposure

| Interaction             | Main biological mechanism                                              | Possible outcome                                 |
|-------------------------|------------------------------------------------------------------------|--------------------------------------------------|
| Nutrition × pesticides  | Nutrient availability modifies detoxification and antioxidant capacity | Altered pesticide tolerance                      |
| Nutrition × microbiome  | Diet determines microbial substrates and community structure           | Changes in nutrient metabolism and gut stability |
| Pesticides × microbiome | Chemicals alter microbial abundance or function                        | Dysbiosis and altered xenobiotic processing      |
| Microbiome × immunity   | Gut microbes regulate barrier function and immune signaling            | Modified pathogen resistance                     |
| Pesticides × immunity   | Chemical stress alters immune-gene expression and defense pathways     | Greater infection susceptibility                 |

|                                    |                                          |                                                          |
|------------------------------------|------------------------------------------|----------------------------------------------------------|
| Nutrition × pathogens              | Dietary quality influences resources     | Variable infection severity available for immune defense |
| Pesticides × nutrition × pathogens | Multiple pathways operate simultaneously | Context-dependent biological cascades                    |

Figure 2 integrates the major reciprocal pathways through which pesticide exposure, nutritional limitation, microbiome dysbiosis, immune dysregulation, climate stress, and pathogen pressure collectively influence pollinator health.

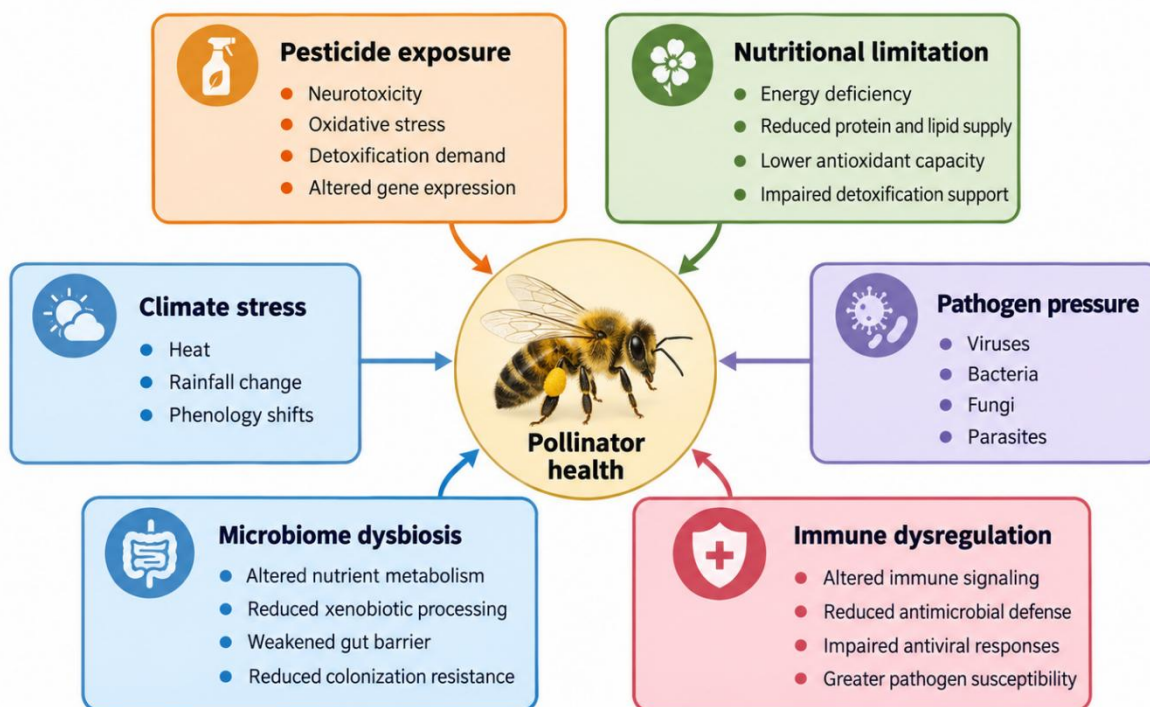


Figure 2. Integrated Multi-Stressor Pathways Shaping Pollinator Health

## 8. From Molecular Disruption to Population Decline: Implications, Mitigation, and Future Directions

### 8.1 Cross-Scale Consequences: Molecular to Ecosystem Levels

Multiple stressors can cause physiological effects in pollinators before visible effects become apparent. These oxidative stress, changes in gene expression, metabolic imbalance, impaired detoxification, disruption of the microbiome and immune dysregulation can be cumulative during chronic exposures and are particularly exacerbated by the presence of pesticides which combine with other factors such as poor nutrition, infections, or bad climate. These molecular responses should be correlated to functional responses at higher level.

This disruption may lead to decreases in survival, development, reproduction, learning, navigation, and foraging efficiency. One of the most significant reproductive effects is in solitary species where each female contributes directly to the recruitment of the population. Assessment should thus go beyond mortality to encompass cognition, development, reproduction, feeding behaviour and recovery of physiology.

Negative impacts on individual social brood-reared bee workers can impact brood provisioning, colony development, queen performance, and colony productivity. Workers may become less efficient over time, leading to decreased resource acquisition and colony maintenance, and reproductive effects may affect the establishment of future colonies. Stress may affect recruitment, species abundance and community composition in wild pollinator populations. These impacts can be cascading, affecting other components of plant–pollinator networks, such as the abundance, diversity, and activity of the pollinators, which could influence reproductive success of both wild and cultivated plants. A change in the number of species of flowers can alter the structure of pollinator networks and competition and resources utilisation between bees, and can also influence the structure of the pollinator communities (Doublet et al., 2022).

Figure 3 summarizes how environmental stressors can propagate from molecular and cellular disruption through individual and population-level effects to broader ecosystem consequences.

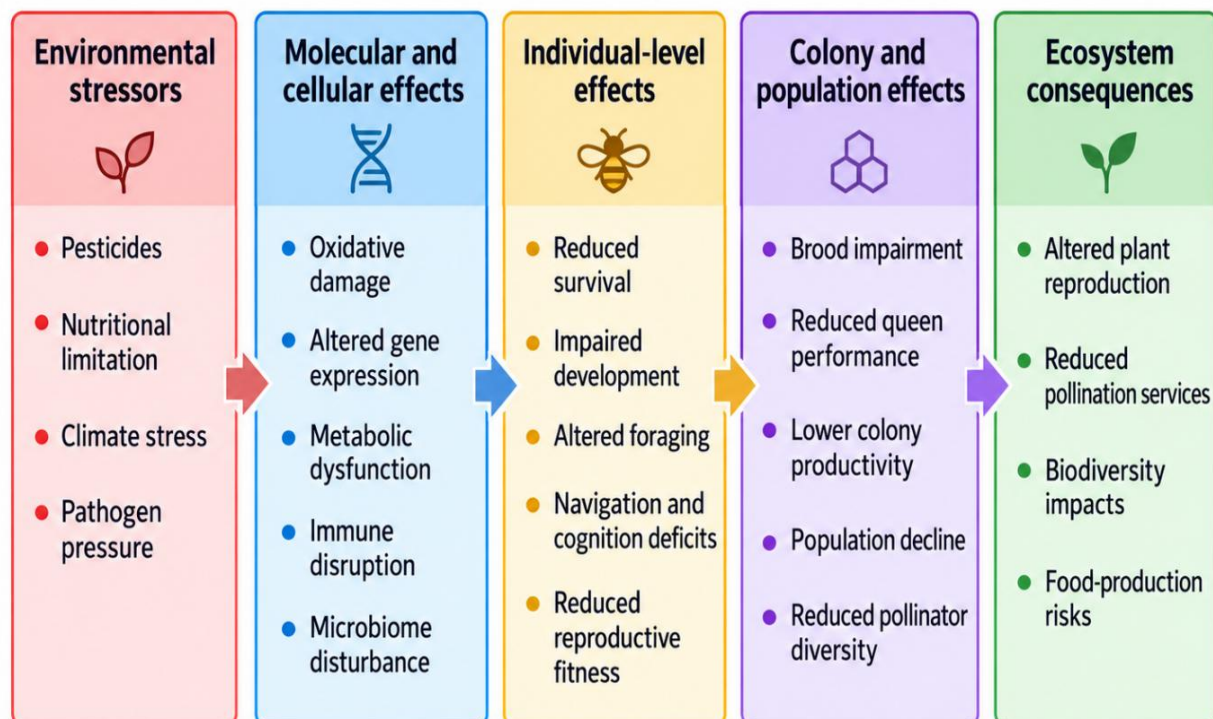


Figure 3. Cross-Scale Progression of Environmental Stress From Molecular Disruption to Ecosystem Consequences

## 8.2 Improving Pesticide Risk Assessment

Risk assessment should move beyond acute mortality tests toward chronic exposure, pesticide mixtures, sublethal endpoints, and multi-stressor testing. More bumblebee and solitary bee involvement is also needed as results can't always be extrapolated from the honey bee. Modern guidance is increasingly supportive of the inclusion of a number of bee groups and more realistic exposure scenarios for evaluating pesticides (European Food Safety Authority [EFSA] et al., 2023). Some practices suggested for pesticide mitigation have limited evidence indicating their effectiveness, however, and should be further field-validated before assuming effectiveness (Straw & Stanley, 2023).

## 8.3 Habitat, Nutritional, and Microbiome-Based Management

Nutrient stress can be alleviated and resilience to other environmental factors increased through improved habitat quality. More stable nectar and pollen sources including floral diversification, wildflower strips, ecological corridors and seasonally continuous forage can be provided. Incorporating flower plantings into agricultural landscapes has been shown to lead to higher abundance and wild bee richness in the area, which is a testament to their usefulness as a practical habitat management practice (Van Drunen et al., 2022). Coordinated action on farms, landscapes, and across policy levels is needed beyond local measures for effective conservation (Stout & Dicks, 2022).

Other microbiome-related strategies, such as probiotics, prebiotics, microbial restoration, and microbiome-derived biomarkers are also being developed as tools to help support pollinator health. These could help reinforce microbial activities related to digestion, pathogen resistance and xenobiotic processing. Their ecological suitability, species specificity, long-term stability and field-scale efficacy are not sufficiently proven, however. Microbiome interventions should therefore complement, rather than replace, habitat restoration, nutritional improvement, and exposure reduction.

## 8.4 Major Knowledge Gaps and Future Priorities

Further studies should reduce the current dependence on *Apis mellifera* and expand evidence for solitary bees, bumblebees, stingless bees and other pollinators. More focus should be paid to discrepancies between the laboratory and field, pesticide mixtures, and standardized multi-stressor protocols, as well as longitudinal responses of the microbiome. Causality of microbial changes and host health is of special significance. Further research should also integrate molecular markers with reproduction, population persistence and ecological function and account for geographic, climatic, sex, caste, species and life-stage differences. Integrated pest and pollinator management provides a valuable pathway for reducing the risk of chemicals and implementing effective crop protection and pollinator conservation strategies (Phan et al., 2025).

## 9. Conclusion

Pollinator health is a complex phenomenon that is influenced by more than one stressor and by their interactions. Exposure to pesticides can affect neural, metabolic, detoxification, and immune functions, and nutritional deficits can reduce the ability to withstand the effects of pesticide exposure. At the same time, the gut microbiome contributes to nutrient metabolism, xenobiotic processing, and immune regulation, meaning that microbial disruption can further alter responses to chemical exposure, poor diet, and infection. These biophysically linked pathways result in biological cascades in which one stressor can enhance, diminish or alter the impact of another stressor.

It is crucial to understand these interactions to account for differences in pollinator susceptibility across species, life stages, ecological conditions and exposure levels. Future studies should move beyond the strong dependence on the managed honey bee and expand to cover more bumblebees, solitary bees, stingless bees and other pollinating insects. There is also a need to pay more attention to chronic and field realistic pesticide exposure, chemical mixtures, realistic nutritional conditions and simultaneous biological stressors. Microbial and molecular indicators should be more consistently related to behavioural, reproductive, colony, population and ecosystem level outcomes.

Habitat enhancement, provision of continual and diverse floral resources, minimisation of hazardous pesticide exposure, better pest-management practices and more robust ecological monitoring will all be necessary to achieve pollinator protection. Risk assessment should similarly incorporate species diversity, sublethal effects, nutritional condition, microbiome responses, and multi-stressor interactions. An integrated biological approach can offer a more realistic basis for conserving pollinator populations, maintaining plant–pollinator networks and protecting the ecological and agricultural functions that rely on the presence of these networks.

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