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Discussion

Discussion: Harnessing microbiome-mediated adaptations in insect pollinators to mitigate climate change impact on crop pollination

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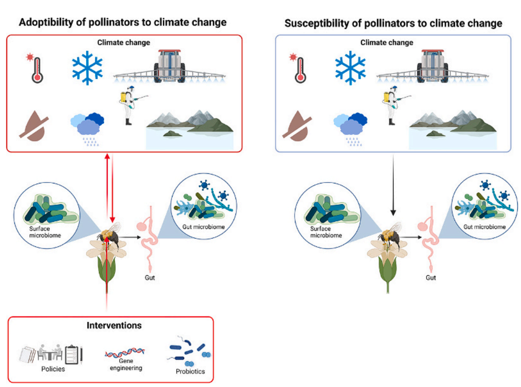
HIGHLIGHTS

- Insect microbiomes shape host physiology, vital for climate resilience.
- Climate impacts on pollinator microbiomes require innovative strategies.
- Resilient microbiomes correlate with stable pollination services.
- Microbiome insights transform agriculture with probiotics, engineering, and conservation.

GRAPHICAL ABSTRACT



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ABSTRACT

Insect pollinators, vital for agriculture and biodiversity, face escalating threats from climate change. We argue and explore the pivotal role of the microbiomes in shaping adaptations of insect pollinator resilience amid climate-induced challenges (climate change and habitat alteration). Examining diverse taxonomic groups, we unravel the interplay between insect physiology, microbiomes, and adaptive mechanisms. Climate-driven alterations in microbiomes impact insect health, behavior, and plant interactions, posing significant effects on agricultural ecosystems. We propose harnessing microbiome-mediated adaptations as a strategic approach to mitigate climate change impacts on crop pollination. Insights into insect-pollinator microbiomes offer transformative avenues for sustainable agriculture, including probiotic interventions (use of EM PROBIOTIC) and microbiome engineering (such as engineering gut bacteria) to induce immune responses and enhanced pollination services. Integrating microbiome insights into conservation practices elucidates strategies for preserving pollinator habitats, optimizing agricultural landscapes, and developing policies to safeguard pollinator health in the face of environmental changes. Finally, we stress interdisciplinary collaboration and the urgency of understanding pollinator microbiome dynamics under climate change in future research.

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1. Introduction

Insect pollinators play a critical role in agriculture, contributing significantly to economic prosperity and ecological balance. Approximately 87.5 % of wild plants rely on insect pollination, with 20 % pollinated by bees. Pollinators in the tropics include moths, butterflies, birds, stingless bees, honeybees, and bats, while temperate regions benefit from honeybees, bumblebees, solitary bees, wasps, and hoverflies. The tropics host over 100,000 species, with approximately 220,000 species in pollinator taxonomic groups. Globally, 1500 crops require insect pollination, contributing to 3–8 % of world crop production (Cameron and Sadd, 2020; Ollerton, 2017; Shah et al., 2023). The economic prosperity and ecological balance are significantly influenced by the specific contributions of different insect pollinators, including bees, moths, and butterflies. Bees, both wild and managed, play a crucial role in providing a wide range of benefits to society, including contributions to food security, farmer and beekeeper livelihoods, social and cultural values, and the maintenance of wider biodiversity and ecosystem stability (Potts et al., 2016). Bee pollination has a substantial economic value for crop production, influencing the economy and contributing to the pollination of various crops (Khalifa et al., 2021). Non-*Apis* bees, also known as wild bees, are valuable for crop pollination, contributing to the pollination of various crops (Greenleaf and Kremen, 2006). Moths, despite being underappreciated, have been recognized for their potential contribution to pollination services. Moths have been found to pollinate four crops of Cucurbitaceae in Asia, indicating that non-bee pollinators may substantially contribute to crop yield (Lu et al., 2021). Butterflies, as potent pollinators and ecological indicators, are important for estimating the general health of an ecosystem.

The declines in pollinator populations have triggered investigations into how land-use change affects insect pollinators and pollination services in agricultural landscapes (Ratto et al., 2022). This decline in pollinator populations also raises concerns about their vulnerability to climate change, a critical issue with significant implications for agricultural ecosystems. (Layek et al., 2023).

The vulnerability of insect pollinators to climate change is a critical concern with significant implications for agricultural ecosystems. This vulnerability has been associated with habitat loss, increased susceptibility to disease and parasites, and pesticide use (Tackenberg et al., 2020). The combined effects of landscape alteration, agricultural intensification, and climate change on animal-mediated pollination reveal potential mismatches in pollination networks, affecting plant-pollinator interactions and leading to indirect evolutionary consequences (González-Varo et al., 2013; Hegland et al., 2009). Additionally, climate change can cause potential disruption of life cycles and species interactions (Potts et al., 2016). Moreover, there are potential consequences of shifts in pollinator phenology under climate change, emphasizing the need to understand the consequences of climate-driven changes in pollinator phenology (Tiusanen et al., 2016).

The relationship between insects and their microbiomes is crucial in shaping various aspects of insect physiology, including essential functions that contribute to their adaptation mechanisms. The gut microbiota emerges as a vital factor in the growth, development, physiology, immunity and evolution of host insects. In the context of insect-plant interactions, the dynamic response of insect gut microbiota to plant secondary metabolites, such as saponin degradation, highlights intricate ecosystem interplay (Mason et al., 2019). Symbiotic relationships, such as Wolbachia infection in adult *Aedes aegypti* mosquitoes, reveal the impacts microbiomes composition, highlighting the complexity (Audsley et al., 2018). Within host-microbiome interactions, larval diapause in *Nasonia vitripennis* reveals the microbiome's role in nutrient allocation and dynamics (Mason et al., 2019). These adaptive functions shape microbial communities, impacting digestive tracts and influencing insect physiology (Engel and Moran, 2013). Microbiomes, through genetic and metabolic interactions, impact insect ecology, physiology, evolution, and behavior, exemplifying their adaptive functions (Vallino et al., 2021). The insect microbiome's composition and function correlate with processes crucial for surviving diverse overwintering pressures (Ferguson et al., 2018). In herbivorous insects, the gut microbiome assumes a critical role in growth, development, and environmental adaptation to host plants (Lefort et al., 2017). The adaptive nature of insect microbiomes is further highlighted by their ability to aid in the breakdown of recalcitrant dietary substrates and facilitate insect social behavior, illustrating their integral role in supporting various physiological processes (Tinker and Ottesen, 2020).

We suggest microbiome-mediated adaptations in insect pollinators as a strategic approach to mitigate the adverse impacts of climate change on crop pollination. By elucidating the complex relationships between insect physiology, microbiomes, and adaptive mechanisms, we propose innovative strategies to enhance the resilience of insect pollinators, safeguarding crucial ecosystem services vital for agriculture and biodiversity.

2. Microbial symbiosis in insect pollinators

Insect digestive systems house diverse microbial communities that significantly impact digestion, energy extraction, and protection against harmful microbes, provide host nutrition and aid in degrading toxic substances, enhancing host tolerance (Mills et al., 2023; Phalnikar et al., 2019; Yang et al., 2022; Yun et al., 2014; Zhang et al., 2022). Influenced by factors such as habitat, diet, developmental stage, and phylogeny, the diversity of these communities reflects the structure and function of the insect digestive system (Schmidt and Engel, 2021). Bacterial symbionts within insects play pivotal roles in host physiology, nutrition, reproduction, and defense against natural enemies (Noman et al., 2020; Paniagua Voirol et al., 2018; Zhao et al., 2022). In the context of insect digestive tracts, significant morphological and physicochemical variations impact microbial community structure (Engel and Moran, 2013). This diversity underscores the intricate relationship between insect hosts and their microbiota (Schmidt and Engel, 2021). Studies of *P. brevitarsis* larvae and *M. domestica* reveal the gut microbiota, concentrated in the distal gut, contributes to the digestion and fermentation of plant cell wall components (Geng et al., 2022; Jing et al., 2020).

Diverse insect pollinators across Diptera, Lepidoptera, and Hymenoptera orders reveal a core microbial community transmitted among beetles to larvae via secretions, impacting insect fitness (Li et al., 2023; Shukla et al., 2018). While plant-feeding insects exhibit variable gut bacterial communities, the modulation of microbial communities by diet composition is evident (Shapiro et al., 2019). Environmental factors, such as Imidacloprid, can impact insect digestive physiology and larval microbiota, influencing insect-microbiome interactions (Raymann et al., 2017).

Microbial communities associated with insects extend beyond the gut, influencing reproduction, virus transmission efficiency, and various aspects of host biology (Cappelli et al., 2022). This is evident in the case of entomopathogenic nematodes and their bacterial symbionts, playing a crucial role in successful colonization and reproduction in insect hosts (Bertoloni Meli and Bashey, 2018). Concentrated in insect intestines, microbial communities regulate host lifestyles, affecting diet and ecological niches (Mills et al., 2023; Xue et al., 2021).

The critical role of insect pollination in agriculture, involving diverse pollinators like beetles, wasps, flies, and bees, underscores the importance of their gut microbiota, shaping broader patterns of microbiome and insect-pollinator host associations (Moreira and Freitas, 2020). Furthermore, microbial signatures on flower surfaces serve as indicators of pollinator visitation, emphasizing the intricate relationship between insects and floral microbiomes (Ushio et al., 2015). The insect microbiome, encompassing bacteria, fungi, viruses, archaea, and protozoa, affects the fitness and behavior of pest insects (Gurung et al., 2019; Nobles and Jackson, 2020). A healthy microbiome, beneficial in dietary supplementation, tolerance to environmental changes, and maintaining host immune system homeostasis, contributes to increased host longevity and reproductive success.

3. Climate-induced changes in microbiomes

Climate change and habitat alterations have caused declines in the abundance, diversity, and body size of insect pollinators, leading to shifts in range, phenology, and ecological relationships, resulting in mismatches between crops and pollinators (Barrett et al., 2023; Hegland et al., 2009). In alpine ecosystems, climate change is expected to have a profound effect, necessitating a better understanding of the insects involved in (Hegland et al., 2009; Lefebvre et al., 2018). Landscape alteration and climatic fluctuations synergistically affect animal-mediated pollination, resulting in spatiotemporal mismatches between interacting species (González-Varo et al., 2013).

The impact of stress resulting from unpredictable climate fluctuations and alterations can give rise to increased instances of resistance within the microbiome of pollinator insects (Gressel, 2018). The more generalist the relations (i.e., multiple pollinator species for a plant or broad diet in pollinators), the more resilient the interactions are under changing climatic conditions (González-Varo et al., 2013). Studies have linked the visitation of diverse pollinator functional groups to the key properties of the floral microbiome under agrochemical disturbance, indicating the potential impact of environmental stressors on microbial diversity and network within the context of climate-induced changes (Wei et al., 2021). Sequence analyses have revealed that honey bee visitation reduced bacterial richness and diversity in seeds, but increased the variability of seed microbial structure and introduced bee-associated taxa (Prado et al., 2020).

The physiological and behavioral implications of climate-induced changes in insect pollinator microbiomes are multifaceted, with significant ecological and evolutionary consequences. Climate change alters the diversity and composition of insect pollinator microbiomes, affecting their physiological and behavioral traits. Physiologically, insect pollinators are susceptible to direct and indirect effects of climate change on their microbiomes. Stressors such as extreme temperatures and habitat alterations disrupt microbial diversity, potentially impacting metabolic processes, immune function, and overall health. Mechanisms of heat tolerance remain poorly studied, and heat shock proteins may be insufficient to mitigate climate-induced stressors on insect pollinator microbiomes (González-Tokman et al., 2020). Furthermore, water loss and high temperatures pose challenges for insect pollinators, making them particularly vulnerable to global warming and aridification (Prudic et al., 2022). Behaviorally, climate-induced changes in insect pollinator microbiomes can influence foraging patterns, phenological synchrony, and interactions with plants. Mutualistic relationships may be at risk of phenological mismatching, particularly if species exhibit disparate responses to temperature changes (Bartomeus et al., 2011). Variation in species responses to abiotic phenological cues under climate change may cause changes in temporal overlap among interacting taxa, with potential demographic consequences (Iler et al., 2013; Mishra et al., 2021).

Disruptions in microbial diversity can have direct effects on the physiological aspects of insect pollinators, impacting metabolic processes and immune function. Specialist species with a comparatively smaller diversity of mutualist interactions may have a higher risk of pollination disruption, leading to potential impacts on metabolic processes and immune function (Aguilar et al., 2006). The cellular processes underlying vertical transmission and nutrient translocation between the insect and microbial partners provide candidate molecular targets for disrupting these symbioses, which can directly affect metabolic processes and immune function in insect pollinators (Douglas, 2015). Microbial symbionts can influence a myriad of insect behavioral and physiological traits, including metabolic processes and immune function (Dong et al., 2022). The diversity and high adaptability of insects are strongly associated with their symbiotic microbes, which include bacteria, fungi, viruses, protozoa, and archaea, impacting metabolic processes and immune function (Zhao et al., 2022). Insect-infecting pathogens could disrupt the pollination process by affecting pollinator population density or traits, leading to potential impacts on metabolic processes and immune function (Recart et al., 2023). The overabundance of β-glucosidases and cellobiose phosphotransferase systems associated with the gut community in wood-feeding beetles can partially explain the enhanced cellulase complex activity, directly impacting metabolic processes (Scully et al., 2014).

The ecological implications of climatic changes in insect pollinator microbiomes are extensive. Insect pollinators are crucial for ecosystem functioning and food production, and disruptions in their microbiomes can have cascading effects on plant-pollinator interactions, biodiversity, and agricultural productivity. Considering the ethical implications of climate-induced stressors on insect pollinator microbiomes is essential, especially for the welfare of individual insect pollinators in the Hymenoptera and Diptera (Barrett et al., 2023). The transmission of non-specialized microbes to developing seeds through insect pollination could have important implications for the assembly of the seed microbiota and plant health.

4. Resilience of microbiome enhanced pollination services

The resilience of pollination services is linked to the stability of crop pollinator occurrences, influenced by the composition of bee communities (Fig. 1). In light of accelerating anthropogenic-induced environmental changes, it became crucial to assess the resilience of crop pollination services (Hutchinson et al., 2022). Engel et al. (Engel and Moran, 2013) reported the vital contributions of insect gut microbiota, encompassing nutritional support, protection against parasites, immune response modulation, and communication. Furthermore, Kühsel et al. (Kühsel and Blüthgen, 2015) suggested that high diversity promotes thermal resilience in pollinator communities within intensively managed grasslands, indicating increased resilience in species-rich pollinator communities despite land-use intensification.

The floral microbiome, shaped by pollinator visitation, significantly enhances pollinator resilience. Wei et al. (Wei et al., 2021) found that different pollinator functional groups influenced microbial properties under agrochemical disturbance, shaping the resilience of the floral microbiome. Additionally, Kaphiem et al. (Kapheim et al., 2021) emphasized the microbiome's impact on multiple facets of pollinator health, fortifying pollinator resilience amid challenging environmental conditions. Attributes like the degree of pollination specialization enhance pollen transfer efficiency, reflecting resilience and stability in the community (Fantinato et al., 2019). The diverse response diversity in pollinators, holds implications for the resilience of pollination services, ensuring adaptability to environmental changes (Miyashita et al., 2021).

Understanding the ecological dynamics of the almond floral microbiome concerning crop management and pollination is crucial for comprehending pollinator resilience (Schaeffer et al., 2020). Agricultural intensification tends to diminish native pollinator abundance and diversity underscores the imperative need to consider pollinator resilience within the context of crop management practices.

5. Microbiome insights in sustainable agriculture

Microbiome insights in sustainable agriculture are extensive and transformative, offering various interventions, including the strategic use of probiotics. This paradigm shift is supported by a growing body of research highlighting the crucial role of microbiomes in agricultural ecosystems. The transformative potential of microbiome insights extends beyond insects, encompassing a broader spectrum of applications for sustainable agriculture (De Smet et al., 2018; Kim and Anderson, 2018; Wang et al., 2019). From improving fish health in aquaculture to enhancing plant function and exploring insects as a sustainable protein source for animal feed, interventions based on microbiome insights

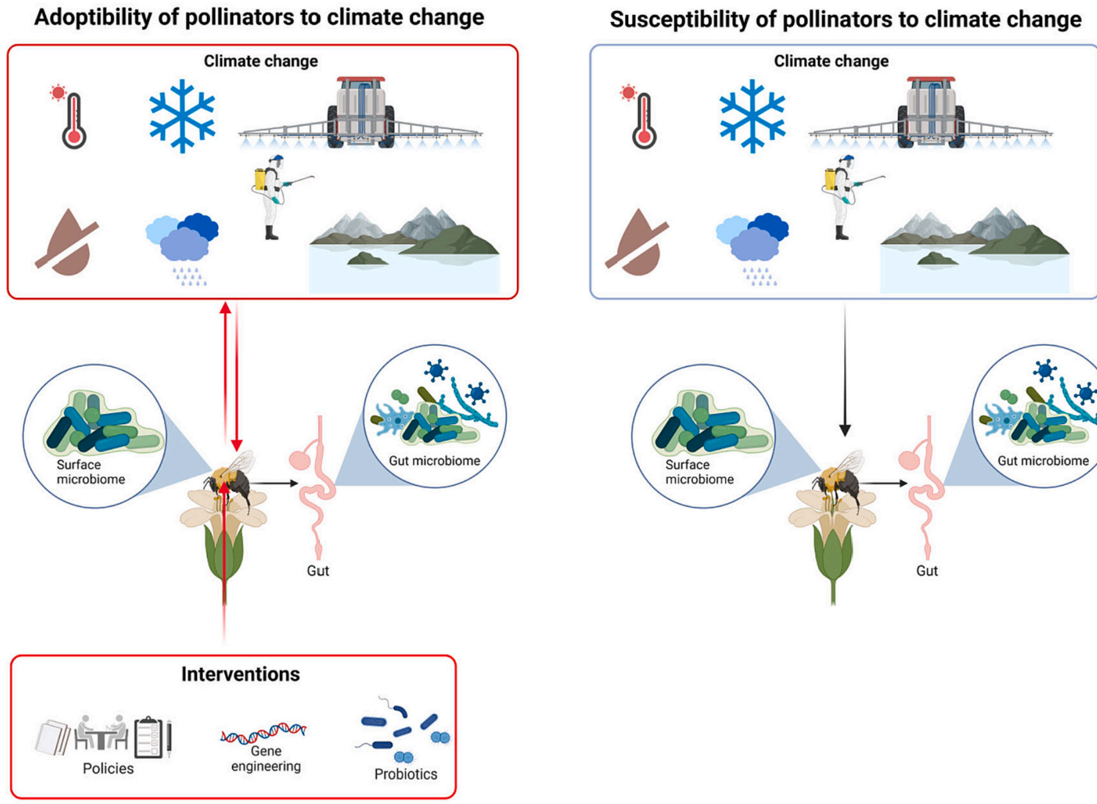

Fig. 1. Interconnected network of insect pollinators, microbiomes, and environmental factors.

showcase a multifaceted approach to advancing agricultural practices.

5.1. Microbiome communities in pest and disease management

The microbiome community of insects, including pests, serves as a valuable resource for sustainable pest and disease management. Understanding pest insect microbiomes facilitates the development of microbe-based tools for control, reducing reliance on chemical pesticides and promoting environmentally conscious pest management practices (Qadri et al., 2020). Insect microbiomes also impact soil microbiomes, affecting plant health and pest resistance (van Dijk et al., 2022). Interventions involving microbiome manipulation contribute substantively to sustainable pest and disease management in agriculture.

5.2. Microbiome engineering in agriculture

Microbiome-based engineering of the rhizosphere influence soil health and plant growth and emerges as a strategy to manage abiotic stresses and enhance plant resilience within agricultural systems (Tyagi et al., 2022). This insight extends to insects and plants, offering the prospect of tailored and sustainable agricultural systems (Pradhan et al., 2022). This integrative approach includes plant-based, meta-organism-based, and microbiome-based engineering to optimize agricultural practices.

5.3. Microbiome contributions to pollination and crop yields

Microbiome communities in pollinators, such as bees, play a pivotal role in crop pollination and plant health. Using insights from pollinator microbiome communities offers a pathway to develop microbe-based interventions, improving pollination services and subsequently increasing crop yields (Pang et al., 2021). Furthermore, interventions grounded in microbiome insights hold significant promise for enhancing pollinator health, subsequently improving crop yields. For instance, a study demonstrated the manipulation of bee gene expression by engineering a symbiotic gut bacterium, *Snodgrassella alvi*. This engineered bacterium induced eukaryotic RNA interference (RNAi) immune responses, leading to altered bee physiology, behavior, and improved survival after viral challenges (Leonard et al., 2020). By modulating the gut microbiome community of pollinators and using microbial inoculants, plant-microbe interactions, and microbiome engineering, these interventions contribute to the overall sustainability of agriculture (Berg et al., 2021; Koch et al., 2022; Pradhan et al., 2022; Ray et al., 2020; Raymann et al., 2017; Schaeffer et al., 2023; Stiemsma and Michels, 2018). Understanding the dynamics of microbiome communities in pollinators and their environments informs targeted interventions that promote the establishment of resilient and beneficial microbiome communities, ultimately benefiting both pollinator health and crop yields.

5.4. Probiotics for insect and soil health

Probiotics emerge as a potent tool for fostering a gut microbiome community in insects that curtails pathogens and enhances overall insect health. Deploying probiotic interventions represents a promising avenue to fortify the resilience and health of insects within agricultural ecosystems (Deutscher et al., 2019). The application of the commercial probiotic mix EM® PROBIOTIC FOR BEES enhanced honey bee colony health, administering EM® for bees via sugar syrup resulted in reduced Nosema spp. spore counts, increased colony strength, and positive physiological changes in treated adult bees (Tlak Gajger et al., 2020). In addition, probiotics can play a role in soil health by influencing microbiome communities and contributing to sustainable agricultural practices (Peixoto et al., 2022).

6. Integrating microbiome insights into conservation practices for pollinator habitats

Microbiome insights play a crucial role in shaping conservation practices, especially in preserving pollinator habitats. Understanding the complex relationships among pollinators, their microbiomes, and the environment is essential for developing effective strategies to safeguard and enhance pollinator health.

6.1. Habitat preservation and restoration

Microbiome insights guide the preservation and restoration of natural habitats critical for maintaining diverse and healthy pollinator microbiomes (Davis et al., 2023; Hadley and Betts, 2012). Conservation efforts should prioritize the protection and restoration of these habitats to support robust pollinator communities.

6.2. Landscape management for connectivity

Understanding the impact of landscape fragmentation on pollinator microbiomes informs landscape management practices (Hadley and Betts, 2012). Conservation actions should concentrate on maintaining connectivity and promoting habitat diversity to sustain healthy pollinator populations.

6.3. Ecosystem services and economic value

Conservation practices are informed by recognizing the economic value of pollination services provided by pollinators and their associated microbiomes (Tibesigwa et al., 2019). Preserving natural habitats helps maintain healthy pollinator communities, thus supporting ecosystem services.

6.4. Smart habitat design and optimization

Microbiome insights inform the design of pollinator habitats to optimize conditions for healthy microbiomes (Anders et al., 2023). Conservation efforts should focus on creating and maintaining habitats that support diverse and beneficial microbial communities associated with pollinators.

6.5. Citizen science, data mapping, and localized conservation actions

Utilizing citizen science data to map wild pollinator habitat preferences and corridors helps prioritize conservation actions in critical areas for maintaining healthy pollinator microbiomes (Serret et al., 2022; Vieli et al., 2021). Microbiome insights also guide local conservation actions aimed at preserving pollinator habitats and promoting healthy microbiomes, with localized efforts having a global impact.

6.6. Solar facilities, habitat management, and agriculture

Microbiome insights guide habitat management practices at solar energy facilities and agricultural landscapes to create and maintain pollinator habitats (Forbes and Northfield, 2017; Mishra et al., 2023). Conservation actions should concentrate on providing and preserving habitat to support pollinator microbiomes, recognizing the positive relationship between pollinator habitat enhancement and increased crop yields. Understanding the dynamics of the floral microbiome informs conservation strategies aimed at preserving and restoring habitats that support diverse and healthy pollinator microbiomes.

6.7. Microbiome-informed management of agricultural landscapes

Microbiome insights guide the management of agricultural landscapes to support biodiversity and ecosystem health:

- Microbiome insights inform the design of agricultural landscapes to include diverse and suitable habitats for pollinators (Gong et al., 2021; Walston et al., 2018). This involves creating pollinator-friendly habitats, such as hedgerows, wildflower strips, and semi-natural areas, to support diverse pollinator microbiomes and enhance ecosystem health.
- Conservation practices are informed by understanding the impact of landscape structure on pollinator microbiomes (Rahimi et al., 2021; Sasaki et al., 2021). Preserving natural habitats and semi-natural areas within agricultural landscapes can support diverse pollinator communities and their associated microbiomes, contributing to ecosystem health.
- Microbiome insights inform the management of agricultural landscapes to support ecosystem services provided by pollinators (Braman et al., 2022). By preserving and enhancing pollinator habitats, agricultural landscapes can benefit from improved pollination services and enhanced biodiversity.
- Agricultural landscapes can be managed to provide diverse floral resources supporting pollinator microbiomes (Fouks and Wagoner, 2019). This involves planting diverse flowering plants and managing floral resources to enhance pollinator health and ecosystem services.
- Understanding the role of pollinator microbiomes in agricultural landscapes informs integrated pest management practices that minimize the use of pesticides and support pollinator health (Schaeffer et al., 2020). This contributes to the conservation of pollinator biodiversity and ecosystem health.
- Microbiome insights inform agroecological practices supporting pollinator health and biodiversity in agricultural landscapes (Moreira and Freitas, 2020; Naharki and Regmi, 2020). By adopting agroecological approaches, such as organic farming and agroforestry, agricultural landscapes can support diverse pollinator communities and ecosystem health.

7. Developing policies for pollinator health

In the crafting of policies aimed at preserving pollinator health, especially those informed by microbiome insights, a comprehensive assessment of various factors influencing agricultural landscapes is crucial (Dicks et al., 2016). This includes evaluating the impact of farming practices, landscape management, and conservation strategies on pollinator microbiomes. Prioritizing the preservation and restoration of diverse and suitable habitats for pollinators within agricultural landscapes should be at the forefront of these policies. This involves creating pollinator-friendly environments, such as hedgerows, wildflower strips, and semi-natural areas, to support diverse pollinator communities and their associated microbiomes (Aslan et al., 2022). Furthermore, the policies should uphold the ecosystem services provided by pollinators and advance biodiversity conservation within agricultural landscapes. Conservation strategies should focus on enhancing the local availability of semi-natural habitats and creating well-managed habitats to counteract the decline of pollinators and protect pollination services. Improving pollinator conservation via multiple means demonstrates the need for a holistic approach to policy restructuring and budgeting to consider both welfare and conservation simultaneously. The implementation of targeted landscape-level management practices is crucial for halting and reversing the decline in biodiversity, promoting biodiversity-mediated ecosystem services, and enhancing the resilience and adaptability of ecosystems (Jiao et al., 2014). Advocating for sustainable land use practices that bolster pollinator health and biodiversity should be a key focus of these policies. This may involve adopting agroecological approaches, practicing organic farming, and embracing integrated pest management strategies to minimize pesticide use and support pollinator microbiomes (Raymann et al., 2017).

The policies should actively encourage the provision of diverse floral resources within agricultural landscapes. This encompasses planting a variety of flowering plants and managing floral resources to promote pollinator health and enhance ecosystem services (Cui et al., 2021). Moreover, unwavering support for research and conservation strategies aimed at preserving and restoring habitats that sustain diverse and healthy pollinator communities is essential.

Championing public engagement and fostering empathy for pollinator conservation initiatives should be another dimension of these policies. This entails adopting an empathetic approach to engage and empower the public for conservation action. Additionally, educational programs should be developed to raise awareness about the significance of pollinator health and biodiversity conservation (Sturm et al., 2021). This includes developing effective mechanisms to support native bee conservation policy to integrate adaptive management strategies and raise awareness of the importance of pollinators among the general public and special interest groups through the dissemination of high-quality and easy-to-understand information.

The key policy recommendations for preserving pollinator health consists of a wide range of measures, including evidence-based decision-making, adaptive management strategies, public awareness campaigns, and the integration of biodiversity conservation into environmental policies. These recommendations emphasize the need for comprehensive, coordinated, and transdisciplinary efforts to address the decline of pollinators and secure pollination services for future generations.

8. Challenges and future directions

Understanding the microbiomes of pollinators and addressing associated challenges is essential for advancing research and informing conservation and management practices. Methodological constraints, such as difficulties in sampling and characterizing microbial communities, underscore the need for standardized approaches (Engel et al., 2016; Pornon et al., 2016). The high diversity of microbial communities poses a continuing methodological challenge in identifying the functional roles and interactions of specific taxa (Benadi and Pauw, 2018; Koch et al., 2022).

Environmental factors, including floral resources, agrochemical exposure, and habitat fragmentation, influence pollinator microbiomes, requiring comprehensive longitudinal studies (Schaeffer et al., 2020; Vannette, 2020). Complex interactions between pollinators and their microbial communities necessitate experimental studies to understand the effects of host physiology, behavior, and environmental factors on microbiome composition and function (Graystock et al., 2015; Wei et al., 2021). Investigating the transmission and dispersal of microbial communities within and between pollinator species requires innovative experimental and observational approaches (Calderone, 2012; Rothman et al., 2019).

There is extensive research on managed pollinator species, whereas lack of in-depth studies on the microbiomes of wild pollinators such as solitary bees and bumblebees. Additionally, the root microbiome plays a crucial role in plant health, and plants can control the composition of their microbiome, adding complexity to the study of pollinator microbiomes. Understanding the broad-scale patterns of gut microbiome and host associations in insect pollinators is essential for identifying general patterns driving host microbial community composition and functioning.

The ecological impacts of pollinator microbiomes on plant-pollinator interactions, disease transmission, and ecosystem functioning are not fully understood, emphasizing the importance of integrating microbiome data with ecological and functional studies (Brown, 2022; Shell and Rehan, 2022). Translating microbiome insights into conservation and management practices for pollinator health and biodiversity conservation necessitates interdisciplinary collaboration and applied research (Hietaranta et al., 2023; Kantsa et al., 2018).

Understanding the impact of anthropogenic disturbance on pollinator microbiomes and the resilience of microbial communities to environmental stressors is a critical research priority, particularly investigating the effects of land use change, climate change, and agrochemical exposure (Lautenbach et al., 2012; Rebolleda Gómez and Ashman, 2019). The importance of pollinators in changing landscapes for world crops has been established, with pollinators being essential for the production of numerous crops (Klein et al., 2007). However, the unresolved question of how pollinators mediate microbiome assembly in the face of anthropogenic disturbance remains a major challenge. Integrating microbiome data with other ecological and environmental datasets to comprehend the drivers and consequences of pollinator microbiome dynamics is a methodological challenge, requiring the development of analytical frameworks for integrating multi-omics data and ecological metadata (Li et al., 2023; Williams et al., 2015).

The interplay between pollinators, plants, and microbes adds another layer of complexity to the study of pollinator microbiomes. For instance, the role of nectar bacteria in weakening plant-pollinator mutualism and the impact of pollen-borne microbes on bee fitness underscore the relationships between pollinators and their microbiota. Additionally, the importance of pollen-borne microbes for wild bee development and fitness further emphasizes the need to understand the dispersal of microbes in pollinator networks. Understanding the interplay between pollinators, plants, and microbes, as well as the impact of management practices and environmental disturbances, is crucial for unraveling the challenges faced in studying pollinator microbiomes.

[1] Explore the influence of climate change on pollinator microbiomes, examining microbial responses to temperature shifts, precipitation patterns, and extreme weather events. Understanding these impacts is crucial for predicting and mitigating potential effects on pollinator health and ecosystem services.

[2] Investigate microbial adaptation to climate change within pollinator microbiomes. Assess the genetic and functional diversity of microbial communities to understand their capacity to adapt to changing environmental conditions and mediate pollinator responses to climate change.

[3] Assess the resilience of pollinator microbiomes to climate change in different landscapes. Investigate how landscape composition and structure influence the stability and diversity of pollinator microbiomes. Identify landscape management strategies that support resilient pollinator microbiomes.

[4] Develop conservation strategies considering the role of pollinator microbiomes in the context of climate change. Investigate how conservation practices, such as habitat restoration, landscape connectivity, and agroecological approaches, can support the resilience of pollinator microbiomes and promote pollinator health under changing climatic conditions.

[5] Investigate the transmission dynamics of pollinator-associated microbes in the context of climate change. Assess how changes in pollinator behavior, floral resource availability, and habitat suitability influence the transmission and dispersal of microbial communities. Explore how these dynamics may be affected by climate change.

[6] Evaluate the implications of climate change for pollinator-mediated ecosystem services in the context of microbial interactions. Investigate how changes in pollinator microbiomes may impact pollination efficiency, plant-pollinator interactions, and the provision of ecosystem services. Explore how these effects may be influenced by climate change.

[7] Assess potential impacts of climate change on pollinator biodiversity and the role of microbiomes. Investigate how changes in pollinator microbiomes may influence pollinator species richness, abundance, and community composition. Explore how these changes may affect plant-pollinator interactions and ecosystem functioning.

[8] Develop and evaluate management practices that promote the resilience of pollinator microbiomes in the face of climate change. Investigate how agricultural and landscape management

practices, such as floral resource enhancement, pesticide reduction, and habitat restoration, can support the health and diversity of pollinator microbiomes under changing climatic conditions.

[9] Investigate potential interactions between pollinator microbiomes and invasive plant species in the context of climate change. Assess how invasive species may influence the composition and function of pollinator microbiomes and how these interactions may be affected by changing environmental conditions.

[10] Explore the implications of climate change for pollinator microbiomes and policy implications for biodiversity conservation and ecosystem services.

CRediT authorship contribution statement

Sakhawat Shah: Writing – review & editing, Writing – original draft. **Muhammad Ilyas:** Writing – review & editing. **Sufen Bian:** Writing – review & editing. **Feng-Lian Yang:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

References

Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol. Lett. 9, 968–980.

Anders, M., Grass, I., Linden, V.M.G., Taylor, P.J., Westphal, C., 2023. Smart orchard design improves crop pollination. J. Appl. Ecol. 60, 624–637.

Aslan, C.E., Haubensak, K.A., Grady, K.C., 2022. Effective and feasible mechanisms to support native invertebrate pollinators in agricultural landscapes: a meta-analysis. Ecosphere 13, e3982.

Audsley, M.D., Seleznev, A., Joubert, D.A., Woolfit, M., O'Neill, S.L., McGraw, E.A., 2018. Wolbachia infection alters the relative abundance of resident bacteria in adult Aedes aegypti mosquitoes, but not larvae. Mol. Ecol. 27, 297–309.

Barrett, M., Fischer, B., Buchmann, S., 2023. Informing policy and practice on insect pollinator declines: tensions between conservation and animal welfare. Front. Ecol. Evol. 10, 1071251.

Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S., Winfree, R., 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. Proc. Natl. Acad. Sci. 108, 20645–20649.

Benadi, G., Pauw, A., 2018. Frequency dependence of pollinator visitation rates suggests that pollination niches can allow plant species coexistence. J. Ecol. 106, 1892–1901.

Berg, G., Kusstatscher, P., Abdelfattah, A., Cernava, T., Smalla, K., 2021. Microbiome modulation—toward a better understanding of plant microbiome response to microbial inoculants. Front. Microbiol. 12, 650610.

Bertoloni Meli, S., Bashey, F., 2018. Trade-off between reproductive and anti-competitor abilities in an insect–parasitic nematode–bacteria symbiosis. Ecol. Evol. 8, 10847–10856.

Braman, S.K., Pennisi, S.V., Fair, C.G., Quick, J.C., 2022. Pollinator cultivar choice: an assessment of season-long pollinator visitation among coreopsis, aster, and salvia cultivars. Front. Sustain. Cities 4, 988966.

Brown, M.J.F., 2022. Complex networks of parasites and pollinators: moving towards a healthy balance. Philos. Trans. R. Soc. B 377, 20210161.

Calderone, N.W., 2012. Insect pollinated crops, insect pollinators and US agriculture: trend analysis of aggregate data for the period 1992–2009. PLoS One 7, e37235.

Cameron, S.A., Sadd, B.M., 2020. Global trends in bumble bee health. Annu. Rev. Entomol. 65, 209–232.

Cappelli, A., Petrelli, D., Gasperi, G., Serrao, A.G.M., Ricci, I., Damiani, C., Favia, G., 2022. Bacterial symbionts in *Ceratitis capitata*. Insects 13, 474.

Cui, Z., Huntley, R.B., Zeng, Q., Steven, B., 2021. Temporal and spatial dynamics in the apple flower microbiome in the presence of the phytopathogen Erwinia amylovora. ISME J. 15, 318–329.

Davis, A.E., Bickel, D.J., Saunders, M.E., Rader, R., 2023. Crop-pollinating D iptera have diverse diets and habitat needs in both larval and adult stages. Ecol. Appl. 33, e2859.

De Smet, J., Wynants, E., Cos, P., Van Campenhout, L., 2018. Microbial community dynamics during rearing of black soldier fly larvae (Hermetia illucens) and impact on exploitation potential. Appl. Environ. Microbiol. 84, e02722-17.

Deutscher, A.T., Chapman, T.A., Shuttleworth, L.A., Riegler, M., Reynolds, O.L., 2019. Tephritid-microbial interactions to enhance fruit fly performance in sterile insect technique programs. BMC Microbiol. 19, 1–14.

Dicks, L.V., Viana, B., Bommarco, R., Brosi, B., del Arizmendi, M., Cunningham, S.A., Galetto, L., Hill, R., Lopes, A.V., Pires, C., 2016. Ten policies for pollinators. Science 80-.). 354, 975–976.

Dong, Y., Zhang, Z.-R., Mishra, S., Wong, A.C.-N., Huang, J.-F., Wang, B., Peng, Y.-Q., Gao, J., 2022. Diversity and metabolic potentials of microbial communities associated with pollinator and cheater fig wasps in fig-fig wasp mutualism system. Front. Microbiol. 4365.

Douglas, A.E., 2015. Multiorganismal insects: diversity and function of resident microorganisms. Annu. Rev. Entomol. 60, 17.

Engel, P., Moran, N.A., 2013. The gut microbiota of insects–diversity in structure and function. FEMS Microbiol. Rev. 37, 699–735.

Engel, P., Kwong, W.K., McFrederick, Q., Anderson, K.E., Barribeau, S.M., Chandler, J.A., Cornman, R.S., Dainat, J., De Miranda, J.R., Doublet, V., 2016. The bee microbiome: impact on bee health and model for evolution and ecology of host-microbe interactions. MBio 7, 10–1128.

Fantinato, E., Del Vecchio, S., Gaetan, C., Buffa, G., 2019. The resilience of pollination interactions: importance of temporal phases. J. Plant Ecol. 12, 157–162.

Ferguson, L.V., Dhakal, P., Lebenzon, J.E., Heinrichs, D.E., Bucking, C., Sinclair, B.J., 2018. Seasonal shifts in the insect gut microbiome are concurrent with changes in cold tolerance and immunity. Funct. Ecol. 32, 2357–2368.

Forbes, S.J., Northfield, T.D., 2017. Increased pollinator habitat enhances cacao fruit set and predator conservation. Ecol. Appl. 27, 887–899.

Fouks, B., Wagoner, K.M., 2019. Pollinator parasites and the evolution of floral traits. Ecol. Evol. 9, 6722–6737.

Geng, J., Sui, Z., Dou, W., Miao, Y., Wang, T., Wei, X., Chen, S., Zhang, Z., Xiao, J., Huang, D., 2022. 16S rRNA gene sequencing reveals specific gut microbes common to medicinal insects. Front. Microbiol. 13, 892767.

Gong, C., Li, L., Axmarcher, J.C., Yu, Z., Liu, Y., 2021. Family graveyards form underappreciated local plant diversity hotspots in China's agricultural landscapes. Sci. Rep. 11, 2011.

González-Tokman, D., Córdoba-Aguilar, A., Dáttilo, W., Lira-Noriega, A., Sánchez-Guillén, R.A., Villalobos, F., 2020. Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world. Biol. Rev. 95, 802–821.

González-Varo, J.P., Biesmeijer, J.C., Bommarco, R., Potts, S.G., Schweiger, O., Smith, H. G., Steffan-Dewenter, I., Szentgyörgyi, H., Woyciechowski, M., Vilà, M., 2013. Combined effects of global change pressures on animal-mediated pollination. Trends Ecol. Evol. 28, 524–530.

Graystock, P., Goulson, D., Hughes, W.O.H., 2015. Parasites in bloom: flowers aid dispersal and transmission of pollinator parasites within and between bee species. Proc. R. Soc. B Biol. Sci. 282, 20151371.

Greenleaf, S.S., Kremen, C., 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. Proc. Natl. Acad. Sci. 103, 13890–13895.

Gressel, J., 2018. Microbiome facilitated pest resistance: potential problems and uses. Pest Manag. Sci. 74, 511–515.

Gurung, K., Wertheim, B., Falcao Salles, J., 2019. The microbiome of pest insects: it is not just bacteria. Entomol. Exp. Appl. 167, 156–170.

Hadley, A.S., Betts, M.G., 2012. The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. Biol. Rev. 87, 526–544.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A., Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? Ecol. Lett. 12, 184–195.

Hietaranta, E., Juottonen, H., Kytöviita, M.-M., 2023. Honeybees affect floral microbiome composition in a central food source for wild pollinators in boreal ecosystems. Oecologia 201, 59–72.

Hutchinson, L.A., Oliver, T.H., Breeze, T.D., Greenwell, M.P., Powney, G.D., Garratt, M.P. D., 2022. Stability of crop pollinator occurrence is influenced by bee community composition. Front. Sustain. Food Syst. 6, 943309.

Iler, A.M., Inouye, D.W., Høye, T.T., Miller-Rushing, A.J., Burkle, L.A., Johnston, E.B., 2013. Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. Glob. Chang. Biol. 19, 2348–2359.

Jiao, Y., Liang, L., Okuro, T., Takeuchi, K., 2014. Ecosystem services and biodiversity of traditional agricultural landscapes: a case study of the Hani terraces in Southwest China. Biocultural Landscapes Divers. Funct. Values 81–88.

Jing, T.-Z., Qi, F.-H., Wang, Z.-Y., 2020. Most dominant roles of insect gut bacteria: digestion, detoxification, or essential nutrient provision? Microbiome 8, 1–20.

Kantsa, A., Raguso, R.A., Dyer, A.G., Olesen, J.M., Tscheulin, T., Petanidou, T., 2018. Disentangling the role of floral sensory stimuli in pollination networks. Nat. Commun. 9, 1041.

Kapheim, K.M., Johnson, M.M., Jolley, M., 2021. Composition and acquisition of the microbiome in solitary, ground-nesting alkali bees. Sci. Rep. 11, 2993.

Khalifa, S.A.M., Elshafiey, E.H., Shetaia, A.A., El-Wahed, A.A.A., Algethami, A.F., Musharraf, S.G., AlAjmi, M.F., Zhao, C., Masry, S.H.D., Abdel-Daim, M.M., 2021. Overview of bee pollination and its economic value for crop production. Insects 12, 688.

Kim, Y.C., Anderson, A.J., 2018. Rhizosphere pseudomonads as probiotics improving plant health. Mol. Plant Pathol. 19, 2349–2359.

Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. B Biol. Sci. 274, 303–313.

Koch, H., Welcome, V., Kendal-Smith, A., Thursfield, L., Farrell, I.W., Langat, M.K., Brown, M.J.F., Stevenson, P.C., 2022. Host and gut microbiome modulate the

antiparasitic activity of nectar metabolites in a bumblebee pollinator. Philos. Trans. R. Soc. B 377, 20210162.
Kühsel, S., Blüthgen, N., 2015. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. Nat. Commun. 6, 7989.
Lautenbach, S., Seppelt, R., Liebscher, J., Dormann, C.F., 2012. Spatial and temporal trends of global pollination benefit. PLoS One 7, e35954.
Layek, U., Kundu, A., Das, N., Mondal, R., Karmakar, P., 2023. Intercropping with Pigeonpea (Cajanus cajan L. Millsp.): an assessment of its influence on the assemblage of pollinators and yield of neighbouring non-leguminous crops. Life 13, 193.
Lefebvre, V., Villemant, C., Fontaine, C., Daugeron, C., 2018. Altitudinal, temporal and trophic partitioning of flower-visitors in alpine communities. Sci. Rep. 8, 4706.
Lefort, M.-C., Boyer, S., Glare, T.R., 2017. A response to Pennisi-"how do gut microbiomes help herbivores", a hint into next-generation biocontrol solutions. Rethink. Ecol. 1, 9–13.
Leonard, S.P., Powell, J.E., Perutka, J., Geng, P., Heckmann, L.C., Horak, R.D., Davies, B. W., Ellington, A.D., Barrick, J.E., Moran, N.A., 2020. Engineered symbionts activate honey bee immunity and limit pathogens. Science (80-.) 367, 573–576.
Li, J., Sauers, L., Zhuang, D., Ren, H., Guo, J., Wang, L., Zhuang, M., Guo, Y., Zhang, Z., Wu, J., 2023. Divergence and convergence of gut microbiomes of wild insect pollinators. MBio 14, e01270-23.
Lu, Q., Liu, C., Huang, S., 2021. Moths pollinate four crops of Cucurbitaceae in Asia. J. Appl. Entomol. 145, 499–507.
Mason, C.J., Ray, S., Shikano, I., Peiffer, M., Jones, A.G., Luthe, D.S., Hoover, K., Felton, G.W., 2019. Plant defenses interact with insect enteric bacteria by initiating a leaky gut syndrome. Proc. Natl. Acad. Sci. 116, 15991–15996.
Mills, T.J.T., Nelson, T.M., Pearson, L.A., Neilan, B.A., 2023. Hive transplantation has minimal impact on the Core gut microbiome of the Australian stingless bee, *Tetragonula carbonaria*. Microb. Ecol. 1–11.
Mishra, A., Kumar, R., Richa, R., 2021. Biodiversity conservation to mitigate the impact of climate change on agro-ecosystems. Biol. Divers. Curr. status Conserv. Policies 1, 89–107.
Mishra, S., Zhu, M., Bernknopf, R., Walston, L., 2023. Valuation of pollination services from habitat management: a case study of utility scale solar energy facilities in the United States. Environ. Res. Commun. 5, 065006 https://doi.org/10.1088/2515-7620/acda7f.
Miyashita, T., Hayashi, S., Taki, H., 2021. Diverse Response Diversity in Pollinators: Implications to the Resilience of Pollination Services in Buckwheat.
Moreira, M.M., Freitas, L., 2020. Review of the pollination system by small diverse insects. Neotrop. Entomol. 49, 472–481.
Naharki, K., Regmi, S., 2020. Risk assessment of pesticidal toxicity and threats on pollinators: a review on honey bee. Turkish J. Agric. Sci. Technol. 8, 2556–2561.
Nobles, S., Jackson, C.R., 2020. Effects of life stage, site, and species on the dragonfly gut microbiome. Microorganisms 8, 183.
Noman, M.S., Liu, L., Bai, Z., Li, Z., 2020. Tephritidae bacterial symbionts: potentials for pest management. Bull. Entomol. Res. 110, 1–14.
Ollerton, J., 2017. Pollinator diversity: distribution, ecological function, and conservation. Annu. Rev. Ecol. Evol. Syst. 48.
Pang, Z., Chen, J., Wang, T., Gao, C., Li, Z., Guo, L., Xu, J., Cheng, Y., 2021. Linking plant secondary metabolites and plant microbiomes: a review. Front. Plant Sci. 12, 621276.
Paniagua Voirol, L.R., Frago, E., Kaltenpoth, M., Hilker, M., Fatouros, N.E., 2018. Bacterial symbionts in Lepidoptera: their diversity, transmission, and impact on the host. Front. Microbiol. 9, 556.
Peixoto, R.S., Voolstra, C.R., Sweet, M., Duarte, C.M., Carvalho, S., Villela, H., Lunshof, J. E., Gram, L., Woodhams, D.C., Walter, J., 2022. Harnessing the microbiome to prevent global biodiversity loss. Nat. Microbiol. 7, 1726–1735.
Phalnikar, K., Kunte, K., Agashe, D., 2019. Disrupting butterfly caterpillar microbiomes does not impact their survival and development. Proc. R. Soc. B 286, 20192438.
Pornon, A., Escaravage, N., Burrus, M., Holota, H., Khimoun, A., Mariette, J., Pellizzari, C., Iribar, A., Etienne, R., Taberlet, P., 2016. Using metabarcoding to reveal and quantify plant-pollinator interactions. Sci. Rep. 6, 27282.
Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., 2016. Safeguarding pollinators and their values to human well-being. Nature 540, 220–229.
Pradhan, S., Tyagi, R., Sharma, S., 2022. Combating biotic stresses in plants by synthetic microbial communities: principles, applications and challenges. J. Appl. Microbiol. 133, 2742–2759.
Prado, A., Marolleau, B., Vaissière, B.E., Barret, M., Torres-Cortes, G., 2020. Insect pollination: an ecological process involved in the assembly of the seed microbiota. Sci. Rep. 10, 3575.
Prudic, K.L., Cruz, T.M.P., Winzer, J.I.B., Oliver, J.C., Melkonoff, N.A., Verbais, H., Hogan, A., 2022. Botanical gardens are local hotspots for urban butterflies in arid environments. Insects 13, 865.
Qadri, M., Short, S., Gast, K., Hernandez, J., Wong, A.C.-N., 2020. Microbiome innovation in agriculture: development of microbial based tools for insect pest management. Front. Sustain. Food Syst. 4, 547751.
Rahimi, E., Barghjelveh, S., Dong, P., 2021. Estimating landscape structure effects on pollination for management of agricultural landscapes. Ecol. Process. 10, 1–12.
Ratto, F., Breeze, T.D., Cole, L.J., Garratt, M.P.D., Kleijn, D., Kunin, B., Michez, D., O'Connor, R., Ollerton, J., Paxton, R.J., 2022. Rapid assessment of insect pollination services to inform decision-making. Conserv. Biol. 36, e13886.
Ray, P., Lakshmanan, V., Labbé, J.L., Craven, K.D., 2020. Microbe to microbiome: a paradigm shift in the application of microorganisms for sustainable agriculture. Front. Microbiol. 11, 622926.
Raymann, K., Shaffer, Z., Moran, N.A., 2017. Antibiotic exposure perturbs the gut microbiota and elevates mortality in honeybees. PLoS Biol. 15, e2001861.
Rebolleda Gómez, M., Ashman, T., 2019. Floral organs act as environmental filters and interact with pollinators to structure the yellow monkeyflower (Mimulus guttatus) floral microbiome. Mol. Ecol. 28, 5155–5171.
Recart, W., Bernhard, R., Ng, I., Garcia, K., Fleming-Davies, A.E., 2023. Meta-analysis of the effects of insect pathogens: implications for plant reproduction. Pathogens 12, 347.
Rothman, J.A., Leger, L., Graystock, P., Russell, K., McFrederick, Q.S., 2019. The bumble bee microbiome increases survival of bees exposed to selenate toxicity. Environ. Microbiol. 21, 3417–3429.
Sasaki, K., Hotes, S., Ichinose, T., Doko, T., Wolters, V., 2021. Hotspots of agricultural ecosystem services and farmland biodiversity overlap with areas at risk of land abandonment in Japan. Land 10, 1031.
Schaeffer, R.N., Crowder, D.W., Illán, J.G., Beck, J.J., Fukami, T., Williams, N.M., Vannette, R.L., 2020. Ecological dynamics of the almond floral microbiome in relation to crop management and pollination. bioRxiv 2011–2020.
Schaeffer, R.N., Crowder, D.W., Illán, J.G., Beck, J.J., Fukami, T., Williams, N.M., Vannette, R.L., 2023. Disease management during bloom affects the floral microbiome but not pollination in a mass-flowering crop. J. Appl. Ecol. 60, 64–76.
Schmidt, K., Engel, P., 2021. Mechanisms underlying gut microbiota–host interactions in insects. J. Exp. Biol. 224, jeb207696.
Scully, E.D., Geib, S.M., Carlson, J.E., Tien, M., McKenna, D., Hoover, K., 2014. Functional genomics and microbiome profiling of the Asian longhorned beetle (Anoplophora glabripennis) reveal insights into the digestive physiology and nutritional ecology of wood feeding beetles. BMC Genomics 15, 1–21.
Serret, H., Andersen, D., Deguines, N., Clauzel, C., Park, W.-H., Jang, Y., 2022. Towards ecological management and sustainable urban planning in Seoul, South Korea: mapping wild pollinator habitat preferences and corridors using citizen science data. Animals 12, 1469.
Shah, S., Ilyas, M., Li, R., Yang, J., Yang, F.-L., 2023. Microplastics and nanoplastics effects on plant–pollinator interaction and pollination biology. Environ. Sci. Technol. 57, 6415–6424. https://doi.org/10.1021/acs.est.2c07733.
Shapiro, L.R., Youngblom, M., Scully, E.D., Rocha, J., Paulson, J.N., Klepac-Ceraj, V., Cibrián-Jaramillo, A., López-Uribe, M.M., 2019. Bacterial communities of herbivores and pollinators that have co-evolved Cucurbita spp. bioRxiv 691378.
Shell, W.A., Rehan, S.M., 2022. Comparative metagenomics reveals expanded insights into intra-and interspecific variation among wild bee microbiomes. Commun. Biol. 5, 603.
Shukla, S.P., Vogel, H., Heckel, D.G., Vilcinskas, A., Kaltenpoth, M., 2018. Burying beetles regulate the microbiome of carcasses and use it to transmit a core microbiota to their offspring. Mol. Ecol. 27, 1980–1991.
Stiemsma, L.T., Michels, K.B., 2018. The role of the microbiome in the developmental origins of health and disease. Pediatrics 141.
Sturm, U., Straka, T.M., Moormann, A., Egerer, M., 2021. Fascination and joy: emotions predict urban gardeners' pro-pollinator behaviour. Insects 12, 785.
Tackenberg, M.C., Giannoni-Guzmán, M.A., Sanchez-Perez, E., Doll, C.A., Agosto-Rivera, J.L., Broadie, K., Moore, D., McMahon, D.G., 2020. Neonicotinoids disrupt circadian rhythms and sleep in honey bees. Sci. Rep. 10, 17929.
Tibesigwa, B., Siikamäki, J., Lokina, R., Alvsilver, J., 2019. Naturally available wild pollination services have economic value for nature dependent smallholder crop farms in Tanzania. Sci. Rep. 9, 3434.
Tinker, K.A., Ottesen, E.A., 2020. Phylosymbiosis across deeply diverging lineages of omnivorous cockroaches (order Blattodea). Appl. Environ. Microbiol. 86, e02513–e02519.
Tiusanen, M., Hebert, P.D.N., Schmidt, N.M., Roslin, T., 2016. One fly to rule them all—muscid flies are the key pollinators in the Arctic. Proc. R. Soc. B Biol. Sci. 283, 20161271.
Tlak Gajger, I., Vlainić, J., Šoštarić, P., Prešern, J., Bubnič, J., Smodiš Škerl, M.I., 2020. Effects on some therapeutical, biochemical, and immunological parameters of honey bee (Apis mellifera) exposed to probiotic treatments, in field and laboratory conditions. Insects 11, 638.
Tyagi, R., Pradhan, S., Bhattacharjee, A., Dubey, S., Sharma, S., 2022. Management of abiotic stresses by microbiome-based engineering of the rhizosphere. J. Appl. Microbiol. 133, 254–272.
Ushio, M., Yamasaki, E., Takasu, H., Nagano, A.J., Fujinaga, S., Honjo, M.N., Ikemoto, M., Sakai, S., Kudoh, H., 2015. Microbial communities on flower surfaces act as signatures of pollinator visitation. Sci. Rep. 5, 8695.
Vallino, M., Rossi, M., Ottati, S., Martino, G., Galetto, L., Marzachì, C., Abbà, S., 2021. Bacteriophage-host association in the phytoplasma insect vector Euscelidius variegatus. Pathogens 10, 612.
van Dijk, L.J.A., Abdelfattah, A., Ehrlén, J., Tack, A.J.M., 2022. Soil microbiomes drive aboveground plant–pathogen–insect interactions. Oikos 2022, e09366.
Vannette, R.L., 2020. The floral microbiome: plant, pollinator, and microbial perspectives. Annu. Rev. Ecol. Evol. Syst. 51, 363–386.
Vieli, L., Murúa, M.M., Flores-Prado, L., Carvallo, G.O., Valdivia, C.E., Muschett, G., López-Aliste, M., Andía, C., Jofré-Pérez, C., Fontúrbel, F.E., 2021. Local actions to tackle a global problem: a multidimensional assessment of the pollination crisis in Chile. Diversity 13, 571.
Walston, L.J., Mishra, S.K., Hartmann, H.M., Hlohowskyj, I., McCall, J., Macknick, J., 2018. Examining the potential for agricultural benefits from pollinator habitat at solar facilities in the United States. Environ. Sci. Technol. 52, 7566–7576.
Wang, A., Ran, C., Wang, Y., Zhang, Z., Ding, Q., Yang, Y., Olsen, R.E., Ringø, E., Bindelle, J., Zhou, Z., 2019. Use of probiotics in aquaculture of China—a review of the past decade. Fish Shellfish Immunol. 86, 734–755.

Wei, N., Russell, A.L., Jarrett, A.R., Ashman, T., 2021. Pollinators mediate floral microbial diversity and microbial network under agrochemical disturbance. Mol. Ecol. 30, 2235–2247.

Williams, N.M., Ward, K.L., Pope, N., Isaacs, R., Wilson, J., May, E.A., Ellis, J., Daniels, J., Pence, A., Ullmann, K., 2015. Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. Ecol. Appl. 25, 2119–2131.

Xue, H., Zhu, X., Wang, L., Zhang, K., Li, D., Ji, J., Niu, L., Wu, C., Gao, X., Luo, J., 2021. Gut bacterial diversity in different life cycle stages of Adelphocoris suturalis (Hemiptera: Miridae). Front. Microbiol. 12, 670383.

Yang, Y., Liu, X., Xu, H., Liu, Y., Lu, Z., 2022. Effects of host plant and insect generation on shaping of the gut microbiota in the rice leaffolder, *Cnaphalocrocis medinalis*. Front. Microbiol. 13, 824224.

Yun, J.-H., Roh, S.W., Whon, T.W., Jung, M.-J., Kim, M.-S., Park, D.-S., Yoon, C., Nam, Y.-D., Kim, Y.-J., Choi, J.-H., 2014. Insect gut bacterial diversity determined by environmental habitat, diet, developmental stage, and phylogeny of host. Appl. Environ. Microbiol. 80, 5254–5264.

Zhang, J., Chen, C., Zhu, K., Ma, H., Fu, Z., Tan, H., Wang, X., 2022. Variation in gut microbial communities of Chilo suppressalis in the typical bivoltine areas of northern China. J. Appl. Entomol. 146, 860–874.

Zhao, M., Lin, X., Guo, X., 2022. The role of insect symbiotic bacteria in metabolizing phytochemicals and agrochemicals. Insects 13, 583.