Environmental Science & Technology

pubs.acs.org/est

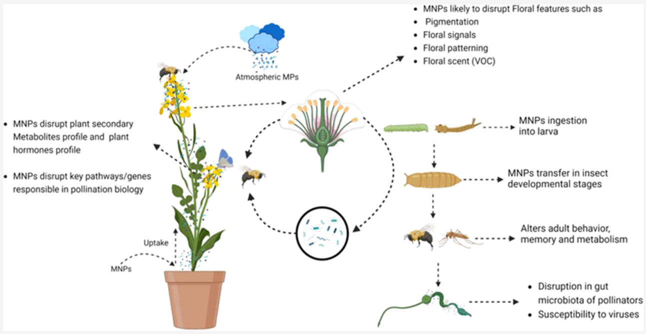
Perspective

Microplastics and Nanoplastics Effects on Plant−Pollinator Interaction and Pollination Biology

Sakhawat Shah, Muhammad Ilyas, Rui Li, Jie Yang,* and Feng-Lian Yang*

Cite This: *Environ. Sci. Technol.* 2023, 57, 6415−6424

ABSTRACT: Microplastics and nanoplastics (MNPs) contamination is an emerging environmental and public health concern, and these particles have been reported both in aquatic and terrestrial ecosystems. Recent studies have expanded our understanding of the adverse effects of MNPs pollution on human, terrestrial, and aquatic animals, insects, and plants. In this perspective, we describe the adverse effects of MNPs particles on pollinator and plant health and discuss the mechanisms by which MNPs disrupt the pollination process. We discuss the evidence and integrate transcriptome studies to investigate the negative effects of MNPs on the molecular biology of pollination, which may cause delay or inhibit the pollination services. We conclude by addressing challenges to plant−pollinator health from MNPs pollution and argue that such harmful effects disrupt the communication between plant and pollinator for a successful pollination process.



KEYWORDS: *Micro and nanoplastics, Pollination, Pollinators, Pollination biology*

■ INTRODUCTION

Pollination is essential for the sexual reproduction of all seed plants and provides benefits to the human population, which involves the transfer of pollen grains from the stamen (male reproductive organ) to the stigma (female reproductive organ). Self-pollination or autogamy, geitonogamy, and cross pollination are the major different types of pollination.[1] Cross pollination is accomplished naturally through insects (entomophily) and winds (anemophily) but can also be performed by hand to produce offspring with desired characters, such as pest resistance or color.[2]

Anemophily or wind pollination contributes to at least 10% of angiosperm plant pollination and has evolved 65 times from animal pollinated ancestors, providing reproductive assurance when insect pollinators are scarce.[3−5] For the initiation and success of wind pollination, plant must release and disperse pollen in airflows and catch airborne pollen;[6] therefore, anemophily plants possess and adopt several traits like unscented flowers, small or absent petals, greenish or whitish floral color, feathery styles, and few or one ovule per flower.[3] Several factors contribute to the process of pollen release in wind pollination angiosperms such as structure and diversity of stamen,[7−9] environmental and meteorological drivers such as solar radiation, relative humidity, temperature, and wind speed,[10−12] and biomechanics of pollen release such as aerodynamics and mechanical and recessive forces.[6,13−17] The molecular mechanism of wind pollination has been reviewed recently by Fattorini and Glover.[1]

Insect pollination or entomophily refers to the transfer of pollen grains from anthers to stigmas by insects and is crucial for almost all terrestrial plant reproduction and vital for the sustainability and conservation of global flora and fauna. A total of 87.5% of all wild plants depends on insect pollination,[18] of which 20% pollinate from bees.[19] Moths, butterflies, birds, stingless bees, honeybees, and bats are the pollinators in the tropics, whereas honeybees, bumblebees, solitary bees, wasps, and hoverflies provide pollination services in temperate regions.[20] It is estimated that there are 100,000 or more species present in the tropics and also around 220,000 species present in pollinator taxonomic groups of flowering plants.[21] Globally, 1500 crops need insect pollination,[20,22] and from 3% to 8% of the world crop production is dependent on insect pollination.[23]

In recent years, the decline in pollinator abundance and distribution received global attention,[18,24−26] as different regions in the world reported reductions in different species

Published: April 17, 2023

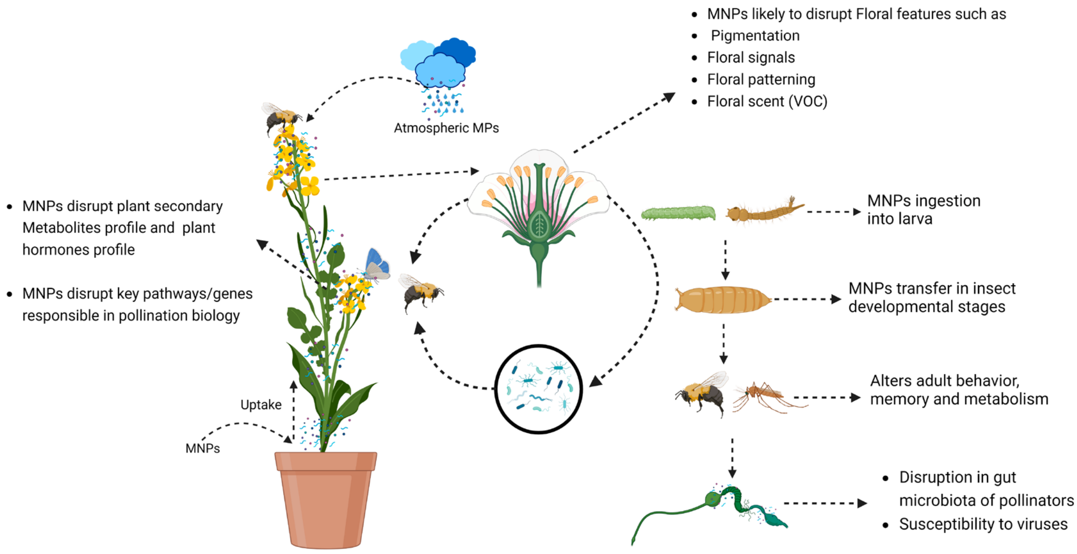


Figure 1. Overview of MNPs on pollination biology and plant−pollinator interactions. Plant exposure to MNPs shows growth retardation and morphological abnormalities in different tissues. Molecular profile of plant exposed to MNPs stresses which disrupt plant secondary metabolites and plant hormones that play key roles in pollination and pollinator attraction. Key genes and enzymes responsible for maintaining floral features such as pigmentation, floral signals, and producing or emiting volatile organic compounds (VOCs) are disrupted with MNPs exposure. MNPs negatively affect pollinator body size and disrupt the pollination process by altering pollinator behavior, memory, and metabolism.

of pollinators,[27−31] which pose major risks to food production and security, ecosystem biodiversity, and plant health.[32] Studies reported several factors such as change in agricultural landscape,[33,34] pathogens and parasites,[35,36] climate change,[37,38] indiscriminate use of synthetic and broad-spectrum pesticides,[39−41] introduction of invasive species,[42,43] air pollution,[44,45] unfavorable environmental and meteorological conditions,[46] pests,[36] fragmentation, and habitat destruction[21] for the decline of the worldwide pollinator population.

Plastic pollution accumulation in soil, water, and in other areas of the environment is considered "poorly reversible" and poses a major threat to human health, biodiversity, and terrestrial and aquatic ecosystems.[47] A total of 79% of all generated plastic waste is accumulated in the natural environment, and it will exceed 12,000 Mt by 2050.[48] The commonly used plastics are synthesized from fossil hydrocarbon derivatives such as ethylene and propylene, which are not biodegradable and hence accumulate in landfills or the natural environment.[48,49] Plastic debris deteriorates and turns into fragments, spheres, and fibers which are called microplastics (MPs 1−5000 um) and nanoplastics (NPs < 1um),[50] and the presence and pollution of micro and nanoplastics (MNPs) are reported in almost all niches of the ecosystem. A vast number of studies documented the presence of MPs in the environment; but due to technical limitations, the detection of NPs in the environment remains largely unknown. Studies suggested that MNPs pollution in ecosystems negatively affects the survival and health of animals and plants and disrupts the communication mechanism between plants and insects, especially pollinators. This perspective targets recent advances to synthesize current approaches to measure the effects of MNPs on pollinators and plant health, to understand the MNPs uptake mechanisms by plants and insects, and to identify direct or indirect effects of MNPs on pollination biology.

■ EFFECTS OF MNPS ON POLLINATORS

Pollinator health should be assessed across species by characterizing individuals, colonies, and populations to effectively observe the vulnerability, adaptability, and resilience of different pollinator species to their environmental context. Hence, the term "pollinator health" is defined as the state that permits the individuals even in the presence of pathogens to live longer and reproduce more.[51] Several individual level aspects such as body size, growth, reproduction with adoptability, and resilience to environmental conditions are aspects of pollinator health considered at a population level.[51] Here, we highlight the effects of MNPs on individual and population healths of several insect species, with special reference to pollinators such as honeybee health, and how they affect the pollination process and ecosystem services. The effects of MNPs on pollinators and the interactions between plants and pollinators are summarized in Figure 1.

■ EFFECTS OF MNPS ON BODY SIZE AND GROWTH OF INSECTS

Body size is one of the most striking and key features of all organisms, and several factors positively or negatively affect the body size such as feeding, resource acquisition, and nutritional availability.[52,53] In insects, larval feeding and growth are critically regulated by juvenile hormones along with the prothoracicotropic hormone (PTTH) and Ecdysteroids activity. During the last larval instar, PTTH stimulates the secretion of Ecdysteroids, by which insects stop feeding, and usually the last larval instar mass determines adult size, as many adult insects do not feed.[54−56] The adult body size in many insects such as Drosophila is dependent on the activity of insulin and insulin-like growth factor signaling, which influence both adult body size and growth rate.[54,57,58]

Exposure or feeding of MNPs negatively regulates the body size and growth of several insect species. Fragments and fibers of MNPs at the rate of 52% and 38%, respectively, are observed in honeybees collected from urban and suburban

https://doi.org/10.1021/acs.est.2c07733
Environ. Sci. Technol. 2023, 57, 6415−6424

areas.[59] The oral exposure of polystyrene MPs significantly reduced the body weight and growth of honeybees, and the exposure of 100 nm polystyrene particles leads to 91.67% reduction in growth and whole-body weight of honeybees compared with a normal control.[60] In another study, it is reported that MNPs negatively impact the body size (body length and head capsule) of *Chironomus tepper*.[61] Insects and other invertebrates exhibit varying degrees and diverse responses to different sizes and concentrations of MNPs.[62,63]

This growing body of evidence suggests that oral delivery of MNPs to organisms causes adverse effects on individual health by blocking digestive tracts, inhibiting or altering feeding behavior, which causes reduction in growth, whole body weight, and size.[64,65]

■ EFFECTS OF MNPS ON GUT MICROBIOTA OF INSECTS

Bacteria in the guts of insects, animals, and humans offer a variety of useful services to the host body, including the provision of nutrients, control of development and physiology, digestion of lipids and proteins, detoxification and modification of plant secondary compounds, defense against predators, parasites, and pathogens, immunity to unfavorable conditions, and communication between and within species,[66−69] and for these and several other beneficial functions, the host insects rely on gut microbiota.[70] The gut microbiota of insects affect the interaction of insects with crop plants, such as crop pests and pollinators.[66] The gut microbiota of pollinators or herbivores impact the behavior and physiology of the host insect, and these bacteria are critical for pollinator foraging behavior and herbivory of pests.[71,72]

The gut microbiota of pollinators such as honeybees and bumblebees are dominated by eight bacterial species,[73] which protect the host body against parasites and show tolerance to xenobiotics.[66,74] The disruption of gut microbiota of pollinators by insecticides or herbicides causes susceptibility to chemicals which affects bee health and their effectiveness as pollinators.[75] The effects of MNPs pollution on the gut microbiota of pollinator insects and other animals have been undertaken that cause inflammation, susceptibility to chemicals, induce and initiate intestinal injury, and disrupt gut microbial distribution.[76−79] A laboratory study by Wang et al.[80] showed that exposure of honeybees to polystyrene MPs caused significant decrease in diversity of honeybee gut microbiota, with alterations in the expression of detoxification, antioxidants, and immune-related genes in guts. Dosage-dependent effects of MPs have been observed as the highest concentration of MPs altering the highest number of gut microbial taxa or vice versa. Here, 50 mg/L of MPs significantly decreased alpha diversity indices (richness and distribution) and reduced the optimal function of bee gut microbiome. *Proteobacteria*, *Commensalibacter*, *Alpha proteobacteria*, *Acetobacteraceae*, and *Klebsiella* were altered at high doses while *Firmicutes Bacilli*, *Lactobacillus*, and its subtaxa were altered at low doses (25 mg/L) of MPs. MPs increased the abundance of *Lactobacillus* and *Gilliamella* species with opportunistic colonizers such as *Bombella*, *Klebsiella*, and *Serratia* species.[80] MPs do not cause direct toxicity to pollinators as the mortality rates among MP-fed pollinators were not higher compared with the control; however, the alterations in composition and diversity of gut microbiota show the negative effects on physiology and sublethal effects on pollinators. When bees were exposed to MPs accompanied by antibiotics, the lethality of MPs increased dramatically and depleted the gut microbiota of bees. MNPs are able to carry different chemicals, pesticides, and other xenobiotics, which increase the pollution of MNPs and lethality on pollinators health.[81] Due to this, the chemical effects of MPs could be far higher than the physical effects. MNPs bioaccumulate in the guts of pollinators, as observed via fluorescence microscopy, and interact with gut bacteria, leading to a significant alteration in diversity and composition of predominant groups of bacteria such as *Proteobacteria*, *Firmicutes*, and *Actinobacteria.* These bacteria are vital for various processes such as metabolism, nectar processing, and immunomodulation and protect the pollinators against xenobiotics and abiotic stresses.[82] MNPs accumulation in gut tissues and interactions with molecules, biological membranes, and organelles cause immunity suppression, oxidative stress, change in membrane permeability, and inflammation which may lead to alteration in gut microbial community structure and diversity. In another study, the oral feeding of 100 nm of polystyrene MNPs to honeybees induced intestinal dysplasia, and the MNPs accumulated in rectum, where bee gut symbionts colonized.[60] MNPs exposure caused loss in body weight and adhered to the germination pore of pollens. The deprivation of pollinators from gut microbiome caused loss in body weight.[83] Similar to other studies, the MNPs deplete the expression of several genes related to detoxification, immunity, and metabolism. The effects of MNPs have also been seen on the health and metabolic disorders of flies and mosquitoes, which caused changes in gut microbiota, reduced energy storage and metabolism such as triglyceride level, affected female reproduction, and decreased fatty acid metabolism.[84−86]

MNPs both at micro and nanoscale impact the health of pollinators by disrupting the gut microbiota of bees and other insect species. The ability of MNPs to carry secondary substances and the raw material used for the synthesis of plastics increases the harm to pollinator gut microbiota environments. Continuous exposure to MNPs pollution at a low level can causes susceptibility of gut microbiota, alteration of several important genes associated with vital processes like detoxification, and immunity harm of pollinator health and impacts the effectiveness in different ecosystems.

■ SUSCEPTIBILITY TO VIRAL INFECTION OF BEES

MNPs have the ability to absorb pollutants and other chemicals, which enhances the impacts of MNPs on host health.[87] Pollinators often have large foraging areas and interact actively with air, water, soil, and plants, and pollutants from these sources are transferred into host bodies. During nectar collection, other substances such as honeydew, water, and plant exudates come in contact, and if these products are contaminated with pollutants and chemicals, pollinators would suck these too.[88] When bees were feed on microplastics presented in a water and sucrose solution, they did not distinguish nor showed feeding deterrence from the solution having microplastics.[89] Deng et al.[90] collected honeybees at different regions in China and showed that 66.7% of bee samples presented different types of MNPs in gut, trachea, and other tissues. In a laboratory experiment, when bees ingested MPs, the particles accumulated in the midgut, damaging intestinal tissue and entering the hemolymph, Malpighian tubes, and trachea, significantly decreasing the survival rate of the bees. The enzymes and genes related to immunity, detoxification, lipid metabolism, and the respiratory system were disrupted with MPs ingestion and accumulation. Bees ingested MPs along with Israeli acute paralysis virus (IAPV) RNA (considered cause of bee colony decline), showing susceptibility to the pathogen infestation.[90] The mortality rate of bees ingested with MPs + IAPV RNA was higher compared to IAPV alone, while the expression profile of virus titer was also higher, compared to the IAPV alone group. As discussed in the above section, MNPs are able to carry xenobiotics which make them more toxic for living organisms. MNPs are also capable of translocating in between various tissues and cells, breaking down the biological barriers and penetrating biological membranes.[91,92] For example, if MNPs carry pesticides or pathogens and enter into the guts of pollinators, the toxicity of these xenobiotics increased, as MNPs alone can alter and disrupt gut microbiota and cause inflammation to biological membranes. Organisms infected with MNPs have compromised immunity as MNPs accumulation caused disruption in several detoxification and immunity related genes and caused oxidative stress, and these organisms are unable to cope with MNPs accumulation along with other pathogens.[90] These reports conclude that MNPs pollution pose a threat to pollinator health and pollination ecosystems and may have implications for human health through ingestion of bee products.

■ IMPACTS OF MNPS ON POLLINATION BIOLOGY

Flowering plants developed and evolved various characteristics in order to attract or influence the success of pollinators.[1] These traits include but are not limited to different floral features such as pigmentation, floral signals, floral pattering, floral scents, and nectar secondary metabolites.[1] The adaptation of floral traits is vital for the attraction of pollinators, which plants adopt through genetic mutation, bring developmental change and enhanced fitness.[93,94] These adaptations by plant to influence pollinators have great impacts on pollination biology.[1,95]

The communications between plants and pollinators are reciprocally beneficial for each other, as pollinators enhance plant reproductive success through pollen export and collection, while nectar and pollen serve as nutrition for pollinators, which are called floral rewards.[96,97] The chemistry of nectar is composed of sugars, amino acids, and volatile organic compounds, which provide nutrition, heat source, nesting materials, and mating, sleeping, and brooding sites for pollinators.[98,99] Plant hormones such as jasmonate in coordination with auxin induce the secretion and synthesis of nectar.[100] Polystyrene MPs are reported to disturb the regulatory network of phytohormones in different studied plants.[101] The auxin levels in leaves significantly decreased with MPs treatment in barley. The MNPs in other crops such as tomato, cucumber, and barley affect the phytohormones profiles in leaves and roots.[102] The effects of MNPs on the hormonal level are different for different plants, as studies showed that the biosynthesis of jasmonate in tomato is severely affected, compared to auxins, ethylene, and gibberellins.[102] Similarly, the exposure of plants to MNPs downregulates the fatty acids and affects amino acid profiling, which may disrupt the chemistry of nectar.[102] The disruption of phytohormonal and biochemical profiles of plants by MNPs may disrupt the production and synthesis of nectar, which affect the biology of pollination and may delay or inhibit interactions between plants and pollinators.

The synergy between angiosperm plants and pollinators depends on effective interactions,[103,104] which involve different signals such as visual, olfactory, thermal, and tactile stimuli, and pollinators choose flowers through floral displays.[105] Experimental evidence suggests that plants attract and stimulate more pollinators by emitting both olfactory and visual cues compared to only olfactory or visual stimuli.[106,107] However, insect sense these stimuli through their cognitive behavior, learning memory, innate preferences, and pre-existence biases.[1,99] Studies showed that MNPs possess adverse effects on pollinators learning, memory, cognition, foraging, and feeding behaviors,[89] which may cause disruption in communication between plant and pollinator cues and affect pollination biology.

■ MNPS EFFECTS ON PIGMENTATIONS

Colorful flowers attract pollinators for pollination, and the color of a flower is determined through pigmentation by carotenoids, flavonoids, and betalains.[108] Chromoplasts are organelles which synthesize and store carotenoids in flowers and other tissues of plants.[109] Besides the role in pollinator attraction, these pigments have other vital roles in photosynthesis and in responses to environmental cues.[109] It has been experimentally proved that the disruptions in content, synthesis, and/or mutation in biosynthetic pathways of carotenoids in flowering plants negatively affect the pollinators visits to plants and affect the pollination biology.[110−113] Similarly, the difference in pigmentation establishes floral patterns and mediates plant pollinator interactions.[108] Several types of MNPs caused chronic carotenoids stress in plants.[114] For a prolonged period of time, plants exposed to MNPs showed severe disruption in different pigment levels including carotenoids.[115] These studies conclude that MNPs like other abiotic stressors such as heavy metals affect the level and synthesis of plant carotenoids by interfering with chlorophyll pathways via inhibition of enzymes such as Protochlorophyllide reductase and Aminolaevulinic acid dehydratase involved in the biosynthesis of carotenoids.[114,115] The disruption of carotenoids profiles in plants by MNPs may have severe implications for plant and pollinator effective interactions and could possibly alter the pollination biology.

■ MNPS EFFECTS ON VOLATILE ORGANIC COMPOUNDS

Flowers produce scents, which are a mix of plant volatile organic compounds (VOCs).[116] Chemically, VOCs are lipophilic in nature, with low boiling points and high vapor pressure at ambient temperatures.[117] Terpenoids, benzenoids, phenylpropanoids, and fatty acid derivatives are the major classes of plant floral VOCs, while terpenoids are considered the largest and diverse class of floral VOCs.[118,119] Flowers emit these volatiles to attract and guide pollinators toward the flowers from long distances and influence their probing and landing behavior.[97,120] Despite this, floral VOCs also have many other functions such as protection against microbes and prevention of pollen and nectar robbers.[121,122] Experimental evidence suggests that blocking the expression of genes associated with VOCs metabolite biosynthesis and disruption in metabolomic profiles of VOCs negatively affect the pollinator visits to flowers.[123,124] The metabolomic analysis of several plants exposed to MNPs showed downregulation in secondary metabolites, while a significant decline was noticed in metabolites involved in biosynthesis of terpenoids.[102] Different plants react differently to MNPs stress; however,

https://doi.org/10.1021/acs.est.2c07733
Environ. Sci. Technol. 2023, 57, 6415−6424

the effects on terpenoids and other metabolites involved in plant VOCs are obvious. The decline in VOCs biosynthetic compounds with MNPs stress in plants may have severe repercussions for pollination, as VOCs are vital for pollinator attraction.

Several studies reported the transcriptome of *Arabidopsis thaliana*, wheat, and rice plants and its tissues such as root, shoot, and leaf, in response to different MNPs stresses. We analyzed the differentially expressed (DE) genes and investigated the enrichment of DE gene pathways in response to MNPs stresses in relation with those pathways involved in the molecular mechanism of pollination biology. The effects of MNPs stress on plant physiology and morphology such as cytotoxicity, genotoxicity, nutritional and oxidative stress, changes in plant photosynthesis, and metabolism are summarized and reviewed by Wang et al.[125]

EFFECTS OF MNPS ON MOLECULAR BIOLOGY OF POLLINATION

The RNA-Seq analyses of plants in response to MNPs particles show DE genes enriched in anthocyanin-containing compounds, anthocyanin biosynthesis and metabolic processes, flavonoids biosynthetic and metabolic processes, phenylpropanoids metabolic process, phenylalanine metabolic process, terpenoid biosynthesis and metabolic processes, triterpenoid biosynthesis, terpene synthase activity, carotenoid biosynthesis, and circadian rhythm.[126−129]

Anthocyanin, betalains, and carotenoids are the major groups of plant chemically distinct pigments, are responsible for attractive flower color displays, and attract pollinators.[130] Anthocyanin is a phenylpropanoid-derived water-soluble pigment, possessing a vast distribution of any floral pigments and producing blue, black, purple, pink, and red colors. The biosynthesis, regulation, chemistry, and distribution of anthocyanin is extensively documented.[130,131] Members of R2R3MYB and basic helix−loop−helix (bHLH) families that form a complex with WR-repeat (WDR) proteins controlled the synthesis of anthocyanin, and the function and interaction of these complexes in anthocyanin synthesis are conserved across divergent taxa.[108,132,133] Similar to flower color, floral patternings, such as pigment spots, stripes, and bicolor, are important signals for pollinator attraction and mediate plant−pollinator interactions.[134] R2R3MYBs are important complexes of pigmentation intensity and patterning in plants.[108] Likewise, venation is also regulated by R2R3MYB and anthocyanin-pigmented venation stimulates pollinator visitation rates.[135] Carotenoids are terpenoid-derived lipid soluble and in the yellow−red range,[136] while betalains are tyrosine-derived pigments, ranging from yellow or red−purple, found only in caryophyllales.[137] The biosynthesis, transport, storage, and regulation of betalain and carotenoids are extensively described.[109,130] The carotenoid biosynthesis starts with C5 IPP and DMAPP formation through the MEP (methylerythritol) pathway, which also produces several volatiles involved in pollinator attraction.[136,138] The production of betalains is mutually exclusive with anthocyanin, and both pigments use arogenate as a precursor, However, betalains are synthesized from tyrosine, while anthocyanins are derived from phenylalanine.[1,139]

Positively and negatively charged polystyrene NPs, PS-NH_2 and PS-SO_3H, respectively, accumulate in roots and shoots of *A. thaliana*.[128] The RNA-Seq revealed that positively charged NPs caused higher impact on gene expression, compared with negatively charged NPs. PS-NH_2 upregulated the mRNA expression of genes, functioning in anthocyanin and flavonoids biosynthesis and metabolic processes. The genes involved in phenylpropanoids and carotenoids biosyntheses are also disrupted with NPs accumulation.[128] Similarly, the RNA-Seq analysis of two rice species, exposed to polystyrene MPs, showed disruption in genes related to phenylpropanoid metabolic processes and flavonoid biosynthesis,[126] while the transcriptome of *Arabidopsis* exposed to degradable plastic poly(butylene adipate-*co*-terephthalate) (PBAT) showed disruption in genes involved in anthocyanin biosynthesis and metabolic processes, phenylpropanoids metabolic process, and flavonoid biosynthesis and metabolic processes.[127] The wheat root and leaf RNA-Seq, exposed to polystyrene NPs, showed DE genes related to phenylalanine metabolism and phenylpropanoid biosynthesis.[129] These studies conclude that different plant species and their tissues exposed to different types of MNPs severely disrupt the biosynthesis and metabolism of plant pigments. Despite the type of MNPs, the molecular pathways of both anthocyanin and carotenoids are disrupted in all studied plants, which indicate the harmful effects of MNPs on pigments. These studies did not evaluate the impact of MNPs stress on floral pigments; however, it is confirmed that flower color could be influenced by the accumulation of flavonoids elsewhere in the plant.[130] We speculate that MNPs have the potential to influence flower hue and pollinator interaction and attraction by manipulating the molecular mechanism of biosynthetic and metabolic pathways of major pigments groups.

The production, regulation, and emission of floral VOCs are important for pollinator attraction and guidance.[140] Terpenoids are the largest floral volatile class, while phenylpropanoids derived from the amino acid phenylalanine are the second largest class of plant VOCs.[141−143] The MNPs stress in several plants caused the disruption of terpenoids biosynthesis and metabolism, terpene synthase activity, and triterpenoid biosynthesis pathways.[126,128] The disruption in these pathways could have greater impact on the production and emission of floral volatiles. Similarly, the circadian clock and rhythm of both pollinators and plants tightly regulate the emission of VOCs and influence flower seeking behavior.[144] The role of the circadian clock in VOCs emission and pollinator attraction has been established.[145] The RNA-Seq analysis of *A. thaliana* showed disruption in genes involved in the circadian clock and rhythm metabolism.[128] The alteration in the circadian rhythm by MNPs could affect volatile emission and pollinator attraction, as studies suggested that disruption in plant circadian rhythm impacted pollinator visitation preference.[146]

FUTURE PERSPECTIVES

MNPs pollution affects the health of pollinators and plants several ways and disrupts the plant−pollinator interactions and communication. We have focused on the key events in pollination biology which are potentially disrupted by MNPs contamination and adversely affect the process of pollination. We highlighted the direct impacts of MNPs contamination on pollinator health, such as metabolic alteration, reduced immunity, growth, impaired hormonal activities, on the negative affects on gut microbiota, on the adverse effects on plant health, such as negatively regulating plant growth, immunity, root and shoot structures, metabolic alteration, susceptibility to biotic and abiotic stresses, and on the

https://doi.org/10.1021/acs.est.2c07733
Environ. Sci. Technol. 2023, 57, 6415−6424

alteration of enzymatic and endocrine activities. These effects directly or indirectly alter the pollination process and pose threats to all stakeholders involved in the pollination process.

Studies about MNPs contamination in ecosystems mainly focused on the uptake and distribution of MNPs particles in plant and insect tissues and its adverse effects on individual health. To the best of our knowledge, no study has undertaken the direct impacts of MNPs contamination on pollination biology.

1. To elucidate the in-depth understanding of the possible adverse effects of MNPs contamination on plant–pollinator interactions and pollination biology, future field and laboratory studies should addess the dynamics and roles in stress response, which could explain in plants and pollinators the different factors, key genes, and pathways.
2. For effective communication between plant and pollinator, plant floral features and pollinator behavior play vital role for the success of the pollination process. Future studies should highlight the interaction of plant–pollinator in MNPs stress conditions, and effects on pollinator behavior will create a more comprehensive context for the exploration of possible adverse effects of MNPs on pollination biology.
3. Modern molecular biology techniques and extensive genomic, transcriptomic, and metabolomic resources must be utilized to determine the effects of MNPs on genotypes of plant and pollinator and elucidate the target genes. Experimental procedures such as CRISPR and RNAi along with genomic resources will enable the analyses of many candidate genes.
4. Field studies, surveys, soil analysis, and monitoring and observation of pollinators would help to assess plant yield losses in terms of pollination disruption and decline in pollinator populations with MNPs contamination.
5. A comprehensive understanding of the mechanisms of plant–pollinator interactions, pollination biology, and response of plant–pollinator to MNPs stresses requires knowledge and skills drawn from several disciplines. The advancements in molecular biology, genetic techniques, and modern bioinformatics tools greatly enhance how to deal with big data and unsolved questions and address systems involved in stress responses.

■ AUTHOR INFORMATION

Corresponding Authors

Feng-Lian Yang – *Hubei Key Laboratory of Insect Resources Utilization and Sustainable Pest Management, College of Plant Science and Technology, Huazhong Agricultural University, 430070 Wuhan, Hubei, People's Republic of China*; Email: yangfenglian@mail.hzau.edu.cn

Jie Yang – *CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 666316 Menglun, China*; Email: yangjie@xtbg.org.cn

Authors

Sakhawat Shah – *Hubei Key Laboratory of Insect Resources Utilization and Sustainable Pest Management, College of Plant Science and Technology, Huazhong Agricultural University, 430070 Wuhan, Hubei, People's Republic of China*; orcid.org/0000-0003-0275-5450

Muhammad Ilyas – *CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 666316 Menglun, China; Chinese Academy of Sciences, 100045 Beijing, China*

Rui Li – *Hubei Key Laboratory of Insect Resources Utilization and Sustainable Pest Management, College of Plant Science and Technology, Huazhong Agricultural University, 430070 Wuhan, Hubei, People's Republic of China*

Complete contact information is available at: https://pubs.acs.org/10.1021/acs.est.2c07733

Author Contributions

All authors contributed equally their experience and knowledge via group discussions to the concepts and recommendations provided in this perspective. In addition, F.-L.Y and J.Y led the discussions, and S.S, M.I., and R.L. contributed to the writing of the manuscript. All authors approved the final manuscript.

Notes

The authors declare no competing financial interest.

Biography

Dr. Feng-Lian Yang is from the College of Plant Science and Technology, Huazhong Agricultural University, China. Her research focuses on the interrelationships between plants and stored product pests. Her research group has been exploring the molecular mechanisms of materials from plants against stored grain pests and studying nanoparticles loaded with these materials from plants.

■ ACKNOWLEDGMENTS

This research was funded by the National Natural Science Foundation of China (31871955), Hubei Provincial Natural Science Foundation of China (2017CFB541), National Key R&D Program of China (2022YFF1302401), Huazhong Agricultural University scholarship to Sakhawat Shah, and the China Scholarship Council (CSC) to Muhammad Ilyas.

■ REFERENCES

(1) Fattorini, R.; Glover, B. J. Molecular mechanisms of pollination biology. *Annu. Rev. Plant Biol.* **2020**, *71*, 487–515.

(2) Crespel, L; Mouchotte Methods of Cross-Breeding. In *Reference Module in Life Sciences*; Elsevier, 2017.

(3) Friedman, J.; Barrett, S. C. H. Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants. *Ann. Bot* **2009**, *103*, 1515–1527.

(4) Ackerman, J. D. Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. In *Pollen and pollination*; Springer, 2000; pp 167–185.

(5) Linder, H. P. Morphology and evolution of wind pollination, 1998; 123–135.

(6) Timerman, D.; Barrett, S. C. H. The biomechanics of pollen release: new perspectives on the evolution of wind pollination in angiosperms. *Biol. Rev.* **2021**, *96*, 2146−2163.
(7) Pacini, E. From anther and pollen ripening to pollen presentation. In *Pollen and Pollination*; Springer, 2000; pp 19−43.
(8) Kellogg, E. A. *Flowering Plants. Monocots*; The Families and Genera of Vascular Plants Series; Springer, 2015; *13*; pp 973−978.
(9) Scott, R. J.; Spielman, M.; Dickinson, H. Stamen structure and function. *Plant Cell* **2004**, *16*, S46−S60.
(10) Jones, A. M.; Harrison, R. M. The effects of meteorological factors on atmospheric bioaerosol concentrations—a review. *Sci. Total Environ.* **2004**, *326*, 151−180.
(11) Van Hout, R.; Chamecki, M.; Brush, G.; et al. The influence of local meteorological conditions on the circadian rhythm of corn (Zea mays L.) pollen emission. *Agric For Meteorol* **2008**, *148*, 1078−1092.
(12) Linskens, H. F.; Cresti, M. Effect of temperature, humidity, and light on the dehiscence of tobacco anthers. In *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 1988.
(13) De Langre, E. Effects of wind on plants. *Annu. Rev. Fluid Mech* **2008**, *40*, 141−168.
(14) Urzay, J.; Llewellyn Smith, S. G.; Thompson, E.; Glover, B. J. Wind gusts and plant aeroelasticity effects on the aerodynamics of pollen shedding: a hypothetical turbulence-initiated wind-pollination mechanism. *J. Theor. Biol.* **2009**, *259*, 785−792.
(15) de Langre, E. Plant vibrations at all scales: a review. *J. Exp Bot* **2019**, *70*, 3521−3531.
(16) Lin, H.; Gomez, I.; Meredith, J. C. Pollenkitt wetting mechanism enables species-specific tunable pollen adhesion. *Langmuir* **2013**, *29*, 3012−3023.
(17) Timerman, D.; Barrett, S. C. H. Comparative analysis of pollen release biomechanics in Thalictrum: implications for evolutionary transitions between animal and wind pollination. *New Phytol* **2019**, *224*, 1121−1132.
(18) Ollerton, J. Pollinator diversity: distribution, ecological function, and conservation. *Annu. Rev. Ecol Evol Syst* **2017**, *48*, 353.
(19) Cameron, S. A.; Sadd, B. M. Global trends in bumble bee health. *Annu. Rev. Entomol* **2020**, *65*, 209−232.
(20) Klein, A.-M.; Vaissière, B. E.; Cane, J. H.; et al. Importance of pollinators in changing landscapes for world crops. *Proc. R Soc. B Biol. Sci.* **2007**, *274*, 303−313.
(21) Kevan, P. G.; Viana, B. F. The global decline of pollination services. *Biodiversity* **2003**, *4*, 3−8.
(22) Hanley, N.; Breeze, T. D.; Ellis, C.; Goulson, D. Measuring the economic value of pollination services: Principles, evidence and knowledge gaps. *Ecosyst Serv* **2015**, *14*, 124−132.
(23) Aizen, M. A.; Garibaldi, L. A.; Cunningham, S. A.; Klein, A. M. How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Ann. Bot* **2009**, *103*, 1579−1588.
(24) Potts, S. G.; Biesmeijer, J. C.; Kremen, C.; et al. Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* **2010**, *25*, 345−353.
(25) Sánchez-Bayo, F.; Wyckhuys, K. A. G. Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv* **2019**, *232*, 8−27.
(26) Hallmann, C. A.; Sorg, M.; Jongejans, E.; et al. More than 75% decline over 27 years in total flying insect biomass in protected areas. *PLoS One* **2017**, *12*, No. e0185809.
(27) Rasmont, P.; Franzen, M.; Lecocq, T.; Harpke, A.; Roberts, S.; Biesmeijer, K.; Castro, L.; Cederberg, B.; Dvorak, L.; Fitzpatrick, U.; Gonseth, Y.; Haubruge, E.; Mahe, G.; Manino, A.; Michez, D.; Neumayer, J.; Odegaard, F.; Paukkunen, J.; Pawlikowski, T.; Potts, S.; Reemer, M.; Settele, J.; Straka, J.; Schweiger, O. Climatic risk and distribution atlas of European bumblebees. *Pensoft Publishers* **2015**, *10*, 1.
(28) Bommarco, R.; Lundin, O.; Smith, H. G.; Rundlöf, M. Drastic historic shifts in bumble-bee community composition in Sweden. *Proc. R Soc. B Biol. Sci.* **2012**, *279*, 309−315.
(29) Cameron, S. A.; Lozier, J. D.; Strange, J. P.; et al. Patterns of widespread decline in North American bumble bees. *Proc. Natl. Acad. Sci.* **2011**, *108*, 662−667.
(30) Connop, S.; Hill, T.; Steer, J.; Shaw, P. The role of dietary breadth in national bumblebee (Bombus) declines: Simple correlation? *Biol. Conserv* **2010**, *143*, 2739−2746.
(31) Morales, C. L.; Arbetman, M. P.; Cameron, S. A.; Aizen, M. A. Rapid ecological replacement of a native bumble bee by invasive species. *Front Ecol Environ* **2013**, *11*, 529−534.
(32) Lander, T. Network modelling, citizen science and targeted interventions to predict, monitor and reverse bee decline. *Plants, People, Planet* **2020**, *2*, 111−120.
(33) Winfree, R.; Aguilar, R.; Vázquez, D. P.; et al. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* **2009**, *90*, 2068−2076.
(34) Scheper, J.; Holzschuh, A.; Kuussaari, M.; et al. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss-a meta-analysis. *Ecol Lett.* **2013**, *16*, 912−920.
(35) Vanbergen, A. J; Initiative, t. I. P. Initiative the IP. Threats to an ecosystem service: pressures on pollinators. *Front Ecol Environ* **2013**, *11*, 251−259.
(36) Grozinger, C. M.; Flenniken, M. L. Bee viruses: Ecology, pathogenicity, and impacts. *Annu. Rev. Entomol* **2019**, *64*, 205.
(37) Franzén, M.; Öckinger, E. Climate-driven changes in pollinator assemblages during the last 60 years in an Arctic mountain region in Northern Scandinavia. *J. Insect Conserv* **2012**, *16*, 227−238.
(38) Rader, R.; Reilly, J.; Bartomeus, I.; Winfree, R. Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Glob Chang Biol.* **2013**, *19*, 3103−3110.
(39) Whitehorn, P. R.; O'connor, S.; Wackers, F. L.; Goulson, D. Neonicotinoid pesticide reduces bumble bee colony growth and queen production. *Science (80-)* **2012**, *336*, 351−352.
(40) Di Prisco, G.; Cavaliere, V.; Annoscia, D.; et al. Neonicotinoid clothianidin adversely affects insect immunity and promotes replication of a viral pathogen in honey bees. *Proc. Natl. Acad. Sci.* **2013**, *110*, 18466−18471.
(41) Pettis, J. S.; Vanengelsdorp, D.; Johnson, J.; Dively, G. Pesticide exposure in honey bees results in increased levels of the gut pathogen Nosema. *Naturwissenschaften* **2012**, *99*, 153−158.
(42) Goulson, D. Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol Evol Syst* **2003**, *34*, 1−26.
(43) Sugiura, S.; Tsuru, T.; Yamaura, Y. Effects of an invasive alien tree on the diversity and temporal dynamics of an insect assemblage on an oceanic island. *Biol. Invasions* **2013**, *15*, 157−169.
(44) Leonard, R. J.; Pettit, T. J.; Irga, P.; et al. Acute exposure to urban air pollution impairs olfactory learning and memory in honeybees. *Ecotoxicology* **2019**, *28*, 1056−1062.
(45) Thimmegowda, G. G.; Mullen, S.; Sottilare, K.; et al. A field-based quantitative analysis of sublethal effects of air pollution on pollinators. *Proc. Natl. Acad. Sci.* **2020**, *117*, 20653−20661.
(46) Ryalls, J. M. W.; Langford, B.; Mullinger, N. J.; et al. Anthropogenic air pollutants reduce insect-mediated pollination services. *Environ. Pollut.* **2022**, *297*, 118847.
(47) MacLeod, M.; Arp, H. P. H.; Tekman, M. B.; Jahnke, A. The global threat from plastic pollution. *Science (80-)* **2021**, *373*, 61−65.
(48) Geyer, R.; Jambeck, J. R.; Law, K. L. Production, use, and fate of all plastics ever made. *Sci. Adv.* **2017**, *3*, No. e1700782.
(49) Barnes, D. K. A.; Galgani, F.; Thompson, R. C.; Barlaz, M. Accumulation and fragmentation of plastic debris in global environments. *Philos. Trans R Soc. B Biol. Sci.* **2009**, *364*, 1985−1998.
(50) Hale, R. C.; Seeley, M. E.; La Guardia, M. J.; Mai, L.; Zeng, E. Y. A global perspective on microplastics. *J. Geophys Res. Ocean* **2020**, *125*, No. e2018JC014719.
(51) Lopez-Uribe, M. M.; Ricigliano, V. A.; Simone-Finstrom, M. Defining Pollinator Health: A Holistic Approach Based on Ecological, Genetic, and Physiological Factors. *Annual Review of Animal Biosciences* **2020**, *8*, 269−294.
(52) Chown, S. L.; Gaston, K. J. Body size variation in insects: a macroecological perspective. *Biol. Rev.* **2010**, *85*, 139−169.

(53) Nee, S.; Lawton, J. H. Body size and biodiversity. *Nature* **1996**, *380*, 672−673.
(54) Edgar, B. A. How flies get their size: genetics meets physiology. *Nat. Rev. Genet* **2006**, *7*, 907−916.
(55) Nijhout, H. F.; Davidowitz, G.; Roff, D. A. A quantitative analysis of the mechanism that controls body size in Manduca sexta. *J. Biol.* **2006**, *5*, 16.
(56) Fischer, K.; Fiedler, K. Reaction norms for age and size at maturity in response to temperature: a test of the compound interest hypothesis. *Evol Ecol* **2002**, *16*, 333−349.
(57) Emlen, D. J.; Corley Lavine, L.; Ewen-Campen, B. On the origin and evolutionary diversification of beetle horns. *Proc. Natl. Acad. Sci.* **2007**, *104*, 8661−8668.
(58) Mirth, C. K.; Riddiford, L. M. Size assessment and growth control: how adult size is determined in insects. *Bioessays* **2007**, *29*, 344−355.
(59) Edo, C.; Fernández-Alba, A. R.; Vejsnæs, F.; et al. Honeybees as active samplers for microplastics. *Sci. Total Environ.* **2021**, *767*, 144481.
(60) Wang, K.; Zhu, L.; Rao, L.; et al. Nano-and micro-polystyrene plastics disturb gut microbiota and intestinal immune system in honeybee. *Sci. Total Environ.* **2022**, *842*, 156819.
(61) Ziajahromi, S.; Kumar, A.; Neale, P. A.; Leusch, F. D. L. Environmentally relevant concentrations of polyethylene microplastics negatively impact the survival, growth and emergence of sediment-dwelling invertebrates. *Environ. Pollut.* **2018**, *236*, 425−431.
(62) Souza Machado, A. A.; Kloas, W.; Zarfl, C.; Hempel, S.; Rillig, M. C. Microplastics as an emerging threat to terrestrial ecosystems. *Glob Chang Biol.* **2018**, *24*, 1405−1416.
(63) Muhammad, A.; Zhou, X.; He, J.; et al. Toxic effects of acute exposure to polystyrene microplastics and nanoplastics on the model insect, silkworm Bombyx mori. *Environ. Pollut.* **2021**, *285*, 117255.
(64) Critchell, K.; Hoogenboom, M. O. Effects of microplastic exposure on the body condition and behaviour of planktivorous reef fish (Acanthochromis polyacanthus). *PLoS One* **2018**, *13*, No. e0193308.
(65) Derraik, J. G. B. The pollution of the marine environment by plastic debris: a review. *Mar. Pollut. Bull.* **2002**, *44*, 842−852.
(66) Engel, P.; Moran, N. A. The gut microbiota of insects-diversity in structure and function. *FEMS Microbiol Rev.* **2013**, *37*, 699−735.
(67) Douglas, A. E. Multiorganismal insects: diversity and function of resident microorganisms. *Annu. Rev. Entomol* **2015**, *60*, 17.
(68) Lynch, S. V.; Pedersen, O. The human intestinal microbiome in health and disease. *N Engl J. Med.* **2016**, *375*, 2369−2379.
(69) Bik, E. M.; Ugalde, J. A.; Cousins, J.; et al. Microbial biotransformations in the human distal gut. *Br. J. Pharmacol.* **2018**, *175*, 4404−4414.
(70) Jing, T.-Z.; Qi, F.-H.; Wang, Z.-Y. Most dominant roles of insect gut bacteria: digestion, detoxification, or essential nutrient provision? *Microbiome* **2020**, *8*, 1−20.
(71) Fierer, N.; Strickland, M. S.; Liptzin, D.; et al. Global patterns in belowground communities. *Ecol Lett.* **2009**, *12*, 1238−1249.
(72) Fox-Dobbs, K.; Doak, D. F.; Brody, A. K.; Palmer, T. M. Termites create spatial structure and govern ecosystem function by affecting N2 fixation in an East African savanna. *Ecology* **2010**, *91*, 1296−1307.
(73) Kwong, W. K.; Moran, N. A. Gut microbial communities of social bees. *Nat. Rev. Microbiol* **2016**, *14*, 374−384.
(74) Zheng, H.; Nishida, A.; Kwong, W. K.; Koch, H.; Engel, P.; Steele, M. I.; Moran, N. A. Metabolism of toxic sugars by strains of the bee gut symbiont Gilliamella apicola. *MBio* **2016**, *7*, No. e01326.
(75) Motta, E. V. S.; Raymann, K.; Moran, N. A. Glyphosate perturbs the gut microbiota of honey bees. *Proc. Natl. Acad. Sci.* **2018**, *115*, 10305−10310.
(76) Lu, L.; Wan, Z.; Luo, T.; et al. Polystyrene microplastics induce gut microbiota dysbiosis and hepatic lipid metabolism disorder in mice. *Sci. Total Environ.* **2018**, *631*, 449−458.
(77) Qiao, R.; Deng, Y.; Zhang, S.; et al. Accumulation of different shapes of microplastics initiates intestinal injury and gut microbiota dysbiosis in the gut of zebrafish. *Chemosphere* **2019**, *236*, 124334.
(78) Li, B.; Ding, Y.; Cheng, X.; et al. Polyethylene microplastics affect the distribution of gut microbiota and inflammation development in mice. *Chemosphere* **2020**, *244*, 125492.
(79) Wang, S.; Shi, W.; Huang, Z.; et al. Complete digestion/biodegradation of polystyrene microplastics by greater wax moth (Galleria mellonella) larvae: Direct in vivo evidence, gut microbiota independence, and potential metabolic pathways. *J. Hazard Mater.* **2022**, *423*, 127213.
(80) Wang, K.; Li, J.; Zhao, L.; et al. Gut microbiota protects honey bees (Apis mellifera L.) against polystyrene microplastics exposure risks. *J. Hazard Mater.* **2021**, *402*, 123828.
(81) Li, J.; Zhang, K.; Zhang, H. Adsorption of antibiotics on microplastics. *Environ. Pollut.* **2018**, *237*, 460−467.
(82) Kakumanu, M. L.; Reeves, A. M.; Anderson, T. D.; Rodrigues, R. R.; Williams, M. A. Honey bee gut microbiome is altered by in-hive pesticide exposures. *Front Microbiol* **2016**, *7*, 1255.
(83) Zheng, H.; Powell, J. E.; Steele, M. I.; et al. Honeybee gut microbiota promotes host weight gain via bacterial metabolism and hormonal signaling. *Proc. Natl. Acad. Sci.* **2017**, *114*, 4775−4780.
(84) Zhang, Y.; Wolosker, M. B.; Zhao, Y.; et al. Exposure to microplastics cause gut damage, locomotor dysfunction, epigenetic silencing, and aggravate cadmium (Cd) toxicity in Drosophila. *Sci. Total Environ.* **2020**, *744*, 140979.
(85) Shen, J.; Liang, B.; Zhang, D.; et al. Effects of PET microplastics on the physiology of Drosophila. *Chemosphere* **2021**, *283*, 131289.
(86) Malafaia, G.; da Luz, T. M.; Guimarães, A. T. B.; da Costa Araújo, A. P. Polyethylene microplastics are ingested and induce biochemical changes in Culex quinquefasciatus (Diptera: Culicidae) freshwater insect larvae. *Ecotoxicol Environ. Contam* **2020**, *15*, 79−89.
(87) O'Donovan, S.; Mestre, N. C.; Abel, S.; Fonseca, T. G.; Carteny, C. C.; Cormier, B.; Keiter, S. H.; Bebianno, M. J. Ecotoxicological effects of chemical contaminants adsorbed to microplastics in the clam Scrobicularia plana. *Front Mar Sci.* **2018**, *5*, 143.
(88) Al Naggar, Y.; Brinkmann, M.; Sayes, C. M.; et al. Are honey bees at risk from microplastics? *Toxics* **2021**, *9*, 109.
(89) Buteler, M.; Alma, A. M.; Stadler, T.; et al. Acute toxicity of microplastic fibers to honeybees and effects on foraging behavior. *Sci. Total Environ.* **2022**, *822*, 153320.
(90) Deng, Y.; Jiang, X.; Zhao, H.; et al. Microplastic polystyrene ingestion promotes the susceptibility of honeybee to viral infection. *Environ. Sci. Technol.* **2021**, *55*, 11680−11692.
(91) Farrell, P.; Nelson, K. Trophic level transfer of microplastic: Mytilus edulis (L.) to Carcinus maenas (L.). *Environ. Pollut.* **2013**, *177*, 1−3.
(92) Dawson, A. L.; Kawaguchi, S.; King, C. K.; Townsend, K. A.; King, R.; Huston, W. M.; Bengtson Nash, S. M. Turning microplastics into nanoplastics through digestive fragmentation by Antarctic krill. *Nat. Commun.* **2018**, *9*, 1001.
(93) Bateman, R. M. Evolutionary-developmental change in the growth architecture of fossil rhizomorphic lycopsids: scenarios constructed on cladistic foundations. *Biol. Rev.* **1994**, *69*, 527−597.
(94) Cronk, Q. C. B.; Bateman, R. M.; Hawkins, J. A. *Developmental Genetics and Plant Evolution*l CRC Press, 2004.
(95) Ronse De Craene, L. Understanding the role of floral development in the evolution of angiosperm flowers: clarifications from a historical and physico-dynamic perspective. *J. Plant Res.* **2018**, *131*, 367−393.
(96) De la Barrera, E.; Nobel, P. S. Nectar: properties, floral aspects, and speculations on origin. *Trends Plant Sci.* **2004**, *9*, 65−69.
(97) Borghi, M.; Fernie, A. R.; Schiestl, F. P.; Bouwmeester, H. J. The sexual advantage of looking, smelling, and tasting good: the metabolic network that produces signals for pollinators. *Trends Plant Sci.* **2017**, *22*, 338−350.

(98) Roy, R.; Schmitt, A. J.; Thomas, J. B.; Carter, C. J. Nectar biology: from molecules to ecosystems. *Plant Sci.* **2017**, *262*, 148−164.
(99) Balamurali, G. S.; Krishna, S.; Somanathan, H. Senses and signals: evolution of floral signals, pollinator sensory systems and the structure of plant-pollinator interactions. *Curr. Sci.* **2015**, *108*, 1852−1861.
(100) Schmitt, A. J.; Roy, R.; Klinkenberg, P. M.; Jia, M.; Carter, C. J. The octadecanoid pathway, but not COI1, is required for nectar secretion in Arabidopsis thaliana. *Front Plant Sci.* **2018**, *9*, na DOI: 10.3389/fpls.2018.01060.
(101) Li, S.; Wang, T.; Guo, J.; et al. Polystyrene microplastics disturb the redox homeostasis, carbohydrate metabolism and phytohormone regulatory network in barley. *J. Hazard Mater.* **2021**, *415*, 125614.
(102) Bouaicha, O.; Tiziani, R.; Maver, M.; et al. Plant species-specific impact of polyethylene microspheres on seedling growth and the metabolome. *Sci. Total Environ.* **2022**, *840*, 156678.
(103) Endler, J. A. Signals, signal conditions, and the direction of evolution. *Am. Nat.* **1992**, *139*, S125−S153.
(104) Klahre, U.; Gurba, A.; Hermann, K.; et al. Pollinator choice in Petunia depends on two major genetic loci for floral scent production. *Curr. Biol.* **2011**, *21*, 730−739.
(105) Raguso, R. A.; Thompson, J. N.; Campbell, D. R. Improving our chemistry: challenges and opportunities in the interdisciplinary study of floral volatiles. *Nat. Prod Rep* **2015**, *32*, 893−903.
(106) Raguso, R. A.; Willis, M. A. Synergy between visual and olfactory cues in nectar feeding by wild hawkmoths, Manduca sexta. *Anim Behav* **2005**, *69*, 407−418.
(107) Peach, D. A. H.; Gries, R.; Zhai, H.; Young, N.; Gries, G. Multimodal floral cues guide mosquitoes to tansy inflorescences. *Sci. Rep* **2019**, *9*, 1−10.
(108) Davies, K. M.; Albert, N. W.; Schwinn, K. E. From landing lights to mimicry: the molecular regulation of flower colouration and mechanisms for pigmentation patterning. *Funct Plant Biol.* **2012**, *39*, 619−638.
(109) Sun, T.; Yuan, H.; Cao, H.; et al. Carotenoid metabolism in plants: the role of plastids. *Mol. Plant* **2018**, *11*, 58−74.
(110) Bradshaw, H. D.; Schemske, D. W. Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature* **2003**, *426*, 176−178.
(111) Bradshaw, C. J. A.; Ehrlich, P. R.; Beattie, A.; Ceballos, G.; Crist, E.; Diamond, J.; Dirzo, R.; Ehrlich, A. H.; Harte, J.; Harte, M. E.; Pyke, G.; Raven, P. H.; Ripple, W. J.; Saltre, F.; Turnbull, C.; Wackernagel, M.; Blumstein, D. T. Underestimating the challenges of avoiding a ghastly future. *Front Conserv Sci.* **2021**, *1*, 9.
(112) Schemske, D. W.; Bradshaw, H. D., Jr Pollinator preference and the evolution of floral traits in monkeyflowers (Mimulus). *Proc. Natl. Acad. Sci.* **1999**, *96*, 11910−11915.
(113) Owen, C. R.; Bradshaw, H. D. Induced mutations affecting pollinator choice in Mimulus lewisii (Phrymaceae). *Arthropod Plant Interact* **2011**, *5*, 235−244.
(114) Pignattelli, S.; Broccoli, A.; Renzi, M. Physiological responses of garden cress (L. sativum) to different types of microplastics. *Sci. Total Environ.* **2020**, *727*, 138609.
(115) Li, Z.; Li, R.; Li, Q.; et al. Physiological response of cucumber (Cucumis sativus L.) leaves to polystyrene nanoplastics pollution. *Chemosphere* **2020**, *255*, 127041.
(116) Ashman, T.-L.; Bradburn, M.; Cole, D. H.; et al. The scent of a male: the role of floral volatiles in pollination of a gender dimorphic plant. *Ecology* **2005**, *86*, 2099−2105.
(117) Dudareva, N.; Pichersky, E. Metabolic engineering of plant volatiles. *Curr. Opin Biotechnol* **2008**, *19*, 181−189.
(118) Muhlemann, J. K.; Klempien, A.; Dudareva, N. Floral volatiles: from biosynthesis to function. *Plant Cell Environ* **2014**, *37*, 1936−1949.
(119) Dudareva, N.; Klempien, A.; Muhlemann, J. K.; Kaplan, I. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. *New Phytol* **2013**, *198*, 16−32.
(120) Cunningham, J. P.; Moore, C. J.; Zalucki, M. P.; West, S. A. Learning, odour preference and flower foraging in moths. *J. Exp Biol.* **2004**, *207*, 87−94.
(121) Kessler, D.; Baldwin, I. T. Making sense of nectar scents: the effects of nectar secondary metabolites on floral visitors of Nicotiana attenuata. *Plant J.* **2007**, *49*, 840−854.
(122) Raguso, R. A. More lessons from linalool: insights gained from a ubiquitous floral volatile. *Curr. Opin Plant Biol.* **2016**, *32*, 31−36.
(123) Kessler, D.; Gase, K.; Baldwin, I. T. Field experiments with transformed plants reveal the sense of floral scents. *Science (80-)* **2008**, *321*, 1200−1202.
(124) Knudsen, J. T.; Eriksson, R.; Gershenzon, J.; Ståhl, B. Diversity and distribution of floral scent. *Bot Rev.* **2006**, *72*, 1−120.
(125) Wang, F.; Feng, X.; Liu, Y.; et al. Micro (nano) plastics and terrestrial plants: Up-to-date knowledge on uptake, translocation, and phytotoxicity. *Resour Conserv Recycl* **2022**, *185*, 106503.
(126) Wu, X.; Hou, H.; Liu, Y.; et al. Microplastics affect rice (Oryza sativa L.) quality by interfering metabolite accumulation and energy expenditure pathways: A field study. *J. Hazard Mater.* **2022**, *422*, 126834.
(127) Liu, J.; Wang, P.; Wang, Y.; et al. Negative effects of poly (butylene adipate-co-terephthalate) microplastics on Arabidopsis and its root-associated microbiome. *J. Hazard Mater.* **2022**, *437*, 129294.
(128) Sun, X.-D.; Yuan, X.-Z.; Jia, Y.; et al. Differentially charged nanoplastics demonstrate distinct accumulation in Arabidopsis thaliana. *Nat. Nanotechnol* **2020**, *15*, 755−760.
(129) Lian, J.; Liu, W.; Sun, Y.; et al. Nanotoxicological effects and transcriptome mechanisms of wheat (Triticum aestivum L.) under stress of polystyrene nanoplastics. *J. Hazard Mater.* **2022**, *423*, 127241.
(130) Grotewold, E. The genetics and biochemistry of floral pigments. *Annu. Rev. Plant Biol.* **2006**, *57*, 761−780.
(131) Gould, K. S. Nature's Swiss army knife: the diverse protective roles of anthocyanins in leaves. *J. Biomed Biotechnol* **2004**, *2004*, 314.
(132) Zhao, D.; Tao, J. Recent advances on the development and regulation of flower color in ornamental plants. *Front Plant Sci.* **2015**, *6*, 261.
(133) Xu, W.; Dubos, C.; Lepiniec, L. Transcriptional control of flavonoid biosynthesis by MYB-bHLH-WDR complexes. *Trends Plant Sci.* **2015**, *20*, 176−185.
(134) Leonard, A. S.; Papaj, D. R. 'X'marks the spot: The possible benefits of nectar guides to bees and plants. *Funct Ecol* **2011**, *25*, 1293−1301.
(135) Shang, Y.; Venail, J.; Mackay, S.; et al. The molecular basis for venation patterning of pigmentation and its effect on pollinator attraction in flowers of Antirrhinum. *New Phytol* **2011**, *189*, 602−615.
(136) Goodwin, T. W.; Britton, G. Distribution and analysis of carotenoids. *Plant Pigment* **1988**, 61−132.
(137) Brockington, S. F.; Walker, R. H.; Glover, B. J.; et al. Complex pigment evolution in the Caryophyllales. *New Phytol* **2011**, *190*, 854−864.
(138) Maeda, H.; Dudareva, N. The shikimate pathway and aromatic amino acid biosynthesis in plants. *Annu. Rev. Plant Biol.* **2012**, *63*, 73−105.
(139) Clement, J. S.; Mabry, T. J.; Wyler, H; Dreiding, A. S. Chemical review and evolutionary significance of the betalains. In *Caryophyllales*; Springer, 1994; pp 247−261.
(140) Ravid, J.; Spitzer-Rimon, B.; Takebayashi, Y.; et al. GA as a regulatory link between the showy floral traits color and scent. *New Phytol* **2017**, *215*, 411−422.
(141) Kaminaga, Y.; Schnepp, J.; Peel, G.; et al. Plant phenylacetaldehyde synthase is a bifunctional homotetrameric enzyme that catalyzes phenylalanine decarboxylation and oxidation. *J. Biol. Chem.* **2006**, *281*, 23357−23366.
(142) Koeduka, T.; Fridman, E.; Gang, D. R.; et al. Eugenol and isoeugenol, characteristic aromatic constituents of spices, are biosynthesized via reduction of a coniferyl alcohol ester. *Proc. Natl. Acad. Sci.* **2006**, *103*, 10128−10133.

(143) Kolosova, N.; Gorenstein, N.; Kish, C. M.; Dudareva, N. Regulation of circadian methyl benzoate emission in diurnally and nocturnally emitting plants. *Plant Cell* **2001**, *13*, 2333−2347.
(144) Fenske, M. P.; Nguyen, L. P.; Horn, E. K.; Riffell, J. A.; Imaizumi, T. Circadian clocks of both plants and pollinators influence flower seeking behavior of the pollinator hawkmoth Manduca sexta. *Sci. Rep* **2018**, *8*, 1−13.
(145) Zeng, L.; Wang, X.; Kang, M.; et al. Regulation of the rhythmic emission of plant volatiles by the circadian clock. *Int. J. Mol. Sci.* **2017**, *18*, 2408.
(146) Fenske, M. P.; Hewett Hazelton, K. D.; Hempton, A. K.; et al. Circadian clock gene LATE ELONGATED HYPOCOTYL directly regulates the timing of floral scent emission in Petunia. *Proc. Natl. Acad. Sci.* **2015**, *112*, 9775−9780.

https://doi.org/10.1021/acs.est.2c07733
Environ. Sci. Technol. 2023, 57, 6415−6424