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SYMPOSIUM

Plant-Pollinator Interactions in the Anthropocene: Why We Need a Systems Approach

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Synopsis Animal-mediated pollination is one of the most ecologically and economically important mutualisms and serves as a remarkable example of cross-kingdom communication and coevolution. Unfortunately, pollinators, plants, and the interactions between them are threatened in the Anthropocene. While pollination emerges from interactions across biological scales, existing research and expertise have developed in distinct silos reflecting traditional fields of study such as ecology, plant physiology, neuroethology, etc. This forward-looking review and perspective is a culmination of the “Plant-pollinator interactions in the Anthropocene” symposium at the 2025 Society for Integrative and Comparative Biology meeting, which collected expertise across these disciplinary silos to identify pressing questions our community needs to tackle in the next decade. In this perspective piece, we argue that an integrative, organismally informed systems approach is critical to unraveling the complexity of how plant-pollinator relationships are impacted by dynamic anthropogenic stressors. Specifically, this calls for an intentional and iterative integration of holistic modeling studies with empirical studies. Modeling the emergent properties driven by organismal interactions in pollination systems can identify impactful variables; this in turn should drive design of empirical studies that elucidate how organisms respond to changing environments in the context of those impactful variables, feeding back into improved models. Repetition of this process will allow better predictive power over pollination stability in changing landscapes. Finally, we consider both existing barriers to this integration, as well as emerging opportunities (such as new technologies) that can help bridge across traditional fields.

Introduction

Animal-mediated pollination is one of the most ecologically and economically important mutualisms, simultaneously connecting trophic levels across geographies and providing food for billions of people (Klein et al. 2007; Reilly et al. 2020). It is a remarkable example of cross-kingdom communication, with plants and animals evolving mutually beneficial interactions (Bronstein 2015). The biological stakeholders in these interactions extend beyond plants and their pollina-

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tors, from microbial partners in soil ecosystems, to the beneficiaries along trophic cascades. Unfortunately, pollinators, plants, and the interactions between them are threatened in the Anthropocene. This combination of risk and importance lends urgency to furthering our understanding of pollination biology (Schweiger et al. 2010). While pollination emerges from interactions across biological scales, existing research and expertise generally occurs in distinct silos reflecting traditional fields of study such as ecology, plant physiology, neuroethology, etc. This forward-looking review and perspective is a culmination of the "Plant-pollinator Interactions in the Anthropocene" symposium at the 2025 Society for Integrative and Comparative Biology meeting, which collected expertise across disciplinary silos to identify pressing questions our community needs to tackle in the next decade. The goal of this collaborative perspective is to locate questions and approaches that will allow us to better predict responses of plant-pollinator interactions to dynamic anthropogenic stressors. Broadly, we argue for the urgency of a systems approach that integrates across scales of biological organization (e.g., from molecular mechanisms to dynamics of species interactions) and research fields (e.g., from neurobiology to community ecology). This organismally informed systems approach should couple modeling and empirical studies to develop a holistic understanding of pollination biology. Computational or modeling approaches allow an investigation of how inter-organismal interactions impact pollination networks (and the associated downstream impacts), identifying which of the variables representing organismal physiology and behavior strongly influence emergent networks and their dynamics. This in turn allows for targeted design of experimental studies to improve how those biological variables are computationally represented. With iteration, this approach should systematically improve our understanding of how pollination systems respond to changing environments. We illustrate the importance of this organismally informed systems approach using two examples of plant-pollinator responses to global change factors: (1) climate change and (2) agricultural landscape transformation.

The interconnected scales at which organisms live drive complexity in plant-pollinator systems

More than a decade ago, Mayer et al. (2011) collated input on pressing questions from 60+ pollination biologists. These questions were organized into thematic areas that also reflected the importance of diverse expertise, including the role of pollinator behavior, expanding understanding of plant-pollinator assemblages, expanding geographic distribution of pollination studies, and conservation. The authors articulate that these large-scale research topics are challenging to address with a single experimental study. In practicing science, we reduce the scale and scope of experiments to better discern relationships between experimental variables and measured responses. However, in reality, organism survival and behavior emerge from interactions between the physiological subsystems that influence inter-organism interactions, resulting in reliably variable contexts (i.e., the staggering phenotypic diversity within and across species). Moreover, these biotic interactions occur in environments that are enormously variable in both space and time (Fig. 1).

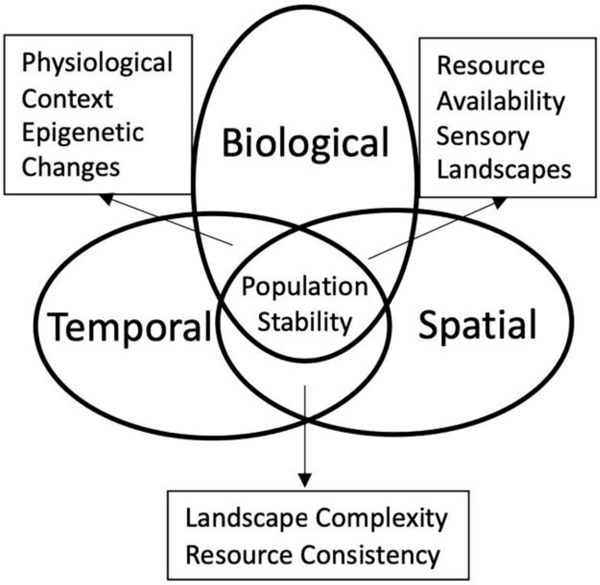

Fig. 1 Understanding the intersection between temporal, spatial, and biological scales is needed for understanding how disruptions at any of those scales could impact plant-pollinator population stability.

Take, for example, diurnal patterns of interactions in plants and pollinators; circadian variability in floral scent production by plants requires metabolic pathways that synthesize volatiles to be linked to a molecular circadian clock (Fenske and Imaizumi 2016). Similarly, circadian variability in odor detection in pollinators necessitates that odor receptors are also linked to a molecular clock (reviewed in Lou et al. 2024). The integration of this clock with scent production and scent detection may result in variable pollinator and/or florivore attraction throughout the circadian cycle (Fig. 2). Temporal scales range from patterns of rapid stimulus-response, to within-lifetime physiological changes, to intergenerational effects. These response time scales are regulated by diverse molecular and physiological mechanisms in both the brain and peripheral systems (Rittschof and

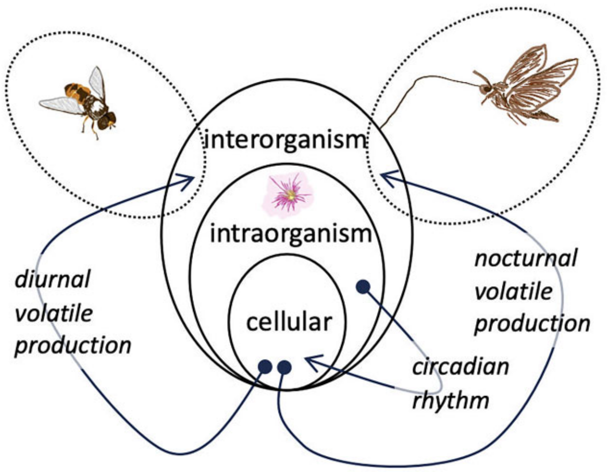

Fig. 2 Example of how changes in intraorganismal functioning can impact plant-pollinator interactions. Petunia flower volatile production shifts along a circadian cycle (Fenske et al. 2015), which could influence which pollinators are attracted to flowers at different times of day (or night). Additionally, diel scent variation can impact the attraction of florivores, such as crickets (Kessler et al. 2015). In agricultural contexts—pesticide application guidelines are framed around diurnal pollination exclusively, even though nocturnal pollinators contribute significantly to yield in many fruits, including apples and blueberries (Cutler et al. 2012; Robertson et al. 2021); thus, not considering the full biological scale of crops could drive pollination limitation and yield decreases.

Hughes 2018; Stein et al. 2018). From an ecological perspective, investigating pollinator-floral interactions on a short time scale will provide valuable information about discrete relationships. However, longer time scales of observation are necessary to reveal seasonal network dynamics (Fig. 3). Environmental variation across space (e.g., from microhabitat variation and resource patchiness to habitat regimes across species ranges) can also significantly affect plant-pollinator interactions. For example, at small spatial scales, variation in temperature and solar radiation can affect both floral nectar production and pollinator foraging patterns (e.g., *via* behavioral thermoregulation) (Souza-Junior et al. 2019; Malovrh et al. 2024). On larger spatial scales, turnover in regional species pools and shifts in home ranges can drive community diversity and evolutionary dynamics. Recent conceptual and empirical advances in landscape ecology (Eigenbrod et al. 2011; Davies and Gray 2015; Zuckerberg et al. 2020) may be particularly relevant for better understanding how spatial environmental complexity affects these organismal and community processes underlying plant-pollinator interactions. In addition, the foraging behavior of pollinators, i.e., the underlying linkage of pollination networks, is spatially variable, with some species travelling substantially shorter distances across landscapes (Fig. 4).

An organismally informed systems approach is needed to elucidate emergent phenomena in plant-pollinator interactions

The complexities of plant-pollinator communities derive from the co-dependence and interactions between species with vastly different life histories whose growth, physiology, and reproduction operate on different temporal and spatial scales. As such, the detailed analysis of pairwise individual interactions between key players of the system has the potential to bring considerable insight into the emergence of more complicated, higher-level patterns (Camazine et al. 2020).

A tighter integration of animal behavior and plant ecology provides helpful insights (Waser and Price 1998). At the level of individual organisms, pollinators mediate plant reproduction by moving pollen to stigmas within and between individual flowers. The null hypothesis might be that pollinators move randomly among flowers, or among individual plants or species, so that pollinators, and thus their service, are diffused across a landscape (Lonsdorf et al. 2009). However, studies in animal behavior show that fine-scale variation and floral pollinator decisions lead to more complex patterns of pollinator service. For instance, many species of bees, butterflies, nectarivore birds, and bats use foraging routes to revisit familiar plants (Lihoreau et al. 2013). These routes are often the result of optimization processes by which animals maximize foraging efficiency based on learning and memory (Lihoreau et al. 2012; Woodgate et al. 2017). Moreover, pollinators' ability to learn effective motor routines to allow pollen extraction from different floral morphologies could affect pollination success (Mayberry et al. 2024). Shifts in foraging behavior can also result from pollinator interactions with species outside the plant-pollinator binary. For example, nectar microbes can cause shifts in bumblebee foraging behavior once learned association between odor and gustatory cues are learned (Schaeffer et al. 2019). Bumblebees will modulate their foraging behavior according to perceived predation risk (Lenz et al. 2012). And the presence of predatory ants increases the likelihood that pollinating wasps instead of non-pollinating wasps will visit figs (Wang et al. 2014). A mechanistic analysis of plant-pollinator systems through consideration of these predictable foraging patterns may have far-reaching implications at higher organizational levels.

At the population level, predicting pollen dispersal through pollinators' movements may help to predict patterns of plant reproduction and outcrossing in turn (Ohashi and Thomson 2009). These predictions could help us better understand plant mating systems and

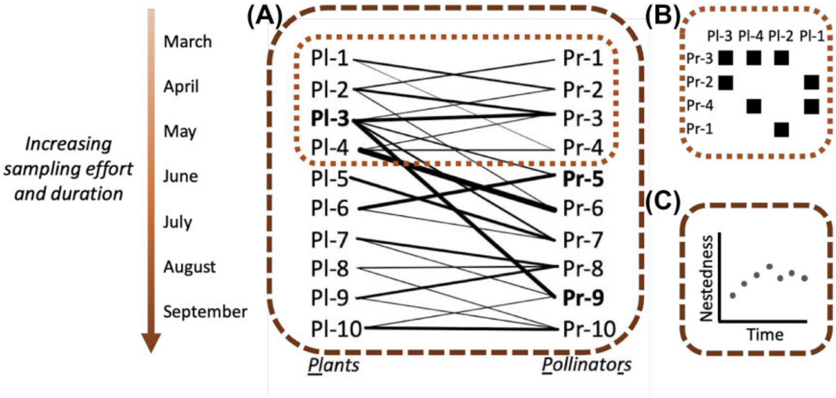

Fig. 3 Short time scales of sampling are inadequate to understand interaction network dynamics. (A) An interaction network for a community comprising 10 plant species (Pl-1 through Pl-10) and ten pollinator species (Pr-1 through Pr-10) ordered according to the onset of flowering or foraging. Lines connecting species represent interactions of varying strengths, indicated by line thickness. The subset of the network that could be detected with a March–May sampling period is enclosed in the dotted outline, whereas the full network that could be detected with a March–September sampling period is enclosed in the dashed outline. (B) The interaction data from the short sampling period may be most useful for calculating static estimates of network properties (such as nestedness, where filled cells in the matrix indicate that a given plant and pollinator species interact). (C) The interaction data from the longer sampling period could be dissected to examine temporal variation in network properties (such as nestedness, where each point in the plot represents a measure of how nested the network is).

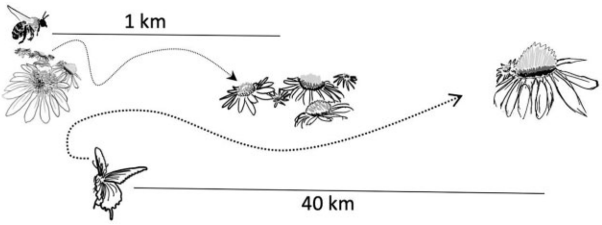

Fig. 4 The spatial characteristics of pollinator foraging ranges will impact gene flow in plant populations. There are established examples of efficacious pollen transfer by both butterflies and bumblebees (Parrey et al. 2021; Burgin et al. 2023). As bumblebees are central-place foragers, their pollen distribution ranges are constrained by the flight distances of workers around their nest location. However, the foraging range of some butterfly species can be substantially larger (Suchan et al. 2019), which will create larger genetic distribution networks. The spatial patterns of gene flow in plant pollinations are necessarily dependent on the foraging dynames of the facilitating pollinator species.

population genetic diversity, with implications for plant ecology and evolution (e.g., (Karron et al. 2009)). Likewise, elucidating conditions under which plant species could be maintained will have conservation implications. Predictions of crop yields based on pollinators' behavior would be beneficial for agriculture (Lihoreau et al. 2024).

At the community level, pollinator preferences and learning bring new insights into species interactions not only from the perspective of plant-pollinator network structure and resilience (e.g., Bascompte and Scheffer 2022), but also how these translate into fitness benefits or costs. This is because pollinator movements among species can lead to conspecific pollen loss and heterospecific pollen deposition, which has implications for biodiversity maintenance (Wei et al. 2021). Moreover, pollinator movements not only distribute pollen, but also serve as vectors for both pollen- and pollinator-pathogens. Integrating pollinator movements into current bipartite interaction networks has the potential to add a spatial dimension to studies of pathogen spread within a plant community via their shared pollinators (Proesmans et al. 2021). This will help us better understand the potential large-scale effects of plant pathogen on maintenance of plant biodiversity and food security (Fetters et al. 2022; Fetters and Ashman 2023). Additionally, plant pathogens may represent a direct threat to pollinator health, as there is at least one documented incidence of a plant virus jumping into an animal (honeybee) host (Li et al. 2014). Finally, pollinator movements will contribute to the distribution of pollinator pathogens—a phenomenon that is particularly problematic in networks with managed-bee species (and their commensurate disease loads) (as reviewed by Graystock et al. 2016).

Systems approaches will improve our understanding of plant-pollinator responses to anthropogenic stressors

A key goal in the study of plant-pollinator interactions is understanding how anthropogenic stressors affect fitness of plants, pollinators, and their interactions (Nicolson and Wright 2017). However, the complexity of these stressors drives several core challenges. First, while focus is often placed on organismal tolerance limits (e.g., thermal minima and maxima), all global change stressors can have significant effects at levels well below immediate mortality effects (e.g., "sublethal" effects of pesticides (Colinet et al. 2015)). Second, stressors do not act in isolation and there is robust, widespread evidence for stressor synergies and context-dependence (Goulson et al. 2015; Harper et al. 2016; Reitmayer et al. 2019; Walker et al. 2019). For example, climate change is modulating daily temperature regimes against a backdrop of constant photoperiod (Walker et al. 2019). However, misalignment of temperature and photoperiod fluctuations can disrupt *Drosophila* circadian networks (Harper et al. 2016). These patterns suggest that the impacts of a stressor depend on the organism experiencing them; what is a strain on one organism may not impact another, a phenomenon that is true within and across species boundaries. Finally, many impacts are delayed, manifesting either in later life stages or accumulating over generations (e.g., stress memory within and across generations) (Philips et al. 2017; Zhang and Tian 2022).

Together, these emerging challenges highlight the importance of utilizing organismal physiology studies of both plants and their pollinators to identify which properties of species exhibit sensitivity versus resilient to anthropogenic change. These properties can then be incorporated into empirical and modeling studies of communities. We argue that this organismally informed systems approach combining insights from organismal biologists, landscape and community ecologists, and ecological modelers provides an ideal framework for understanding and predicting the complex effects of anthropogenic change. This will lead to a better understanding of the consequences for ecological interactions and ultimately individual fitness and ecosystem stability (Fig. 5). We focus on two specific aspects of global change below (climate change and agricultural intensification) to emphasize how an organismal perspective can help us understand the subtle, interactive, and time-delayed effects of stress. This is not an exhaustive review of current stressors, but rather intended to illustrate the importance of accounting for emergent phenomena in the study of plant-pollinator interactions.

Example 1: climate change

Climate change is affecting the physiologies, morphologies, and phenologies of both plants and pollinators (Hegland et al. 2009; Scaven and Rafferty 2013; Forrest 2015; Manincor et al. 2023). These direct, organismal-level effects of warming, drought, and other climatic stressors can scale up to restructure plant-pollinator interactions and alter the costs-benefit structure of mutualisms. In this section, we highlight some of the immediate and delayed effects of climatic change on flowering plants, insect pollinators, and their interactions to illustrate how incorporating temporal perspective into a systems approach can be useful for understanding sublethal stress from organismal to network levels.

On the plant side, the effects of warming and drought on floral traits are among the most immediate and have obvious effects on interactions with pollinators. For example, annual wildflowers subjected to experimental drought produce smaller flowers with more concentrated nectar over the span of a few weeks, causing bees to preferentially visit flowers on unstressed plants (Rose-Person et al. 2024). In addition to this type of rapid physiological response, delayed effects of stress can also influence floral resource availability to pollinators. Within their lifespans, individual plants may flower for shorter periods under warmer climates, thus narrowing the window of time for pollinator foraging (Manincor et al. 2023). If plants produce fewer and/or lower-quality seeds under heat or soil moisture stress (Manincor et al. 2023), plant population sizes and therefore floral resource availability may decline in subsequent generations. On the other hand, seeds developed under warmed conditions can have increased germination rates due to maternal effects (Dwyer and Erickson 2016). Such transgenerational effects and their consequences for interactions with pollinators are a prime example of where an organismally informed systems approach could elucidate emergent impacts of climate change.

Similarly to plants, insect-pollinator responses to climatic stress range from immediate behavioral adjustments to delayed effects resulting from physiological damage. Bees are known to modify their foraging behavior under warming, with individual bumblebee workers making fewer trips to artificial flowers at temperatures of just 32°C (Gérard et al. 2024). Environmental stressors, such as climate warming, can also affect insect pollinator sensory perception and cognition, affecting downstream behavioral performance and interactions with flowers (Klein et al. 2017). Heat waves can affect fertility of male bumblebees by reducing the viability of their spermatozoa, a sublethal effect that could accelerate population declines over generations (Campion et al. 2023). These direct effects on pollinators are likely to affect pollination success of plants, ultimately feeding back to alter selection on floral traits and mating systems (Eckert et al. 2010).

Direct impacts on plants are equally likely to disrupt pollination success. For example, approximately 10% of flowering plants house pollen in poricidal anthers (Russell et al. 2017), including agriculturally vital crops such as tomato, potato, and eggplant (Cooley and

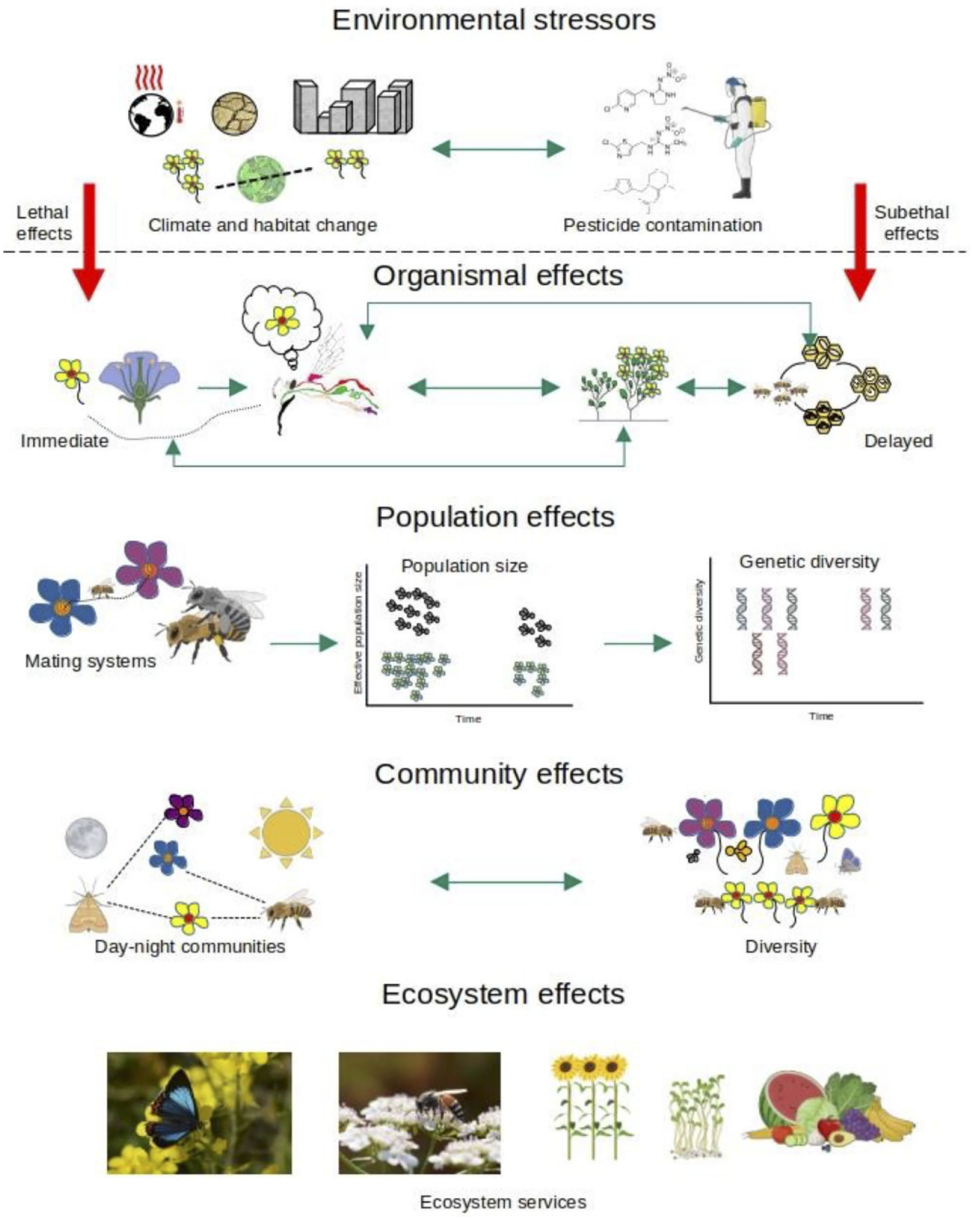

Fig. 5 Conceptual figure depicting some examples of anthropogenic effects on systems biology. Environmental stressors such as climate and habitat change (warming, drought, urbanization, and habitat fragmentation), and pesticide contamination can independently or synergistically (green double-headed arrow) affect either lethally or sublethally (red arrows) across systems biology scales such as organismal, population, and communities. Organismal effects include effects across time (immediate and/or delayed) in both plant, and pollinator physiology, behaviors, and development, which impacts population-level mating strategies, effective population sizes, and genetic diversity. Stressors' effects can be exacerbated at the community scale too, where different communities can be impacted differently. These can directly and indirectly affect ecosystem functions that reduce the capabilities of providing the most efficient ecosystem services to humans. In this figure, red arrows indicate negative effects of stressors on different systems biology; and green arrows represent interactions between different biological processes within scales (figure not to scale, created using biorender.com).

Vallejo-Marn 2021). However, the function of poricidal anthers relies critically on the turgor pressure provided by the plant cell's vacuole against the cell wall to maintain cell rigidity and structural integrity (Alvord et al. 2024). Reductions in turgor may cause the pollen cavities within the poricidal anther to collapse under the weight of the pollinator, while increases in turgor may render the poricidal anther too stiff for the pollinator to vibrate and collect pollen. Temperature and water availability are known to impact the physiological regulation of turgor pressure (Coussement et al. 2021); however, the effects of climate change on poricidal anther turgor is an open question. When we expand the biological scale of this problem past the plant and to the "buzz" pollinators using indirect flight muscle activation to shake pollen from poricidal anthers (Buchmann and Jankauski 2024), the impact of climate change on that flight muscle physiology also becomes relevant. Increased ambient temperature might impact the amount of energy needed to "buzz" individual flowers, or affect thermoregulation strategies (Sepúlveda-Rodríguez et al. 2024). Buzz pollination illustrates how changes in climate can simultaneously impact both plants and pollinators, with potential effects on pollination services.

At the network level, climatic stress alters plant-pollinator interactions via two (non-exclusionary) primary paths. First, by causing gains or losses of species to a community, resulting in novel interaction formation, i.e., interaction turnover. Second, by causing changes within the existing composition of a community that result in interaction rewiring (Fründ 2021). Just as effects on plants and pollinators span timescales, network-level effects of climate change are likely to vary from rapid to gradual. Immediate trait-based changes in response to warming and drought, such as altered quality and quantity of floral rewards and subsequent pollinator foraging adaptations (Valdovinos et al. 2013) would be expected to affect interactions within communities first. As rewiring of pollination networks occurs, transgenerational effects of climatic stress would then be expected to either exacerbate or ameliorate the population declines that lead to interaction turnover. Complex, cascading effects are likely. For example, temporary removal of dominant bumblebees from natural communities in subalpine meadows of the Rocky Mountains caused behavioral changes in the remaining pollinator community, resulting in reduced foraging specialization and likely reduced plant reproduction (Brosi and Briggs 2013). We might expect temporary removal to mimic local extinction events; however, Hiraiwa and Ushimaru found that loss of pollinator functional diversity was more important that species diversity—implying that predicting the effect of species loss is a challenging endeavor (Hiraiwa and Ushimaru 2024). By understanding how immediate, organismal-level responses scale up to longer-term community-level responses, we can start to build a framework for predicting the effects of climate change on interaction networks (Fig. 5).

Example 2: agricultural systems

The transition to industrialized agriculture that accompanied the industrial revolution made growing and harvesting crops more efficient via mechanization, facilitating a shift in workforce from farms to factories. This transition drove ecological and landscape changes. Since the mid-20th century, agricultural landscapes in the US, for example, have become increasingly simplified (e.g., monocultures) and reliant on chemical inputs (e.g., synthetic fertilizers and pesticides) (Meehan et al. 2011), as well as being maintained and harvested with fossil fuel-burning machines (Zabel et al. 2019). Large-scale monocropping came with huge losses of shrublands, grasslands, and temperate forests. These habitat losses in turn drove biodiversity declines, which are particularly pronounced for pollinator species (Burkle et al. 2013) and the plant populations they support, leading to trophic instability (Canelas and Pereira 2022).

Because monoculture crops are phenologically homogenous, they will often create resource-poor landscapes for pollinators. In addition, both regular tilling and soil compaction from heavy machinery reduce nesting habitat for many solitary bees (Christmann 2022). Given losses of native pollinator populations, industrial agriculture is therefore reliant on commercial beekeeping operations to supply pollination services during transient mass-bloom events (Aizen et al. 2009). Despite the domestication of some pollinators, both wild and managed species remain crucial for agriculture. Overall, about 75% of flowering plants and approximately 35% of food crops rely exclusively on pollinators (Eilers et al. 2011; Nicholls and Altieri 2013; Sluijs and Vaage 2016). This includes a wide range of crops that are essential for both food supply and agricultural economy such as fruits (apple, orange, strawberry), vegetables (tomato, cucumber, pepper), nuts (almond, walnut), and oilseeds (canola, sunflower) (Losey and Vaughan 2006; Klein et al. 2008; Aizen et al. 2009; Gallai et al. 2009). Managed honeybee and bumblebee populations alone are an inadequate and inefficient solution. Earlier in this century, the value of wild bees in our intensively managed agricultural landscapes was estimated at $150 billion US dollars in pollination services (Gallai et al. 2009). Short-term pollination services were more recently valued at 1 trillion US dollars (Lippert et al. 2021), with visits from wild, non-bee pollinators making up 39% of overall activity in crops (Rader et al. 2015). In general, wild pollinators have been found to pollinate more effectively, visit more often, and contribute to enhanced fruit sets (Winfree et al. 2008; Garibaldi et al. 2013).

In addition, the presence of wild pollinators can modify honeybee foraging behavior; in some agrosystems this results in more cross-pollination and increased yields (Mallinger and Gratton 2014; Osterman et al. 2023). While not all studies documenting this effect have established a mechanism for their findings, work by Eeraerts et al. (2020) showed that increased bumblebee and wild bee density resulted in a higher probability of row changes by honeybees foraging in a cherry orchard—resulting in higher rates of cross-pollination due to the orchard management practice of planting one cultivar type per row. "Ecological intensification" of agricultural landscapes, i.e., incorporating strategic wildflower strips, can boost abundance and species richness of wild insects (Campbell et al. 2019). In addition to anticipated pollination service benefits, the wildflower strips can attract natural enemies of pest species and reduce crop damage Blaauw and Isaacs 2015, Pollier et al. 2019). However, the agricultural and ecological benefits of this strategy are not universally realized. A recent meta-analysis did not find impacts of wildflower intensification on biological control, and that yield benefits were constrained to landscapes with intermediate natural habitat cover (Grab et al. 2018). Additional complexity arises in conservation contexts, as wildflowers in close proximity to agricultural fields can accumulate neonicotinoids and serve as a chronic exposure pathway for wild pollinators (Boti´as et al. 2015). These results illustrate that balancing the complex trade-offs for sufficient crop yield, opportunity cost of land use, and pollinator health would benefit from using a systems approach to understand the complete suite, both direct and indirect, of stressors that agricultural systems place on plant-pollinator networks.

Direct effects of pesticides cross physiological system, generational, and species boundaries

Within the agricultural setting, pesticides have a particularly complex role in mediating plant-pollinator interactions. While pesticides can control outbreaks that could decimate crop yields, they are also capable of reducing yield through disruption of pollination services (Stanley et al. 2015). Pesticide exposure is widespread among insect pollinators globally and has important impacts on performance, survival, and reproduction (Goulson et al. 2015). Bees and other insect pollinators can be exposed to insecticides through direct contact (e.g., via foliar sprays) or through ingestion of contaminated food resources (e.g., nectar and pollen contamination resulting from seeds treated with systemic insecticides). Neonicotinoids are a particularly important and well-studied class of insecticides that are agonists of nicotinic acetylcholine receptors (nAChRs) in the insect central nervous system. Neonicotinoids have increased dramatically in global use since their introduction in the mid-1990s, and are regularly encountered by pollinators, as illustrated by a global survey of honey from *Apis mellifera* colonies finding the vast majority (∼75%) of samples containing at least one neonicotinoid pesticide (Mitchell et al. 2017) (Fig. 5). There is now widespread evidence that exposure to neonicotinoids can negatively affect colony growth in social pollinators such as bumblebees (Whitehorn et al. 2012), leading to long-term population declines (Janousek et al. 2023).

The mechanisms linking direct physiological impacts of pesticides to impaired growth and population declines in pollinators, especially non-bee pollinators, are less well understood, and reflect the complexity of organismal responses to these insecticides. Many of neonicotinoids' key effects occur at levels well below "lethal" exposure. Neonicotinoids can disrupt physiological and neural processes (e.g., sensory processing, cognitive performance, and metabolism) that in turn impair key aspects of organismal performance and behavior such as foraging, nursing, and thermoregulation at levels well below acute lethal toxicity (Stanley et al. 2015; Crall et al. 2018; Siviter and Muth 2022; Tatarko et al. 2023; Paoli and Giurfa 2024).

In addition to these direct effects, many of the critical impacts of neonicotinoids occur through interactions with the secondary stressors (i.e., synergistic effects) (Siviter et al. 2021). For example, in bumblebees (*Bombus* spp), the effects of imidacloprid (a common neonicotinoid) on locomotor activity depend on body temperature; imidacloprid has strong negative effects on activity at low temperatures (Easton-Calabria et al. 2023), but relatively limited effects at higher temperatures. This physiological interaction at the scale of individual organisms leads to a complex emergent pattern at the colony scale: larger colonies, where average body temperature is higher (as a result of social thermoregulation) are more robust to imidacloprid exposure than smaller, younger colonies (Easton-Calabria et al. 2023).

While application regulations are intended to limit lethal exposure to pollinators (IPM 2025), they do not adequately account for synergistic effects between pesticides and other agrochemicals (e.g., fungicides) or differential toxicity of pesticides across species (Thogmartin et al. 2017; Tosi and Nieh 2019; Wade et al. 2019; Bloom et al. 2021). For example, coapplication of the fungicide propiconazole and the neonicotinoid flupyradifurone synergistically increases honeybee mortality (Tosi and Nieh 2019).

In addition to immediate effects on organismal performance, there is growing recognition that pesticide exposure can have delayed effects (both within and across generations), also known as carryover effects. In solitary bees (*Osmia lignaria*), for example, neonicotinoid exposure can have important delayed effects; exposure to imidacloprid as larvae in 1 year reduced reproductive success when those bees emerged as adults in the subsequent year (Stuligross and Williams 2021). Delayed effects can also be driven by complex biological feedbacks; in honeybees (*Apis mellifera*), direct mortality of foragers reduces long-term colony performance by inducing premature behavioral development in workers (Perry et al. 2015). The temporal dynamics of neonicotinoid exposure (e.g., multiple exposures through an organism's lifespan) may have important implications for sensitivity (i.e., through priming or cumulative exposure increasing susceptibility) and represent an important understudied area. As a whole, the now extensive literature on neonicotinoids and pollinators highlights the remarkable diversity of impacts of these compounds across scales of biological organization and time, underscoring the importance of an integrative, organismal perspective in better understanding pollinator health.

Indirect effects are elucidated by considering impacts of agriculture across biological scales

Agricultural environments can also indirectly disrupt pollination services by disrupting plant-pollinator communication. Pollination, while a main desired outcome of plant-pollinator interactions for both the plants and us human beneficiaries, is (in animal-pollinated plants) the result of a complex cross-species conversation between plants and animals. As such, it is dependent on a combination of signals and signal detection (sensory) systems, primarily plant signals and animal perception (Chittka and Thomson 2001). Agriculture, urbanization, and associated habitat change present unique challenges to these signal-receiver interactions, as they modify signal abundance and the ambient environment, both of which can influence signal detection. For example, a monoculture of *Brassica rapa* will produce more floral volatiles (such as farnesene, linalool, and pinene [Blight et al. 1997]) than a polyculture planting. This monoculture may attract a larger number of pollinators from greater distances (Sprayberry 2018), or may make it difficult for pollinators to assess and target flowers most in need of visitation (from both the nectar production and pollination services prospective) (Gavini et al. 2021). Moreover, floral odors themselves are vulnerable to modification in agricultural environments due to both “subtractive” and “additive” odor pollution. Farm machinery running diesel creates an environment that degrades floral odor signals via reactions between floral odorants and nitrous oxides in diesel exhaust (Girling et al. 2013). This subtractive degradation of floral odors is sufficient to decrease both honeybee and bumblebee responses to learned scents (Girling et al. 2013; Saunier et al. 2022). In addition, pesticides such as fungicides can themselves have strong odors, additively changing the odor landscape. Fungicide odor has been shown to be disruptive to bumblebee foraging behavior in multiple contexts (Sprayberry et al. 2013; David et al. 2022; Yousry et al. n.d.). Finally, flowers grown under fungicide conditions can have modulated floral odor blends, which in turn can impact pollinator attraction to those floral resources (Voß et al. 2023). These signal detection challenges are exacerbated by neonicotinoid exposure, as this can reduce the accuracy of odor encoding in an insect brain (Andrione et al. 2016). While much of this work needs to be ground truthed with direct field testing, recent work has found that presence of fungicides decreases wild bee visitation rates (Bloom et al. 2021). Thus, olfactory plant-pollinator communication can be inhibited by modifications to quantity, quality, and composition of floral signal, as well as modifications to pollinator signal detection ability in agricultural and urban landscapes.

At local spatial scales, consideration of how agriculture changes visual landscapes needs to be considered. For example, habitat change can modify shade cover and alter the quantity and wavelengths of light reaching flowers (Endler 1992), which can influence their detectability and quality assessment by visually oriented pollinators (Finnell and Koski 2021). This may be particularly important for plant-pollinator interactions dependent on long and short wavelength signals, as changes in shade cover have strong effects on relative proportions of long wavelengths of light (Endler 1992), and the relative ease of detection of reds and UV signals (Endler 1992; Obara et al. 2008).

The examples above center around two different sensory modalities: chemical and visual. However, most communication is multi-modal, meaning it contains signal information in multiple sensory modalities. Plant-pollinator interactions are an excellent example of this, as many plants produce both volatiles and visual signals to attract their pollinators; and pollinator sensory biases, in both vision and olfaction, influence which flowers pollinators visit (Kantsa et al. 2018). Pollinator color preference can change with the presence of different olfactory cues in sex-specific ways, as illustrated by the swallowtail butterfly *Papilio xuthus* (Yoshida et al. 2015). Furthermore, these signals are often temporally variable, both across seasons and throughout the day (Abe and Kamo 2003; Fenske and Imaizumi 2016). The temporal variability of sensory signals produced by flowers may result from the complex suite of species interactions that can influence plant fitness. For example, scent can attract both pollinators and florivores (Theis and Adler 2012)—creating a potential push-pull dynamic in selective forces on scent production. In *Cirsium arvense* flowers, circadian fluctuations in scent emission peak when pollinators are active, and are lowest when florivores are active (Theis et al. 2007). In addition to temporal signal variability, it is likely that signal detection by receiver sensory system also changes with season and time of day, though this has been comparatively rarely studied (but see Eilerts et al. 2018; Hirzel et al. 2024). Thus, a more complete understanding of how multimodal integration is impacted by spatiotemporal signal variability is a critical next step in both neuroethology and sustainable agriculture research.

Organismally informed systems biology is crucial to understanding plant-pollinator relationships at scales that are relevant to learning about their resilience to human disruption

In this review, we have presented why an organismal approach is crucial to building an understanding of plant-pollinator relationships that is robust enough to help us predict responses to anthropogenic stressors. Organisms themselves are complex systems whose behavior and physiology are emergent properties of interactions between system components. The plant-pollinator relationships that are a foundation of trophic stability are in turn emergent properties of how (at a minimum) two organisms respond to each other in dynamic environments.

Variability across studies is not the only source of ambiguity in our understanding of plant-pollinator relationships. Additionally, there is important natural physiological and behavioral variability in pollinators. In honeybees and bumblebees, this variability shapes division of labor (Pankiw and Page 2000) and determines the performances of individuals in given tasks (Chittka et al. 2003). In butterflies, sexual dimorphism in color sensitivity (potentially due to a combination of sexual selection and natural selection) (Arikawa et al. 2005; McCulloch et al. 2016) and pollen consumption (Boggs et al. 1981) may facilitate within-species variation in pollinator services. Similarly, pollinators show important variability in their susceptibility to environmental stressors (insecticides, malnutrition, etc.), both within and between species and taxonomic groups. Measuring this variability and studying its evolution in response to stress exposure might help better understand the risks for populations and their potential of resilience, in a much more powerful way than just looking at means/norms of reaction (Cabirol et al. 2023). A systematic analysis of variance could, for instance, help identify tipping points below which populations can tolerate stress and above which action should absolutely be taken. Once again—to fully understand the impact of this kind of variability, we need targeted studies that cross species boundaries and operate at large enough temporal and spatial scales to interrogate impacts on plant-pollinator networks.

Barriers and bridges to integrative organismal biology of plant-pollinator relationships

The importance of organismal approaches to ecology and behavior is easy to accept, but difficult to enact because it requires investigations that manifest at large scales: disciplinary, spatial, and temporal. Large-scale scientific studies have inherent barriers, and this review hopes to elucidate those barriers so that plant-pollinator biologists can build structures to overcome them.

Understanding plant-pollinator interactions requires cognizance across biological scales both within and between organisms. This complexity demands multidisciplinary expertise—a challenge for researchers working in isolation, but easily overcome with targeted collaborative teams. For example, combining the skills of a thermal physiologist, neuroethologist, plant physiologist, and pollination network ecologist could enable studies that address the gaps in our current understanding of how climate warming will impact phenological stability in plant-pollinator interactions. However, a single research team is unlikely to have the resources needed to investigate interactions at necessarily large temporal and spatial scales. Emerging technologies such as advances in computer vision and deep learning of image analysis offer pathways to overcome this limitation (Høye et al. 2021). Tools like image-based monitoring systems can collect data more efficiently across time and space, reducing dependence on traditional labor-intensive methods that utilize human observers. These technologies can also capture interactions between flowers and pollinators, as compared to isolated assays such as vane traps or plant surveys. While automated monitoring techniques offer great potential for monitoring plant-pollinator interactions (Ratnayake et al. 2021), these emerging tools require significant expertise (e.g., in computer vision, deep learning, etc.) that is less common in biology and ecology. Facilitating broader adoption of these techniques for plant-pollinator research will thus require expanding training and teaching opportunities in these skills, as well as emphasis on accessibility (rather than just availability) of techniques.

Even with the increased efficiency of data collection promised by emerging technologies, iterating studies across geographies is likely too much for a single collaborative team. Creating standardized methods and protocols for plant assays and pollinator monitoring could produce datasets that are directly comparable across studies. This comparability would open the door to more robust meta-analyses, delivering deeper insights into ecological patterns and processes.

While the presented strategies will significantly enhance data collection, neither entirely address the challenge of elucidating phenomena that emerge from the integration of biological, spatial, and temporal scales. For example, camera traps distributed throughout a large field site can capture both a large temporal distribution of data for monitored plants, and a large spatial distribution of pollinator species' occurrence, but cannot provide large-scale temporal data for an individual pollinator or measure spatial distribution of an individual plant's pollen transfer. However, a systems-biology approach allows us to leverage organismal data at relevant biological scales to inform computational models in order to illuminate potential emergent patterns. These emergent patterns can in turn be used to design targeted empirical studies, the results of which can refine models. For example, previous network models have indicated that generalist versus specialist pollinators can influence pollination-network dynamics; and that behavior such as adaptive foraging in generalist pollinators has potential impacts on maintenance of biodiversity (Valdovinos et al. 2013). At a pollinator lever, radar tracking allows us to collect spatial and temporal data on the foraging patterns for a small number of individual pollinators (Woodgate et al. 2017, 2021; Brebner et al. 2021). This in turn could empirically inform algorithmic representations of adaptive foraging behavior. At a plant level, while pollinators are learning a landscape, they are more likely to pick up heterospecific pollen. This could impact seed set, as diverse pollen loads are higher in pathogen load and increase disease transmission (Fetters and Ashman 2023), highlighting the complex role of insect behavior in driving tradeoffs between beneficial outcrossing and disease transmission in plants. Empirical data on physiological mechanisms of reduction in seed set could inform more dynamic estimation of seed set in network models. This is a single example of how a model results can indicate which components of underlying interactive systems can substantially influence emergent properties, which allows empirical testing to revise algorithms embedded with models, which will then improve model predictions. Collaborative teams taking this iterative model to empirical study to model approach will improve our ability to understand how plant-pollinator interactions (and thus trophic stability) are impacted by human stressors.

It is worth considering that conservation messaging may be a barrier to effective integration across scales and a holistic understanding of pollination biology. Productive conservation efforts must cross academic and public sectors, with bidirectional information exchange that educates scientists and non-scientists alike. This need for broad-scale communication and education incentivizes generalizing otherwise complex phenomena into major themes, often creating the narrative that pollination communities are monolithic, or a "one size fits all" conservation approach. However, even for well-documented drivers of pollinator declines (e.g., habitat loss, declines in floral resource abundance), broad trends can mask enormous and important variation (e.g., across local ecologies, species' natural history, and community context) (Roulston and Goodell 2011; Valdovinos et al. 2016; Rafferty et al. 2020). Similar nuance exists in conversations about pesticide use, and invasive and naturalized non-native species of plants and pollinators alike (Russo 2016; Mallinger et al. 2017; Iwasaki and Hogendoorn 2022). For example, there are over 8000 species of introduced plants in the continental United States (USGS), in addition to non-wild-type cultivars (Hayes et al. 2025). Oversimplified messaging on the perils of invasive plants would ignore the neutral and potentially positive impacts of non-natives (Rittschof et al. 2023). This could then result in well-intentioned conservation efforts to remove all non-native plants in a landscape, despite eradication being potentially impractical or even detrimental to at-risk communities (Albrecht et al. 2014). Conservation scientists, pollinator biologists working in urban, agricultural, and native landscapes, and other stakeholders like growers would all benefit from greater cross-talk to facilitate a better bi-directional understanding of important variability in pollination systems. For example, the Pollinator Partnership—a nonprofit pollinator conservation and research organization—has developed "Bee Friendly Farming" guides and certification programs, which are based on published research findings, and will need to be updated as our understanding of pollinator conservation improves (Rourke et al.2022; "Bee Friendly Farming Third-Party Certification Manual" 2023). Much as iterative approaches between organismal and modeling studies can build a more nuanced understanding of how variability will impact responses to dynamic stressors, iterative conversations between stakeholders will inform better targeted studies to inform impactful conservation efforts.

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Conflict of interest

The authors have no conflict of interest in this work.

Data availability

No original data are analyzed or presented in this review and perspective piece.

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