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Plant–pollinator conservation from the perspective of systems-ecology

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Ecosystems are interconnected and complex, but conservation has often focused on rehabilitating individual species. A systems-ecology approach aims to support overall structure and maintain functions of the whole ecosystem, and may be especially pertinent for mutualistic plant–pollinator communities. This approach focuses on species interactions as the units to be conserved within the larger ecosystem. Analyzing species interactions is a more holistic approach because it incorporates a broader web of organisms, and considers the plethora of potential indirect influences from interacting partners. In this article, we suggest pollinator researchers focus on plant–pollinator networks to inform conservation programs and best support the coexistence of pollinators and plants within natural and agricultural systems. We propose that a system-ecology perspective is the most promising way to simultaneously improve pollinator conservation, agricultural sustainability, and human well-being.

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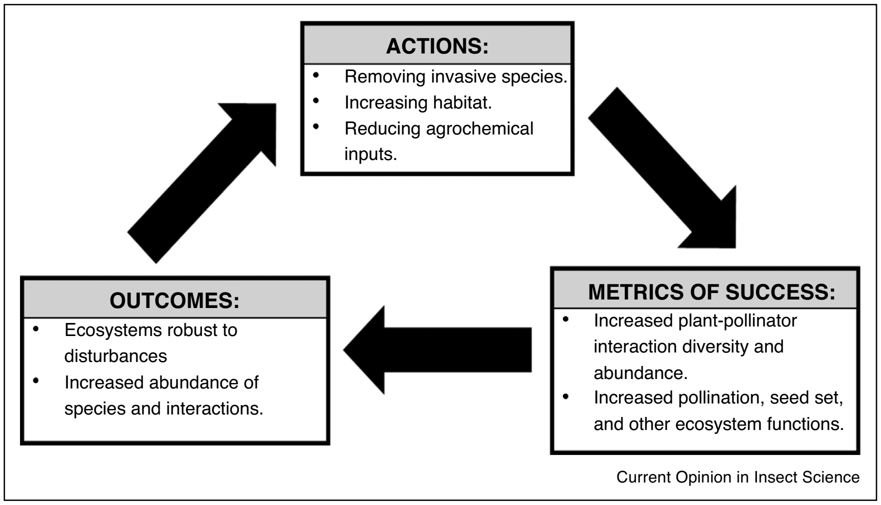
Introduction

Classically, conservation programs have focused strongly on 'saving' individual species. For example, the International Union for the Conservation of Nature's 'Red List' targets species needing conservation to inform management [1]. At the same time, ecologists have long known that species conservation initiatives must be considered within the myriad of ecological interactions in which they occur [2], the ecological community as a whole [3,4], and in the context of human society [5,6]. For example, if the goal is to conserve a target carnivore species (e.g. cheetahs), then it is equally important to also conserve the ecological interactions upon which the animal depends (e.g. herbivorous prey species, the plant communities upon which these herbivores forage on) and reduce conflict between humans and cheetahs (e.g. carnivore killings by ranchers [7]). Although environmental managers started conceptualizing ecosystem-focused conservation strategies 25 years ago [6], many well-meaning conservation programs continue to focus on individual species without consideration of the broader network of ecological and societal interactions [8]. Likewise, conservation practices often focus on one cause of species declines instead of a more realistic scenario including multiple, and likely correlated stressors [9]. While there have been successful examples of single species focused conservation programs, such as the reintroduction of the large blue butterfly in the UK [10] there is also evidence pointing to the limitations of such efforts, for example, the unsuccessful reintroduction of the short-haired bumble bee in the UK [11,12]. Species-specific approaches assume that the true declining status of species and their drivers are already known, however if species-specific conservation fails to identify a species in decline or to correctly evaluate the stressors causing the decline, species protection efforts will likely fall short. In this article, we suggest that traditional species-specific strategies should be complemented by knowledge from a systems-ecology perspective; an awareness of the ecological network of interactions supporting a species may be critical for promoting its successful re-establishment and/or long-term population growth. A system-wide approach strives to support all species and interactions in the ecosystem [4] and therefore has the potential to also protect species that scientists have not been able to detect or establish are in decline.

The conservation of mutualist species in particular requires a perspective in which ecological interactions and communities themselves are the target of conservation action [13,14] (Figure 1). Pollinators are highly sensitive to disturbances and declines of the mutualistic partners they rely on [15–17]. Therefore, extinction or decline of interactions with mutualist partners have the

Figure 1



Systems-ecology conservation structure.
A diagrammatic representation of an adaptive management structure for conservation based on systems-ecology. The actions are similar to a species-specific perspective, however the metrics of success focus on interactions and ecosystem functions and lead to more broad-scale ecological outcomes.

potential to be used as early predictors of population trends for the species with which they interact. However, pollination does not only influence pollinators and plants, but all organisms who feed on the fruits, seeds, and vegetation provided by successfully pollinated plants, affecting everything from soil microbes [18] to higher trophic levels [19,20]. Some pollinators also act as predators, parasites, and herbivores, participating in other ecological networks and functions [21•,22]. A systems-ecology approach to plant–pollinator conservation can support ecosystem structure and functional stability [23] even beyond pollination [24], creating ecosystems that can withstand disturbances that may lead to extinctions in less robust communities [9,13].

Traditional species-specific management may intuitively be considered a better approach for conserving rare, specialized pollinators than considering broader aspects including plant species, interactions, and pollination services. However, species response to stressors is highly variable [25], therefore it may be difficult to create individualized conservation programs for every single declining species, especially when so many are in decline [26]. Under a systems ecology perspective, it becomes clear that even specialized pollinator species often benefit from a network that includes a robust community of plants and pollinators. For example, the Mojave poppy bee is a specialist pollinator which only forages on the Las Vegas bear poppy, and both species are in decline. While the Mojave poppy bee is one of two highly efficient pollinator of the Las Vegas bear poppy, there are 21 other pollinators known to visit the plant and confer some level of pollination, albeit less than the two highly efficient pollinators [27]. With a robust plant–pollinator community that provides additional floral resources to support the other 21 pollinators visiting the Las Vegas bear poppy, the poppy would have higher pollination success due to higher pollinator abundances and neighborhood context effects. This increased pollination success could increase the abundance of the Las Vegas bear poppy, offering more resources to support the specialist Mojave poppy bee. In addition, if the Mojave poppy bee goes extinct, conserving the pollinator community provides a safeguard for the plant, because its larger assembly of interaction partners has been maintained.

A systems-ecology approach can also benefit sustainable agricultural management. Traditional conservationists separate biodiversity conservation from agricultural sustainability, and pollinator populations from crop pollination services, however these elements are highly interconnected. As more land is continuously be used for agriculture in order to sustain the exponentially growing human population, the amount of natural habitat for biodiversity conservation will decrease [28]. While some organisms can only thrive in natural habitats, many pollinators are found and can be useful in agricultural environments, making farmland an ideal space for expanding pollinator conservation efforts. In the spirit of these broader considerations, in this article we discuss themes and examples that highlight the benefits of a systems-ecology perspective for both conservation and sustainable agricultural management.

Conserving biological networks

Considering a systems-ecology perspective, what are the most useful approaches to conservation of plant–pollinator interactions? One methodology gaining traction in recent years is network modelling, which uses plant–pollinator interactions to describe how the structure of interactions may influence species support and function in the community [13,29••,30••]. Network models analyze all observed 'links' between interacting species (plants, pollinators) and how their distributions are patterned, to understand the underlying structure that supports biodiversity [31]. While network analysis often focuses on taxonomic groups (usually species level), the resulting networks could be used to test hypotheses about functional groups (e.g. ground nesting bees) and their roles in plant–pollinator ecology and conservation [32,33]. Analysis of natural plant–pollinator communities has revealed that species are highly interconnected, with the average distance from one species to all other species in the network being 1.5–1.7 interactions [23]. Therefore, even a small shift in interactions between a few species can produce a cascading effect of 'interaction rewiring'. Interactions are not static. For example, pollinators may shift which plant species they visit due to changing competitive pressure and floral resource availability [24,30••,34], even though overall network properties characterizing patterns of link distribution are preserved [35–37].

Analysis of natural plant–pollinator networks have provided hints into the types of interaction structures that best support species and pollination services in the wake of environmental disturbances. For example, plant and pollinator species range from generalist (those that interact with many species) to specialist (those that interact with few species). In a robust system, generalists and specialists coexist within a 'nested' network structure where highly specialized species interact mostly with highly generalized species, forming a core of interacting generalist species that support specialized species that attach onto that core. In one study, eighty percent of analyzed mutualistic networks (pollination and seed dispersal networks) are highly nested, much more than antagonistic networks such as food webs [38]. A nested structure is thought to be a key feature of community stability and the long-term support of biodiversity. This is because generalist species tend to have more stable population abundances from year to year, making them reliable interaction partners for more sensitive specialist species [39–41] whereas specialist species may not have the same reliability if both interaction partners have volatile population abundances. As mentioned in the aforementioned section, increased interaction diversity of the Las Vegas bear poppy makes it a better partner for the rare Mojave poppy bee because the bear poppy can be pollinated to some extent by other pollinators [27], helping to ensure its persistent survival from year-to-year for the poppy bee.

Additionally, while plant–pollinator networks are grouped frequently into 'modules', or clusters of more tightly interacting species, the entire network is connected through key highly generalized species, such that modules are not fully isolated from each other. Loss of interactions connecting one module to another can produce large effects on the overall network [13] and groups of species run the risk of becoming increasingly isolated and eventually completely disconnected from the rest of the network [42]. Changes in the nested and modular structure of networks can occur independently of each other [43], allowing two metrics of network structure to be used to predict future species loss [13]. On the other hand, restoring network structure as characterized by nestedness and well-connected modules can be a prerequisite to reestablish particular mutualists after they have been lost [44], making it a potential tool for preemptive conservation action.

Network structures and dynamics may also provide insights into functional consequences for ecosystem services such as pollination, though there is limited research in this area to date. Even small shifts in the composition of pollinator assemblages could have drastic effects on pollination success, due to pollination efficiency differing between pollinator species and competition with other plants for visits by a limited community of pollinators [45]. Therefore, plant–pollinator communities where species interact with a diverse group of other species (i.e. increased interaction diversity) may be a desirable conservation goal [13] to increase the likelihood of any given plant species meeting its pollination needs and increased floral resource abundance for pollinator species, including specialist species that often interact with generalist species [38]. However, the link between network metrics and pollination function needs further study.

Establishing a standardized method for empirical network analysis, especially with regards to observer bias [33,46,47] and differences in species richness between networks [48], will help bolster use of network analysis in empirical ecological research. While there are still hurdles to network analysis, such as the high labor cost and extensive taxonomic expertise, we believe the benefits outweigh the costs. Taxonomic hurdles are also an issue for species-specific conservation efforts. Network-based approaches have the advantage in that they can be conducted using higher taxonomic groupings (above species level) and still provide insights about plant–pollinator interactions useful for conservation efforts [49]. In addition, populations can be monitored alongside sampling efforts for network analysis; the number of individuals is observed when quantifying interactions and an estimate of the number of individuals of any one species observed can be integrated into networks when quantifying interactions. Therefore, network analysis can be used in conjunction with traditional population analysis to ensure species declines are being detected adequately. While there is still more to learn, network analysis is a highly promising tool for describing the structure and maintenance of interactions across an entire ecosystem to inform system-wide conservation and management practices.

The human dimension in plant–pollinator networks

A more system-wide perspective on the importance of non-managed pollinators to humanity and the entire biosphere is beginning to be emphasized [50,51]. While many conservationists consider agriculture and human needs separate from biodiversity conservation programs, many pollinators are often found in these environments, including some of conservation concern [52,53]. Therefore, sustainable management of agricultural environments can simultaneously conserve biodiversity and increase crop production while reducing our reliance on managed exotic pollinators. Wild bees contribute economically [52] and can fully pollinate crops as efficiently as, or even more efficiently than managed bees [54–56]. In addition, other pollinators such as butterflies, flies, and wasps are becoming increasingly acknowledged for their contribution to the pollination of crops [57].

At the same time, mounting studies are revealing the negative ecological impacts of managed exotic bees, including exotic species invasion [58] and disease transmission [59]. However, conservation policy must also consider economic and social values alongside environmental concerns. The use of exotic managed honey bees in the Americas is justified by their economic contribution to crop production [52] (Figure 2), a result of a species-specific perspective (i.e. the benefits and costs to honey bee presence). However, the agricultural system promoting managed bee use is increasingly shown to be costly [60,61]; and can decrease both economic and conservation benefits, particularly if these managed bees become invasive [62••]. Additionally, other stressors within the structure of our current agricultural system could be confounding the negative 'influence' of exotic managed honey bees [9] and driving our reliance upon them. Only with a systems-ecology perspective can we determine if an alternative system, such as one promoting wild pollinators, can deliver agricultural pollination services with more beneficial environmental and social outcomes.

Industrial agriculture is an example of a practice focused on optimizing productivity of just a few species, often at the expense of biodiversity. For pollinators, industrial agriculture has converted natural systems with continuous floral resources into feast/famine environments dependent on crop bloom periods [63••,64], which may be directly contributing to reduced pollinator diversity in highly agricultural landscapes [52,65]. Humans' reaction to the lack of wild pollinators for crops caused by this land use change has been to supplement pollination services with mobile managed bees transported from crop field to crop field following floral resources (Figure 2). This has set up a 'vicious cycle' of reduced yields from pests or poor pollination, providing impetus to convert more land to agriculture to increase overall production, leading to further decline of pollinator species [66].

It is becoming increasingly apparent that our current form of agriculture and excessive reliance on honey bees for crop pollination cannot be sustained forever [67]. Some countries like the US are already strained under the demand for managed bee pollinators to meet increasing crop acreage: California's 2020 almond crop used approximately 2.4 million [68] of the 2.6 million commercial honey bee colonies in the United States [69]. We have reached a critical juncture in which this species-centric approach for providing agricultural needs of pollination is leading to a breakdown, not only of natural ecosystems, but of the agricultural production systems upon which we humans depend. While we may not be experiencing the costs of these externalities now, we have known for a while that eventually our agricultural production will decrease and become prohibitively costly unless we embrace a more sustainable system [70–73].

An environment supportive of wild pollinators for agriculture can be highly beneficial to human society from a systems-ecology perspective. Wild pollinators require natural habitat within or near agricultural fields, and habitat enhancements are being increasingly used for promoting biocontrol (e.g. supporting pest predator populations; [74••,75]), reducing soil erosion, and improving water quality [52,53], showing a systems-ecology perspective can solve multiple issues simultaneously. Biodiversity benefits go far beyond agricultural production, with natural pollinator existence influencing intrinsic values like improved mental health [76•,77], maintenance of cultural traditions (e.g. 'honey hunting' from wild, native bees [78], religious and cultural symbolism [79•], and ecotourism [80]).

While changing our current approach from one of species-specific management focused on agricultural production to one of system-wide benefits and environmental health will no doubt be challenging and require further research and adjustment [81], it is a necessary step in order to to best apply our the insights from a modern scientific understanding. Emerging research highlights the impending dangers of environmental degradation [82] and effects of climate change [45], which imply that pollinator management should aim at promoting resilient plant–pollinator networks. Now is the time to reassess how we want our ecosystem to operate, considering

Figure 2

Question: Should managed honey bees be used?

	Environmental	Economic	Social	Focus
Species-Specific Perspective:	• Utilizes resources in natural environments. • Can become invasive. • Transmits diseases to wild pollinator populations.	• Increase crop production and yield. • Can be moved to follow floral resources or to low-pollinator environments. • Produces honey and other products.	• Well-liked by the public. • Most well-known pollinator.	The value and influence of this species in isolation.
Systems-Ecology Perspective:	• Negatively influences wild plant-pollinators interactions and functions. • Managed bees are more resistant to expanding industrial agriculture environments.	• Not necessarily better than wild pollinators at increasing crop yield. • Creates "vicious cycle" that increases agricultural costs long-term.	• Biodiversity is beneficial to human quality-of life. • Healthy environments is becoming increasingly important within society.	The value and influence of this species and other potential species within the entire system.

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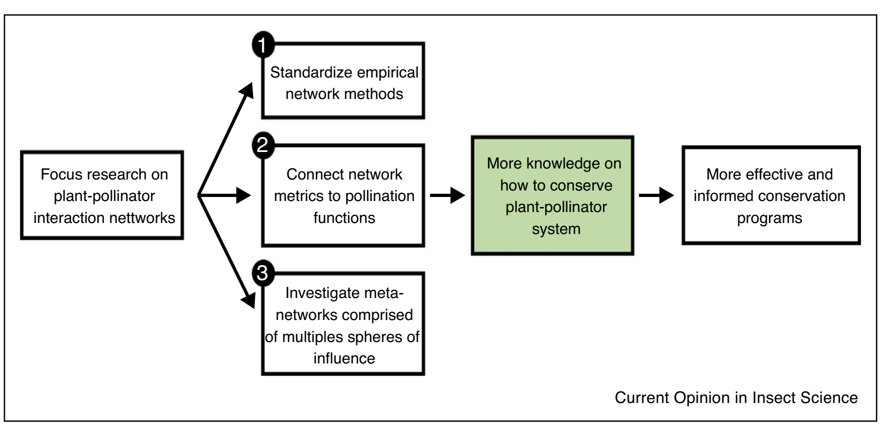
Systems-ecology leads to healthier systems.
Comparison of environmental, economic, and social considerations when determining a management question, such as whether to use managed honey bees, when focusing on species-specific values or systems-ecology values.

environmental, agricultural, and societal interests, when choosing conservation management policies.

Conclusion

In conclusion, ecologists' broader understanding of the diversity and system-wide outcomes needs to be the forefront of plant–pollinator conservation. Species-focused management approaches can lead to systems of unsustainable agricultural production, detrimental environmental outcomes, and decreased human well-being. Alternatively, an ecological interactions systems approach prioritizes the health of the overall system, balancing economic values of crop production with environmental health and services as well as human well-being. While

Figure 3



Future steps.
Our paper concludes that it is pertinent to focus plant–pollinator research on interaction networks for pollinator conservation, with a need to (1) standardize network methods for empirical research, (2) connect network metrics to pollination functions, and (3) broaden our scope to investigate multiple interacting networks. This research will lead to more wholistic information on how to best conserve plant–pollinator systems which will lead to more effective and informed conservation programs.

interaction networks are promising for analyzing an entire plant–pollinator system simultaneously, there are knowledge gaps that need to be filled (Figure 3).

First, we need to establish a scientifically supported standardized procedure for analyzing and comparing interaction networks so future studies produce results that accurately represent the studied ecosystems. There have been multiple studies using simulated networks testing the effect of observer bias and species richness differences [33,46–48], but there is still a great deal of disconnection between theoretical network analysis and its use in empirical studies. Therefore, more work needs to be done compiling our theoretical network knowledge with empirical constraints to produce standardized network analysis methods for field-based research. Second, we need to continue studying the links between statistical network metrics (nestedness, modularity, etc.) with plant community composition and ecosystem function such as floral resource abundance, nesting site availability, seed/fruit production, and pollination. A few studies have found interesting trends in seed production and pollinator competition [29••,30••], but network analysis still requires more evidence directly linking interaction structure to ecosystem function so that network results become widely accepted by pollination ecologists. Third, we cannot simply analyze plant–pollinator networks in isolation, but must start investigating how plant–pollinator interactions integrate with other ecological functions and human spheres such as economic, social, and trade networks [6]. Ecosystems are dynamic and complex, and as we move from an individual-species focus to a systems-ecology perspective, and as our ability to analyze entire communities improves, we need to remember there is still a much larger system at work.

In summary, ecologists have long known that species exist in highly interconnected networks, yet an application of this knowledge to the practical management of pollinator populations using systems perspective lags behind. Conservation and sustainable agriculture initiatives stand to benefit greatly by utilizing emerging findings from empirical studies in systems-ecology, to most effectively conserve plant–pollinator systems based on the latest scientific understanding [83,84]. We suggest this is the best course to follow to support environmental, economic, and societal values in the wake of environmental degradation, species declines, and global climate change, and to maintain sustainable and healthy ecosystems.

Conflict of interest statement

Nothing declared.

CRediT authorship contribution statement

Kate E Borchardt: Conceptualization, Writing - original draft, Writing - review & editing. **Carolina L Morales:** Conceptualization, Writing - review & editing. **Marcelo A Aizen:** Conceptualization, Writing - review & editing. **Amy L Toth:** Conceptualization, Writing - original draft, Writing - review & editing.

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