

The Resilience of Plant–Pollinator Networks

Jordi Bascompte^{1,*} and Marten Scheffer²

¹Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland; email: jordi.bascompte@uzh.ch

²Department of Environmental Sciences, Wageningen University, Wageningen, The Netherlands

Annu. Rev. Entomol. 2023. 68:363–80

First published as a Review in Advance on
October 7, 2022

The *Annual Review of Entomology* is online at
ento.annualreviews.org

<https://doi.org/10.1146/annurev-ento-120120-102424>

Copyright © 2023 by the author(s). This work is licensed under a Creative Commons Attribution 4.0 International License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. See credit lines of images or other third-party material in this article for license information.

*Corresponding author

**ANNUAL
REVIEWS CONNECT**

www.annualreviews.org

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Keywords

mutualistic networks, robustness, ecosystem shifts, global environmental change

Abstract

There is growing awareness of pollinator declines worldwide. Conservation efforts have mainly focused on finding the direct causes, while paying less attention to building a systemic understanding of the fragility of these communities of pollinators. To fill this gap, we need operational measures of network resilience that integrate two different approaches in theoretical ecology. First, we should consider the range of conditions compatible with the stable coexistence of all of the species in a community. Second, we should address the rate and shape of network collapse once this safe operational space is exited. In this review, we describe this integrative approach and consider several mechanisms that may enhance the resilience of pollinator communities, chiefly rewiring the network of interactions, increasing heterogeneity, allowing variance, and enhancing coevolution. The most pressing need is to develop ways to reduce the gap between these theoretical recommendations and practical applications. This perspective shifts the emphasis from traditional approaches focusing on the equilibrium states to strategies that allow pollination networks to cope with global environmental change.

1. INTRODUCTION

Pollinators are declining worldwide, with implications for agricultural productivity (1, 3, 17, 20, 27, 34, 76). Much effort has been allocated to identifying the causes of this decline, ranging from insecticides (48, 98, 108) to parasites (64), loss of abundance and diversity of flowering plants (30, 36, 37, 77), or multiple effects acting simultaneously (18, 27, 40, 76, 89). Assessing the systemic response of these communities, however, largely depends on understanding the way species depend on each other (11, 42, 51, 72, 81). Indeed, the dependencies between plants and their pollinators shape complex interaction networks that can be considered as the architecture of biodiversity (14). These networks map the ways species depend on each other and allow assessment of the degree to which declines in the abundance of one plant species, for example, will translate into declines in the abundance of multiple pollinator species (**Figure 1**).

Species interactions have been incorporated into conservation following the realization that we may have missed an even more insidious type of extinction, that of species interactions (52, 53). A synthesis of 688 published papers showed that species interactions may be more susceptible to global environmental change than species themselves, and that there are clear patterns in the way in which these interactions are eroded (103). Specifically, several drivers of global environmental change such as nitrogen deposition, CO₂ enrichment, climate change, biotic invasions, and land use, have been found to reduce the intensity of mutualistic interactions involving plants, increase the magnitude of pathogen infection, and enhance herbivory (103). As noted in that review, however, one of the major challenges is to scale up these effects of global change on interactions as we move from pairwise interactions all the way to complex networks (**Figure 1**). Climate change, for example, can impact differently across the plant species in a community, inducing differences in the timing of flowering and potential phenological mismatches with pollinators (57). This, in turn, may affect different species of pollinators in contrasting ways beyond what one would predict on a pairwise basis.

One first step toward understanding the community-wide consequences of climate change is coupling species distribution models and pollination networks (13, 47, 65, 73, 87, 93, 95). This work has found two main differences between direct, climatically driven extinctions and subsequent coextinctions (**Figure 2**). First, while the single best predictor of the probability that a species is driven extinct by the direct effects of climate change is its geographic location, the best

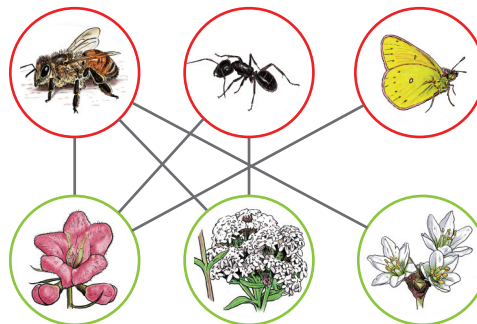


Figure 1

Species interactions shape complex networks of mutual dependency. The example illustrates a subset of the interactions of mutual benefit between plants and their pollinators in a system of hills in the Pampa region in Argentina (83; network *M_PL_072* available at <https://www.web-of-life.es>). Pollinator species are, from left to right, *Apis mellifera*, *Camponotus* sp., and *Colias lesbia*. Plant species are, from left to right, *Gerardia genistifolia*, *Stevia satureiifolia*, and *Nothoscordum bonariense*. Drawings courtesy of A. López-Rojas.

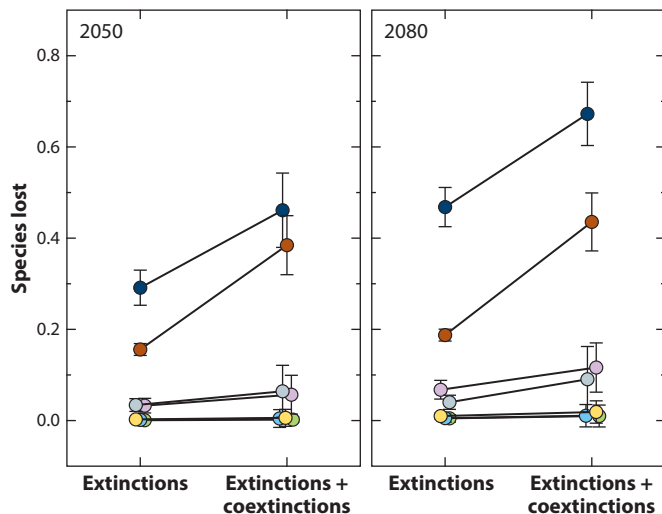


Figure 2

Plant species extinctions and subsequent coextinction cascades predicted in seven pollination networks across two time horizons. Plant extinction probabilities are predicted by species distribution models, assuming that species are independent from each other. The coextinction scenarios assume that the previous climatically induced extinctions can trigger coextinction cascades. In this case, the total fraction of species lost (directly and indirectly) is plotted. The different colors identify the specific networks, with darker and lighter colors representing Mediterranean and Eurosiberian networks, respectively. For visualization purposes, different points are slightly displaced across the *x* axis when they overlap. The figure shows the average and standard deviation of the fraction of species lost across 1,000 replicates. Figure adapted with permission from Reference 13.

predictor of the ultimate fate of a species as a result of the combined effect of extinctions and subsequent coextinctions is network identity, i.e., the specific properties of the network of interactions that species is embedded in (13).

The second main difference between climatically driven extinction events and subsequent coextinctions is that the two processes target a different subset of the plant species (13). Again, knowing that species are part of a web of mutual dependencies is important when assessing the fate of pollinators. This shifts the attention from the species to the interactions.

Our thesis in this review is that we should build a conceptual framework to understand the resilience of plant–pollinator networks. This approach should consider both the boundaries of the safe operational space preserving all species and the rate and shape of network collapse once the boundaries of such a space are crossed. In the following sections, we describe these two components and how they should be brought together.

2. THE STRUCTURAL STABILITY OF POLLINATION NETWORKS

The dominant approach to studying dynamic stability in ecology has revolved around the concept of linear stability (55, 62, 63, 74). Given a solution for a particular combination of parameter values, one looks at whether a system will return to its original solution after being pushed away by an infinitesimally small perturbation. Although it has brought many interesting insights, the approach of linear stability has several limitations that have constrained the way we think about the resilience of natural communities (55). Recently, ecologists have turned toward structural stability as a way of sorting out these limitations (2, 12, 16, 23, 41, 60, 80, 92, 101, 105). Instead of asking

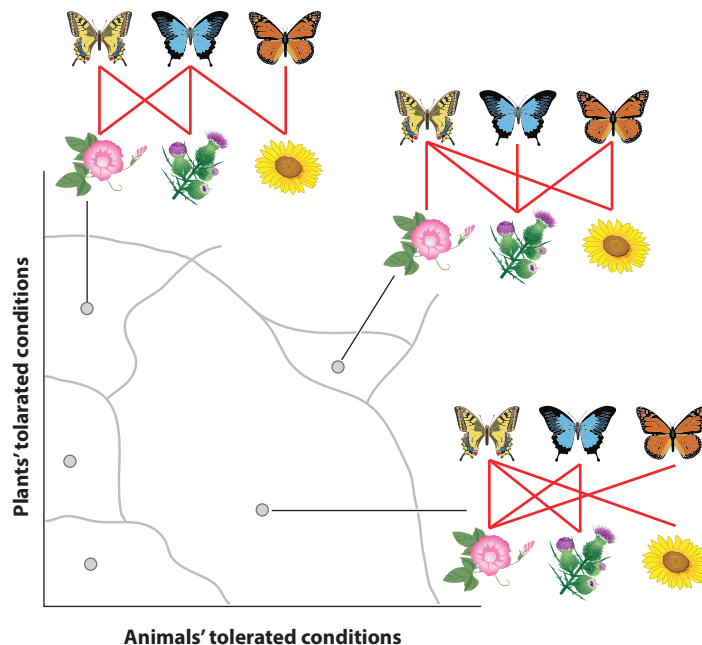


Figure 3

Network resilience can be measured through the concept of structural stability, which refers to the volume of parameter space compatible with the stable coexistence of all species. Different network architectures have different levels of resilience, with the highest corresponding to the nested network at the bottom. Figure adapted with permission from Reference 80 (which adapted it in turn from an equivalent display in the context of developmental biology in Reference 2).

whether a solution is stable for a particular choice of parameter values, structural stability addresses how broad is the range of parameter values compatible with the stable coexistence of all species (**Figure 3**). This is arguably a more operational measure of resilience in the context of global environmental change, which is large and directional. It is very much related to the approach pioneered by C.S. Holling (49). Holling contrasted the traditional concept of engineering resilience, namely, the time required by an ecosystem to return to its equilibrium after a disturbance, with the alternative concept of the capacity of a system to absorb disturbance and reorganize while undergoing change. Holling's brilliant perspective was later adopted by researchers studying tipping points, i.e., the sudden shift to an alternative state once a critical condition value is crossed (Section 3.1). Thus, structural stability represents a common currency between research on tipping points and research on networks.

Using the structural stability concept, we can derive some simple rules of thumb regarding how resilience can be built in complex ecological networks. In this section, we highlight four strategies: rewiring the network of interactions, adding heterogeneity in the nodes, allowing environmental variability, and enhancing coevolution.

2.1. Rewiring the Network

Enhancing resilience by rewiring the network of interactions, i.e., changing the identity of the species with which a focal species interacts, is the approach most directly related to current theoretical work on complex networks. Two main properties of the structure of ecological networks, modularity and nestedness, have received considerable attention. Modularity is defined

as the tendency of a network to be organized in modules, where nodes within a module tend to interact a lot among themselves while showing few interactions with nodes from other modules (44, 69). Nestedness is defined as the tendency for specialists to interact with well-defined subsets of the species with which generalists interact (15).

Haldane & May (46), for example, recommended increasing modularity to foster systemic resilience in the financial sector. Indeed, the possibility that modular networks may increase the persistence of the system by buffering the spreading of a perturbation has been a long-term tenet in theoretical ecology (38, 62, 96). More recently, it has been shown that the resilience induced by modularity may depend on the intensity of perturbations. Specifically, modularity is advantageous only after a minimum level of environmental stochasticity (38). In the absence of perturbations, in contrast, there is a negative correlation between modularity and total metapopulation size.

More relevant for the case of pollination networks, nestedness has been related to species coexistence (16), abundance (99), and community resilience (4, 19, 66, 71, 80, 100). As is the case for modularity, the optimum degree of nestedness could be a compromise between two conflicting tendencies. This trade-off arises from the fact that requiring dynamical stability under external perturbations seems to push the system in a direction in configuration space that is opposite to that required to maintain full feasibility under those same perturbations (12, 82).

Experimentally rewiring the network of plant–pollinator systems has only been done in a few small-scale experimental systems by covering the flowers of a relevant species with a mesh that prevents interaction with large pollinators (10, 32, 78). One could also modify species abundance such that a pollinator would mainly interact with a plant species that has been made more abundant. This, of course, may only work for small systems, rendering it unrealistic for many organisms.

Alternatively, one could ask to what degree a driver of global environmental change, such as habitat loss, affects the architecture of plant–pollinator networks and therefore their resilience (35, 39, 45, 54, 94, 102). For example, a study in sandhill habitats in Florida has shown that the direct effects of habitat loss on species richness and abundance lead indirectly to more modular and connected networks (94). These changes resulted in no net effect on nestedness, since a strong positive indirect effect through species richness was cancelled by negative indirect effects through connectance and abundance (94). Similarly, in a coastal dune marshland, habitat loss resulted in a reduction in species richness and abundance of pollinators. This translated into an increase in modularity, as in the previous study in Florida, and a reduction in nestedness, which was interpreted by the authors as potentially reducing the robustness of these pollination networks (102). Habitat loss has also been found to reduce the specialization of interactions, which has led toward the functional homogenization of the resulting impoverished communities. This has resulted in the formation of opportunistic interactions among generalist species (54). Finally, from a theoretical perspective, a recent metacommunity model has shown that, while mutualistic networks become more connected and nested as habitat is progressively lost, antagonistic networks become more modular (35).

2.2. Increasing Heterogeneity

The second approach to engineering network resilience consists of modifying the heterogeneity of the nodes. This echoes similar recommendations to increase systemic risk in the financial sector. For example, while the increasing tendency for each bank to be equivalent to each other reduces the local risk for each bank, it increases the probability of the entire financial system collapsing (46). In ecology, functional diversity and within-species genetic diversity are good surrogates for heterogeneity. Regarding the former, simple manipulative experiments in plant–pollinator systems have shown that functional diversity may be key to the persistence and functioning of these systems (30, 32).

Regarding the role of genetic diversity, there is ample evidence that it affects ecosystem processes (88, 109, 110). Building from this earlier work, Barbour and colleagues (8) showed that genetic diversity in a focal plant species (*Arabidopsis thaliana*) increases the structural stability of an experimental food web composed of two aphid species feeding on *Arabidopsis* (*Brevicoryne brassicae* and *Lipaphis erysimi*) and their common parasitoid wasp (*Diaeretiella rapae*). In particular, genetic diversity moves the vector of aphid growth rates toward the center of the region in parameter space compatible with the stable coexistence of all species. Notably, this effect is mainly driven by the presence of a keystone gene in the focal plant involved in the synthesis of defenses against herbivores (8). Although these keystone genes may be rare (90), and many traits will be affected by more complex genetic architectures (70), it may be interesting to extend this pilot study to assess whether similar effects of genetic diversity for community resilience are found in plant–pollinator systems (61). As a step in this direction, it has been found that plant plots established with multiple genotypes had more abundant flower visitors, which suggests that genetic diversity may indeed lead to more sustainable natural and agricultural systems (36).

The finding that a keystone gene in a focal plant enhances the persistence of an ecological network suggests that the loss of genetic diversity resulting from anthropogenic influences can result in the simplification of ecological communities. These findings, however, also represent unforeseen opportunities for ecosystem restoration, for example, through maximizing the genetic diversity within pre-adapted populations during introductions. Overall, the study by Barbour and colleagues (8) demonstrates the need to bridge across scales of biological organization, from genes to ecosystems, to understand community persistence.

2.3. Allowing Variance

Allowing variance has been shown to increase the safe operating space for managed systems (21). In sharp contrast, current policies in both biology and the financial sector tend to suppress variance. Indeed, variance in the fluctuations of species or stock prices is perceived as an undesirable property, as it makes it more difficult to plan based on average targets and equilibria. This dominant approach, again, is very much influenced by the main view in ecology, based on the notion of equilibrium.

For example, policies to manage European forests aim to stabilize yield while suppressing disturbances (31). One such disturbance is fire (56). Management practices in Mediterranean-type climate regions aimed at fire suppression have created a short-term benefit but dramatically increased the chance of massively destructive superfires. In contrast, many fire-prone areas of Africa intentionally burn the national parks in the early season (when biomass is not so high) to greatly reduce the likelihood of large, destructive fires in future years (56, 67). Similarly, fish harvesting rules minimizing variance are preferred as a way to maximize profit (50; for details, see 21). The same principles most likely apply as well to the management of pollination of agricultural fields, although specific experimental tests are urgently needed.

In sharp contrast to traditional management approaches, Carpenter and colleagues (21) showed that actions aimed at decreasing variance have the unanticipated effect of reducing the range of conditions compatible with a desirable state. This cancels signals of declining resilience and removes pressures that would otherwise build tolerance of stress. This view adheres to Holling's perspective of the need for ecological systems to persist while undergoing change.

2.4. Allowing Coevolution

Finally, another intrinsic property of real ecological networks is that species are able to coevolve. In contrast to similar networks without this possibility, one can assess to what degree coevolution

increases network resilience. A first step in this direction has been made by de Andreazzi and colleagues (26) in models of antagonistic interactions. These authors showed that, when selection due to antagonistic interactions is stronger than other selective pressures, ecoevolutionary feedbacks lead to lower temporal variation in abundances, which can be used to measure demographic stability. Interestingly, in relation to our first rule of thumb to foster resilience, i.e., rewiring the network (Section 2.1), the structure of the antagonistic network mediates this relationship between coevolution and demographic stability. Specifically, population variability decreased with species richness, connectance, and nestedness and increased with modularity (26).

More recently, Gawecka and collaborators studied the effects of habitat destruction on coevolving metacommunity models (35). They showed that, when the community dynamics are governed by interactions between species, coevolution dampens the effects of habitat loss in mutualistic communities, while the effects on antagonistic communities are more variable. This suggests that the ability to coevolve can be used to increase the resilience of pollinator communities to a greater extent than for other interaction types, such as predator–prey interactions. It is not yet clear whether the same result will be obtained when using measures of resilience such as the ones described in this review and when applying them to empirical settings. In addition, this certainly is the most speculative rule of thumb for building resilient networks, and to our knowledge there is empirical evidence neither for pollinator systems nor, more broadly, for species interaction networks.

Regarding the alternative question of to what degree habitat loss affects the outcome of coevolution, Gawecka and colleagues (35) found that, in the case of mutualism, habitat loss results in a greater heterogeneity of trait values across the landscape. This result can be understood as follows: Habitat loss makes the local species composition more heterogeneous across the landscape. This results in different coevolutionary trajectories.

3. THE COLLAPSE OF POLLINATION NETWORKS

The previous section focused on the resilience of plant–pollinator communities and how to increase such resilience. In this section, we turn to the behavior of the system once the boundaries of the safe operational space are crossed and some species are driven extinct. These extinctions, in turn, can generate a cascade of coextinctions, i.e., groups of species disappearing as a consequence of the extinction of species that they depend on (13, 19, 29, 66, 75, 79, 91, 106) (**Figure 2**). We first briefly review the theory of tipping points and early-warning signals of an impending transition. We then discuss to what extent network collapse can be understood within this perspective.

3.1. Theory of Tipping Points and Early-Warning Signals

Many complex systems ranging from the climate to ecosystems and financial markets show abrupt flips to a new, alternative state as conditions (e.g., CO₂ levels, nutrient concentration, volatility) reach a critical point (9, 85). This makes it difficult to predict the response of the system to such changing conditions. One paradigmatic example within ecology is that of shallow lakes. These lakes are either pristine—characterized by clear water and high diversity—or eutrophic, in which case they are turbid and inhabited by a few dominant species. There are no intermediate states. As the amount of nutrients (e.g., *P*) poured into the lake keeps increasing, the lake is first able to absorb this perturbation and remain in the pristine state. However, its ability to continue absorbing a worsening in conditions is eroded such that, when a critical level of nutrient is reached, the lake shifts to a eutrophic state.

This transition from a pristine to a eutrophic lake can be understood as a particular class of critical transition described by a folding of the function relating a system state to the changing

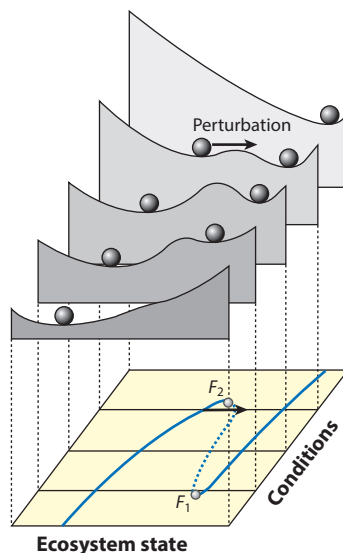


Figure 4

Tipping points and system resilience. The map at the bottom represents the response of a nonlinear system as conditions are changed. The system remains in its original state (*upper branch*) until it reaches a tipping point where it jumps to an alternative steady state (*lower branch*). The graph above illustrates how resilience—represented by the tendency of the ball to return to the valley after being pushed—decreases as the system approaches the tipping point. Figure adapted with permission from Reference 85.

conditions (see **Figure 4**). This induces hysteresis or irreversibility (the path of destruction is not the same as the one of recovery). The most immediate implication is that, once we cross a tipping point, it is not enough to remove the excess of nutrients up to the value at which the transition took place (F_2 in **Figure 4**). The system is trapped in the alternative, eutrophic state. To flip back to the pristine state, it will be necessary to reach much lower levels of nutrients (F_1 in **Figure 4**).

Understanding the basic mechanism of the tipping point requires thinking in terms of dynamical systems and stability. The pristine state is a solution of a dynamical system, as illustrated in **Figure 4**. For low values of environmental degradation, this is a stable solution. Small deviations from such a steady state will fade away, and the system will return to the same equilibrium point (97). These feedback loops are strong as long as the conditions are far from a bifurcation point (e.g., F_2 in **Figure 4**). However, as the level of stress increases, the basin of attraction of the pristine state shrinks. The negative feedback loops are now much weaker. Close to the tipping point (F_1 and F_2), the basin of attraction is very small (the landscape in **Figure 4** is almost flat). Even a small perturbation may now push the system toward the basin of attraction of the alternative state, which will then become stable.

Recent research has shown that there may be generic indicators of the proximity to a tipping point (84, 86). They relate to a property known as critical slowing down, that is, the increase in the time that the system requires to return to its original state after a perturbation.

Two widely used indicators of critical slowing down are an increase in the variability of the system and an increase in its autocorrelation, i.e., the correlation between two successive values in the time series (84). There are two major advantages to such a generic approach. First, we do not need to have a full understanding of the system. Second, the same signals can be applied to multiple systems despite their different natures.

Some recent results can be considered a proof of concept of the utility of early-warning signals as indicators of the proximity to a tipping point (84). However, the systems to which these indicators have been applied to date are easily classified into two alternative states (e.g., pristine versus eutrophic lakes). As a consequence, it is not clear to what degree the framework of tipping points will be appropriate for those systems characterized by many interacting elements for which it is not clear what the alternative state will look like (86). This is the topic of the next section, where we consider pollinator collapse through the lens of a loose interpretation of the concept of a tipping point (104).

3.2. Network Collapse as a Potential Example of a Tipping Point

Lever et al. (59) used a model of a pollination network to explore to what degree network structure affects the rate and shape of network collapse as a driver of pollinator decline is increased. For low values of nestedness, the collapse is partial, with several extinctions taking place as the driver of pollinator decline is increased. By contrast, at high values of nestedness, the network stands until a higher value of perturbation but collapses all at once. Recent theoretical work has tried to assess the universality of such a collapse (33, 68). This is an exciting avenue, although future work should explore the generality of these results when departing from some of the strong assumptions made by the analytical approach, i.e., assuming linear dynamics and homogeneous networks.

In the scenario of a simultaneous network collapse for high nestedness, there is hysteresis. As both nestedness and connectivity increases, the distance between the point of collapse and that of recovery increases (**Figure 5**). As a consequence, the overall service of pollination may be lost abruptly, even if it is provided by a large number of species, and global environmental change increases gradually. If this were to occur in real communities, it would not be enough to revert the driver of global change to the point where the collapse took place. It would be necessary to revert the driver of global change to lower levels.

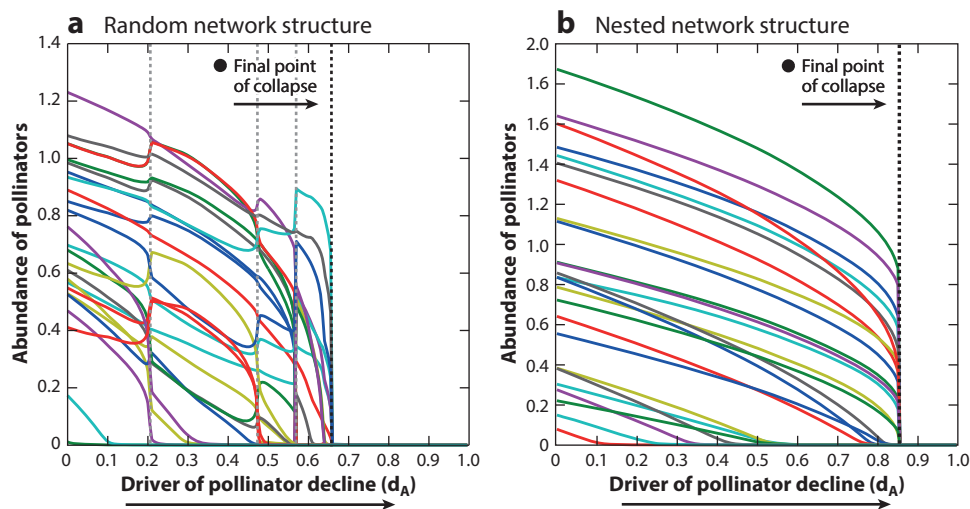


Figure 5

The collapse of a simulated pollination network as the driver of pollinator decline (affecting, e.g., pollinator mortality rates) is increased. The panels represent (a) a randomly built and (b) a nested plant–pollinator community with the same number of species and interactions. The random network experiences multiple episodes of collapse, while the nested network stands for higher levels of pollinator decline but collapses all at once. Figure adapted with permission from Reference 59.

The prospect of an abrupt decline such as the one described in Reference 59 is reminiscent of a tipping point, so we can try to develop similar early-warning signals of network collapse. We turn our attention to this in the next section.

3.3. Early-Warning Indicators of Network Collapse

Previous work using critical slowing down as a generic indicator of ecosystem shifts used the single time series characterizing the system. Recent reviews, in contrast, deal with a high-dimensional system, with as many temporal series as there are species in the community (plants and pollinators). We could, therefore, apply these indices to each one of the time series in the animal set and each one of the time series in the plant set. A relevant question in this context is whether statistics on a given species or those over the ensemble of all species (or one group of species) work better in terms of early-warning indicators. In cases where individual time series serve better, the next question is which are the best species to use.

Dakos & Bascompte (25) addressed this question using a data set of plant–pollinator and plant–seed dispersal networks to parameterize the dynamical model in Reference 16. They progressively reduced mutualistic strength between plants and animals until the entire community was driven extinct. By comparing time series of species far and close to the onset of community collapse, Dakos & Bascompte found that both the variability and the correlation of these time series in biomass increased (**Figure 6, top**). This pattern applies to both plant and animal species. Similar trends were found for aggregate measures of total community biomass (e.g., all plant species together; **Figure 6, bottom**) (25).

Dakos & Bascompte (25) concluded that specialist species serve best as sensor species to monitor the proximity to a tipping point. On top of this result, this paper found that trends in the critical slowing down for each species correlate well with the order of species extinctions. Specialist species are the best indicators of the proximity to a tipping point because they are the first species being

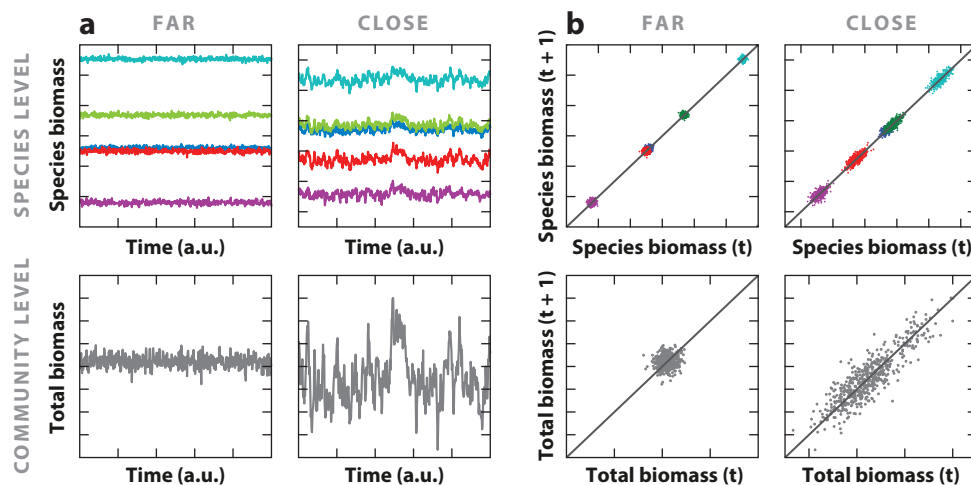


Figure 6

Early-warning indicators of network collapse in the simulated dynamics of a plant–pollinator network (6; network *M_PL_002* available at <https://www.web-of-life.es>). Mutualistic strength was progressively decreased until the network collapsed. Two commonly used indicators of critical slowing down are represented: the (a) variance and (b) autocorrelation of the temporal series of the abundance of each species (top; 5 species out of a total of 107) and the aggregated total community biomass (bottom). Figure adapted with permission from Reference 25.

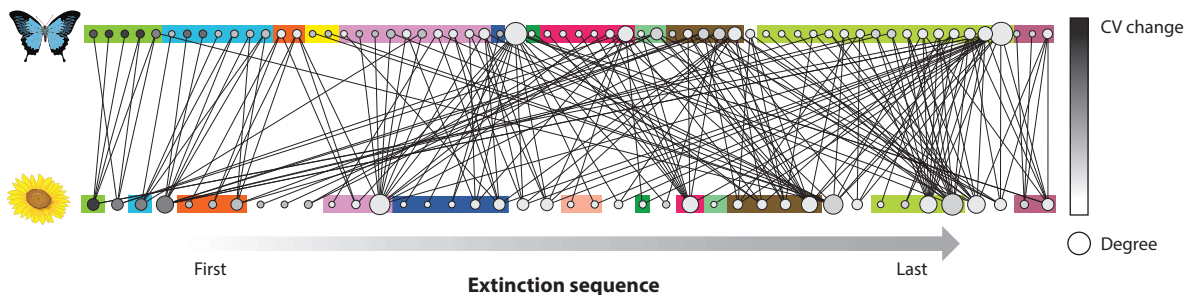


Figure 7

Mapping species resilience based on critical slowing down indicators. The figure represents the pollination network of Cordón del Cepo, Chilean Andes (6; network *M_PL_002* available at <https://www.web-of-life.es>). From left to right, the different species are ranked according to their order of extinction in the numerical simulations. The size and color of each species indicate their number of interactions and change in their coefficient of variability (CV) before the onset of community collapse, respectively. Black colors indicate strong increases in CV. Color boxes group species that went coextinct. There is a positive correlation between the magnitude of the CV change and the order of species extinctions, which can be used to rank species risk of extinction. Figure adapted with permission from Reference 25.

driven extinct. Therefore, this approach could be used as a way of ranking the susceptibility of the different species across a pollination network (**Figure 7**).

Building on the above results, Aparicio and collaborators (5) used a mathematical approach based on the structural observability of dynamical systems to come up with a minimal set of sensor species based exclusively on topological information. This set ensures that one can detect changes in the abundance of all other species in the community as conditions worsen. As any system can contain several such minimal sets of sensors, one can rank species in terms of their presence in a larger number of such sets. A species that appears in all of the minimum set of sensors, therefore, will have a high sensor score, meaning that monitoring this species is essential. Aparicio and collaborators then proceeded to compare the sensor score of a species with its ability to predict the collapse of the community using the same dynamical model as Dakos & Bascompte (25).

While the theory of early-warning signals of ecosystem shifts has been tested experimentally for lakes (22, 107) and laboratory populations (24, 28), no such empirical tests have been developed for networked systems such as those between plants and their pollinators. This would be a much needed direction for future research.

3.4. Predicting the Alternative State

The previous section reviews early-warning signals of the proximity of a pollinator community to an impending transition. Our next question refers to predicting what the alternative state will look like: Is there a single alternative state or several?

Barbour and colleagues (8) showed that an experimental food web mainly collapsed through two paths from the original state of one focal plant, two aphid, and one parasitoid species. Thus, this system transitions either to a scenario with the extinction of all insect species or, more frequently, to a food chain with the parasitoid and one of the aphid species. The second transition was five times more common than the first across replicates (8).

Under some circumstances, one can look at statistical indicators that provide information about the future state of a network. Specifically, Lever et al. (58) found that one such indicator is based on the idea that critical slowing down occurs only for perturbations that bring the system closer to an approaching threshold. As changing conditions undermine the resilience of a network, the size of the disturbance needed to cause a regime shift becomes increasingly small, but it is not

only the size of a disturbance that determines whether a regime shift occurs. The direction of the disturbance in the phase space of a network, i.e., a space in which the abundance of each species is on a separate axis, is also important (41). As conditions change, the network approaches a tipping point, and the distance in this space between the initial stable state and an unstable equilibrium point on the threshold toward the future state becomes increasingly small. Critical slowing down occurs only for perturbations that change abundances in ways that push the network toward this unstable equilibrium point. Because the future state and the threshold toward it are likely to be found in the same direction, this direction of critical slowing down could indicate the relative amount that each species will gain or lose from a regime shift (58).

Lever and colleagues (58) analyzed the time series generated by dynamical models of pollination networks to determine the relative magnitude of fluctuations in the direction of critical slowing down. This measure indicates the future state of the network and becomes increasingly strong as the tipping point is approached. The indicator of direction has one component in the phase space of complex networks for each species. This multidimensional arrow indicates the future state when its components, or scores on the indicator, are directly proportional to the difference in abundance between the initial and the future states. Species with a negative score are thus expected to decrease in abundance, while those with a positive score are expected to increase (58). Interestingly, positive feedbacks, so characteristic of mutualistic systems, are what allow prediction of the alternative state, since delayed negative feedbacks leading to oscillatory or other complex dynamics are relatively weak in comparison to food webs. However, because ecological systems exhibit a combination of different interactions, predicting the alternative state of a plant–pollinator community would become harder once the negative feedbacks involved in competitive interactions have become comparatively large in relation to the strength of positive feedbacks.

3.5. Consequences of Network Collapse for Selection and Evolution of Species

In the previous section, we discuss the possibility of predicting which subset of species and interactions will constitute the alternative state after a pollination network undergoes a (partial) collapse. In this section, we continue this line of reasoning by asking how this alternative state may affect the evolutionary dynamics of the remaining species.

There is growing evidence that the community context can highly influence the (co)evolutionary trajectories of the constituent species. For example, simple models of pollination networks have shown that indirect effects—those between species that do not interact directly but do so through shared partners—can be as relevant as direct effects in shaping trait evolution within complex networks. The role of such indirect effects is stronger for mutualisms of lower specificity, such as those between plants and their pollinators, as opposed to more intimate mutualisms such as those between fish and anemone or between plants and defensive ants (43).

As a particular example, albeit one that illustrates trophic interactions, Barbour and colleagues (7) conducted a field experiment involving a leaf-galling midge (*Iteomyia salicisverruca*) feeding on the willow *Salix hookeriana* and the midge's natural enemies. In the natural, complex food web, the midge was exposed to the two guilds of parasitoids (egg and larval parasitoids), while in a manipulated food web, the larval parasitoid was excluded using mesh bags. This simulates a scenario in which this guild of parasitoids has been driven extinct.

The experiment showed that losing a subset of its natural enemies could make it more difficult for the midge to adapt to future conditions. Specifically, in the complex food web, different combinations of three relevant traits in the midge allowed its survival. In contrast, only one specific trait combination allowed fly survival when the larval parasitoid was excluded (7). This reveals an insidious and unexplored consequence of extinctions, namely, the reduction in the

ability of extant species to adapt in a changing environment. Thus, preserving biodiversity is also crucial for allowing populations to adapt to future environments, an ability that is particularly important in the face of global environmental change.

4. CONCLUDING REMARKS

This review sketches some fresh angles from which to approach an answer to the question of how we may protect the pollination networks on which humanity depends. These angles have been inspired by novel theoretical developments in the fields of networks and tipping points. We do realize, however, that these theories remain rather abstract and may seem far removed from the practical challenges in conservation ecology. Nonetheless, the advances that we highlight do have profound implications for our understanding of the fundamental mechanisms that shape resilience and transitions in ecological communities. We hope that the perspective that we have sketched will inspire efforts to explore ways of linking the new theory to reality.

To summarize the challenge, theory suggests four ways in which the resilience of pollination networks may be enhanced: (a) rewiring the network of interactions, (b) increasing the heterogeneity of the species, (c) allowing variability, and (d) enhancing coevolution. One may think of each of these factors in more concrete terms such as (a) increasing nestedness up to a point that maximizes feasibility without reducing stability, (b) promoting the genetic diversity of species, (c) allowing populations to fluctuate, and (d) fostering the coevolution of local populations. However, this obviously leaves two major challenges: to work out practical ways to do all of this and to test predictions of the theory in real field situations.

The theoretical work also suggests that there is a fundamental trade-off in which enhancing resilience comes at the cost of making a possible future collapse more dramatic. For instance, the higher the resilience caused by features such as the nested structure of model pollinator networks, the more simultaneous this collapse is across species (59). We do not know yet how generic this result is. It will be important to integrate these contrasting aspects of community resilience into a single framework. In addition, translating the framework advocated in this review to the practice of conservation ecology is a major challenge. Are there ways to promote resilience without setting up the system for a major collapse if a tipping point is ultimately reached?

Clearly, the challenges of bringing theory into practice are formidable. However, the insights that we highlight above suggest that a lot may be gained if we design conservation strategies that go beyond preventing the direct loss of independent species. An integrative approach taking the complex web of interactions into account may be worth considering for finding ways to ensure that pollinator communities can thrive in a changing world.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Christina Grozinger for encouraging us to write this review. Discussions with Jelle Lever shaped our thinking, particularly on the relationship between the work by Buzz Holling and related approaches. Klementyna Gawecka, Paulo (Miúdo) Guimarães, Rodrigo Cámara-Leret, Matt Hutchinson, Matt Barbour, and Marília Gaiarsa provided feedback on a previous draft and/or pointed out relevant literature. The Swiss National Science Foundation provided financial support (grant 310030_197201 to J.B.).

LITERATURE CITED

1. Aizen MA, Aguiar S, Biesmeijer JC, Garibaldi LA, Inouye DW, et al. 2019. Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Glob. Change Biol.* 25(10):3516–27
2. Alberch P. 1989. The logic of monsters: evidence for internal constraint in development and evolution. *Geobios* 22:21–57
3. Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, et al. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv. Biol.* 12(1):8–17
4. Allesina S, Tang S. 2012. Stability criteria for complex ecosystems. *Nature* 483(7388):205–8
5. Aparicio A, Velasco-Hernández JX, Moog CH, Liu YY, Angulo MT. 2021. Structure-based identification of sensor species for anticipating critical transitions. *PNAS* 118(51):e2104732118
6. Arroyo MTK, Primack R, Armesto JJ. 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. *Am. J. Bot.* 69:82–97
7. Barbour MA, Greyson-Gaito CJ, Sotoodeh A, Locke B, Bascompte J. 2020. Loss of consumers constrains phenotypic evolution in the resulting food web. *Evol. Lett.* 4(3):266–77
8. Barbour MA, Kliebenstein DJ, Bascompte J. 2022. A keystone gene underlies the persistence of an experimental food web. *Science* 376:70–73
9. Barnosky AD, Hadly EA, Bascompte J, Berlow EL, Brown JH, et al. 2012. Approaching a state shift in Earth's biosphere. *Nature* 486(7401):52–58
10. Bartomeus I, Saavedra S, Rohr RP, Godoy O. 2021. Experimental evidence of the importance of multitrophic structure for species persistence. *PNAS* 118(12):e2023872118
11. Bascompte J. 2009. Disentangling the web of life. *Science* 325(5939):416–19
12. Bascompte J, Ferrera A. 2020. A structural theory of mutualistic networks. In *Theoretical Ecology: Concepts and Applications*, ed. KS McCann, G Gellner, pp. 93–115. Oxford, UK: Oxford Univ. Press
13. Bascompte J, García MB, Ortega R, Rezende EL, Pironon S. 2019. Mutualistic interactions reshuffle the effects of climate change on plants across the tree of life. *Sci. Adv.* 5(5):eaav2539
14. Bascompte J, Jordano P. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 38:567–93
15. Bascompte J, Jordano P, Melián CJ, Olesen JM. 2003. The nested assembly of plant-animal mutualistic networks. *PNAS* 100(16):9383–87
16. Bastolla U, Fortuna MA, Pascual-García A, Ferrera A, Luque B, Bascompte J. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458(7241):1018–20
17. Biesmeijer J, Roberts S, Reemer M, Ohlemüller R, Edwards M, et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313:351–54
18. Bryden J, Gill R, Mitton R, Raine N, Jansen V. 2013. Chronic sublethal stress causes bee colony failure. *Ecol. Lett.* 16:1463–69
19. Burgos E, Ceva H, Perazzo RP, Devoto M, Medan D, et al. 2007. Why nestedness in mutualistic networks? *J. Theor. Biol.* 249(2):307–13
20. Burkle LA, Marlin JC, Knight TM. 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* 339(6127):1611–15
21. Carpenter SR, Brock WA, Folke C, Nes EHV, Scheffer M. 2015. Allowing variance may enlarge the safe operating space for exploited ecosystems. *PNAS* 112(46):14384–89
22. Carpenter SR, Cole JJ, Pace ML, Batt R, Brock WA, et al. 2011. Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332(6033):1079–82
23. Cenci S, Saavedra S. 2018. Structural stability of nonlinear population dynamics. *Phys. Rev. E* 97(1):012401
24. Dai L, Vorselen D, Korolev KS, Gore J. 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* 336(6085):1175–77
25. Dakos V, Bascompte J. 2014. Critical slowing down as early warning for the onset of collapse in mutualistic communities. *PNAS* 111(49):17546–51

26. de Andreazzi CS, Astegiano J, Guimarães PR. 2020. Coevolution by different functional mechanisms modulates the structure and dynamics of antagonistic and mutualistic networks. *Oikos* 129(2):224–37
27. Diaz S, Chapin FI, Potts S. 2005. Biodiversity regulation of ecosystem services. In *Ecosystems and Human Well-Being: Current State and Trends*, Vol. 1, ed. Millenn. Ecosyst. Assess., pp. 297–329. Washington, DC: Island Press
28. Drake JM, Griffen BD. 2010. Early warning signals of extinction in deteriorating environments. *Nature* 467(7314):456–59
29. Dunne JA, Williams RJ, Martinez ND. 2002. Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecol. Lett.* 5(4):558–67
30. Ebeling A, Klein A, Schumacher J, Weisser WW, Tschardt T. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* 117(12):1808–15
31. Fares S, Mugnoz G, Corona P, Palahí M. 2015. Sustainability: five steps for managing Europe's forests. *Nature* 519:407–9
32. Fontaine C, Dajoz I, Meriguet J, Loreau M. 2006. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLOS Biol.* 4(1):e1
33. Gao J, Barzel B, Barabási AL. 2016. Universal resilience patterns in complex networks. *Nature* 530(7590):307–12
34. Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339(6127):1608–11
35. Gawecka KA, Pedraza F, Bascompte J. 2022. Effects of habitat destruction on coevolving metacommunities. *Ecol. Lett.* In press
36. Genung MA, Lessard JP, Brown CB, Bunn WA, Cregger MA, et al. 2010. Non-additive effects of genotypic diversity increase floral abundance and abundance of floral visitors. *PLOS ONE* 5(1):e8711
37. Ghazoul J. 2006. Floral diversity and the facilitation of pollination. *J. Ecol.* 94(2):295–304
38. Gilarranz LJ, Rayfield B, Linan-Cembrano G, Bascompte J, Gonzalez A. 2017. Effects of network modularity on the spread of perturbation impact in experimental metapopulations. *Science* 357(6347):199–201
39. Gonzalez A, Rayfield B, Lindo Z. 2011. The disentangled bank: how loss of habitat fragments and disassembles ecological networks. *Am. J. Bot.* 98(3):503–16
40. Goulson D, Nicholls E, Botías C, Rotheray EL. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347(6229):1255957
41. Grilli J, Adorisio M, Suweis S, Barabás G, Banavar JR, et al. 2017. Feasibility and coexistence of large ecological communities. *Nat. Commun.* 8:523
42. Guimarães PR Jr. 2020. The structure of ecological networks across levels of organization. *Annu. Rev. Ecol. Evol. Syst.* 51:433–60
43. Guimarães PR Jr., Rico-Gray V, Oliveira P, Izzo TJ, dos Reis SF, Thompson JN. 2007. Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. *Curr. Biol.* 17(20):1797–803
44. Guimerà R, Amaral LAN. 2005. Functional cartography of complex metabolic networks. *Nature* 433:895–900
45. Hagen M, Kissling WD, Rasmussen C, Aguiar MAD, Brown LE, et al. 2012. Biodiversity, species interactions and ecological networks in a fragmented world. *Adv. Ecol. Res.* 46:89–210
46. Haldane AG, May RM. 2011. Systemic risk in banking ecosystems. *Nature* 469(7330):351–55
47. Hattab T, Leprieux F, Ben Rais Lasram F, Gravel D, Le Loc'h F, Albouy C. 2016. Forecasting fine-scale changes in the food-web structure of coastal marine communities under climate change. *Ecography* 39(12):1227–37
48. Henry M, Béguin M, Requier F, Rollin O, Odoux JF, et al. 2012. A common pesticide decreases foraging success and survival in honey bees. *Science* 336(6079):348–50
49. Holling CS. 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Evol. Syst.* 4:1–23
50. Holmgren N, Norrström N, Aps R, Kuikka S. 2014. A concept of Bayesian regulation in fisheries management. *PLOS ONE* 9(11):e111614
51. Ings TC, Montoya JM, Bascompte J, Blüthgen N, Brown L, et al. 2009. Ecological networks—beyond food webs. *J. Anim. Ecol.* 78(1):253–69

52. Janzen DH. 1974. The deflowering of Central America. *Nat. Hist.* 83:48–53
53. Janzen DH, Hallwachs W. 2021. To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let's be kind to the survivors. *PNAS* 118(2):e2002546117
54. Jaunker F, Jaunker B, Grass I, Steffan-Dewenter I, Wolters V. 2019. Partitioning wild bee and hoverfly contributions to plant–pollinator network structure in fragmented habitats. *Ecology* 100(2):e02569
55. Justus J. 2014. Ecological and Lyapunov stability. *Philos. Sci.* 75:421–36
56. Kelly LT, Giljohann KM, Duane A, Aquilué N, Archibald S, et al. 2020. Fire and biodiversity in the Anthropocene. *Science* 370(6519):eabb0355
57. Kudo G, Ida TY. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* 94(10):2311–20
58. Lever JJ, van de Leemput IA, Weinans E, Quax R, Dakos V, et al. 2020. Foreseeing the future of mutualistic communities beyond collapse. *Ecol. Lett.* 23(1):2–15
59. Lever JJ, Van Nes EH, Scheffer M, Bascompte J. 2014. The sudden collapse of pollinator communities. *Ecol. Lett.* 17(3):350–59
60. Levine JM, Bascompte J, Adler PB, Allesina S. 2017. Beyond pairwise mechanisms of species coexistence in complex communities. *Nature* 546(7656):56–64
61. López-Urbe MM, Soro A, Jha S. 2017. Conservation genetics of bees: advances in the application of molecular tools to guide bee pollinator conservation. *Conserv. Genet.* 18(3):501–6
62. May RM. 1972. Will a large complex system be stable? *Nature* 238(5364):413–14
63. McCann KS. 2000. The diversity–stability debate. *Nature* 405:228–33
64. Meeus I, Brown M, De Graaf D, Smagghe G. 2011. Effects of invasive parasites on bumble bee declines. *Conserv. Biol.* 25(4):662–71
65. Memmott J, Craze PG, Waser NM, Price MV. 2007. Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* 10(8):710–17
66. Memmott J, Waser NM, Price MV. 2004. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B* 271(1557):2605–11
67. Moreira F, Ascoli D, Safford H, Adams MA, Moreno JM, et al. 2020. Wildfire management in Mediterranean-type regions: paradigm change needed. *Environ. Res. Lett.* 15(1):011001
68. Morone F, Ferraro GD, Makse HA. 2019. The k-core as a predictor of structural collapse in mutualistic ecosystems. *Nat. Phys.* 15(1):95–102
69. Newman MEJ, Girvan M. 2004. Finding and evaluating community structure in networks. *Phys. Rev. E* 69:026113
70. Nosil P, Gompert Z. 2022. Eco–evolutionary effects of keystone genes. *Science* 376(6588):30–31
71. Okuyama T, Holland JN. 2008. Network structural properties mediate the stability of mutualistic communities. *Ecol. Lett.* 11(3):208–16
72. Pascual M, Dunne JA. 2006. *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford, UK: Oxford Univ. Press
73. Pellissier L, Rohr RP, Ndiribe C, Pradervand JN, Salamin N, et al. 2013. Combining food web and species distribution models for improved community projections. *Ecol. Evol.* 3(13):4572–83
74. Pimm SL. 1984. The complexity and stability of ecosystems. *Nature* 307:321–26
75. Pires MM, O'Donnell JL, Burkle LA, Díaz-Castelazo C, Hembry DH, et al. 2020. The indirect paths to cascading effects of extinctions in mutualistic networks. *Ecology* 101(7):e03080
76. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25(6):345–53
77. Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P. 2003. Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* 84(10):2628–42
78. Ramos SE, Schiestl FP. 2019. Rapid plant evolution driven by the interaction of pollination and herbivory. *Science* 364(6436):193–96
79. Rezende EL, Lavabre JE, Guimarães PR, Jordano P, Bascompte J. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448:925–28
80. Rohr RP, Saavedra S, Bascompte J. 2014. On the structural stability of mutualistic systems. *Science* 345(6195):1253497

81. Saavedra S, Rohr RP, Dakos V, Bascompte J. 2013. Estimating the tolerance of species to the effects of global environmental change. *Nat. Commun.* 4:2350
82. Saavedra S, Rohr RP, Olesen JM, Bascompte J. 2016. Nested species interactions promote feasibility over stability during the assembly of a pollinator community. *Ecol. Evol.* 6(4):997–1007
83. Sabatino M, Maceira N, Aizen AM. 2010. Direct effects of habitat area on interaction diversity in pollination webs. *Ecol. Appl.* 20:1491–97
84. Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, et al. 2009. Early-warning signals for critical transitions. *Nature* 461(7260):53–59
85. Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. *Nature* 413(6856):591–96
86. Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, et al. 2012. Anticipating critical transitions. *Science* 338(6105):344–48
87. Schleuning M, Fründ J, Schweiger O, Welk E, Albrecht J, et al. 2016. Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nat. Commun.* 7:13965
88. Shuster S, Lonsdorf E, Wimp G, Bailey J, Whitham T. 2006. Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution* 60(5):991–1003
89. Siviter H, Bailes EJ, Martin CD, Oliver TR, Koricheva J, et al. 2021. Agrochemicals interact synergistically to increase bee mortality. *Nature* 596(7872):389–92
90. Skovmand LH, Xu CC, Servedio MR, Nosil P, Barrett RD, Hendry AP. 2018. Keystone genes. *Trends Ecol. Evol.* 33(9):689–700
91. Solé R, Montoya JM. 2001. Complexity and fragility in ecological networks. *Proc. R. Soc. B* 268(1480):2039–45
92. Song C, Rohr RP, Saavedra S. 2018. A guideline to study the feasibility domain of multi-trophic and changing ecological communities. *J. Theor. Biol.* 450:30–36
93. Sonne J, Maruyama PK, González AMM, Rahbek C, Bascompte J, Dalsgaard B. 2022. Extinction, co-extinction and colonization dynamics in plant–hummingbird networks under climate change. *Nat. Ecol. Evol.* 6:720–29
94. Spiesman BJ, Inouye BD. 2013. Habitat loss alters the architecture of plant–pollinator interaction networks. *Ecology* 94(12):2688–96
95. Staniczenko PP, Sivasubramaniam P, Suttle KB, Pearson RG. 2017. Linking macroecology and community ecology: refining predictions of species distributions using biotic interaction networks. *Ecol. Lett.* 20(6):693–707
96. Stouffer DB, Bascompte J. 2011. Compartmentalization increases food-web persistence. *PNAS* 108(9):3648–52
97. Strogatz SH. 1994. *Nonlinear Dynamics and Chaos*. New York: Perseus Books
98. Stuligross C, Williams NM. 2021. Past insecticide exposure reduces bee reproduction and population growth rate. *PNAS* 118(48):e2109909118
99. Suweis S, Simini F, Banavar JR, Maritan A. 2013. Emergence of structural and dynamical properties of ecological mutualistic networks. *Nature* 500(7463):449–52
100. Thébault E, Fontaine C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329(5993):853–56
101. Thom R. 1994. *Structural Stability and Morphogenesis*. Boston: Addison-Wesley
102. Traveset A, Castro-Urgal R, Rotllán-Puig X, Lázaro A. 2018. Effects of habitat loss on the plant–flower visitor network structure of a dune community. *Oikos* 127(1):45–55
103. Tylianakis JM, Didham RK, Bascompte J, Wardle DA. 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11(12):1351–63
104. van Nes EH, Arani BM, Staal A, van der Bolt B, Flores BM, et al. 2016. What do you mean, “tipping point”? *Trends Ecol. Evol.* 31:902–4
105. Vandermeer JH. 1970. The community matrix and the number of species in a community. *Am. Nat.* 104:73–83
106. Vieira MC, Almeida-Neto M. 2015. A simple stochastic model for complex coextinctions in mutualistic networks: Robustness decreases with connectance. *Ecol. Lett.* 18(2):144–52

107. Wang R, Dearing JA, Langdon PG, Zhang E, Yang X, et al. 2012. Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature* 492(7429):419–22
108. Whitehorn PR, O'Connor S, Wackers FL, Goulson D. 2012. Neonicotinoid pesticide reduces bumble bee colony growth and queen production. *Science* 336(6079):351–52
109. Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* 7(7):510–23
110. Wuest SE, Niklaus PA. 2018. A plant biodiversity effect resolved to a single chromosomal region. *Nat. Ecol. Evol.* 2(12):1933–39

Contents

Complex and Beautiful: Unraveling the Intricate Communication Systems Among Plants and Insects <i>James H. Tumlinson</i>	1
Chemical Ecology of Floral Resources in Conservation Biological Control <i>Stefano Colazza, Ezio Peri, and Antonino Cusumano</i>	13
Management of Insect Pests with Bt Crops in the United States <i>Aaron J. Gassmann and Dominic D. Reisig</i>	31
Iron Homeostasis in Insects <i>Maureen J. Gorman</i>	51
Phoresy and Mites: More Than Just a Free Ride <i>Owen D. Seeman and David Evans Walter</i>	69
Postcopulatory Behavior of Tephritid Flies <i>Diana Pérez-Staples and Solana Abraham</i>	89
The Biology and Ecology of Parasitoid Wasps of Predatory Arthropods <i>Minghui Fei, Rieta Gols, and Jeffrey A. Harvey</i>	109
Dehydration Dynamics in Terrestrial Arthropods: From Water Sensing to Trophic Interactions <i>Joshua B. Benoit, Kevin E. McCluney, Matthew J. DeGennaro, and Julian A.T. Dow</i>	129
Biology and Management of the Spotted Lanternfly, <i>Lycorma delicatula</i> (Hemiptera: Fulgoridae), in the United States <i>Julie M. Urban and Heather Leach</i>	151
Historical and Contemporary Control Options Against Bed Bugs, <i>Cimex</i> spp. <i>Stephen L. Doggett and Chow-Yang Lee</i>	169
Functional Diversity of Vibrational Signaling Systems in Insects <i>Meta Virant-Doberlet, Nataša Stritib-Peljhan, Alenka Žunič-Kosi, and Jernej Polajnar</i>	191
Forest Insect Biosecurity: Processes, Patterns, Predictions, Pitfalls <i>Helen F. Nahrung, Andrew M. Liebhold, Eckehard G. Brockerhoff, and Davide Rassati</i>	211

Stingless Bee (Apidae: Apinae: Meliponini) Ecology <i>David W. Roubik</i>	231
Diapause in Univoltine and Semivoltine Life Cycles <i>Hideharu Numata and Yoshinori Shintani</i>	257
Early Monitoring of Forest Wood-Boring Pests with Remote Sensing <i>Youqing Luo, Huaguo Huang, and Alain Roques</i>	277
<i>Spodoptera frugiperda</i> : Ecology, Evolution, and Management Options of an Invasive Species <i>Wee Tek Tay, Robert L. Meagher Jr., Cecilia Czapak, and Astrid T. Groot</i>	299
Molecular Mechanisms of Winter Survival <i>Nicholas M. Teets, Katie E. Marshall, and Julie A. Reynolds</i>	319
Arthropod and Pathogen Damage on Fossil and Modern Plants: Exploring the Origins and Evolution of Herbivory on Land <i>Conrad C. Labandeira and Torsten Wappler</i>	341
The Resilience of Plant–Pollinator Networks <i>Jordi Bascompte and Marten Scheffer</i>	363
The Mechanisms of Silkworm Resistance to the Baculovirus and Antiviral Breeding <i>Zhaoyang Hu, Feifei Zhu, and Keping Chen</i>	381
Diversity, Form, and Postembryonic Development of Paleozoic Insects <i>Jakub Prokop, André Nel, and Michael S. Engel</i>	401
Molecular Mechanisms Underlying Host Plant Specificity in Aphids <i>Po-Yuan Shib, Akiko Sugio, and Jean-Christophe Simon</i>	431
Adaptive Plasticity of Insect Eggs in Response to Environmental Challenges <i>Monika Hilker, Hassan Salem, and Nina E. Fatouros</i>	451

Errata

An online log of corrections to *Annual Review of Entomology* articles may be found at
<http://www.annualreviews.org/errata/ento>

Related Articles

From the *Annual Review of Animal Biosciences*, Volume 10 (2022)

Translating Basic Research to Animal Agriculture

George E. Seidel Jr.

Concepts and Consequences of a Core Gut Microbiota for Animal Growth and Development

Daphne Perlman, Marina Martínez-Álvarez, Sarah Morais, Ianina Altsbuler, Live H. Hagen, Elie Jami, Rainer Roebe, Phillip B. Pope, and Itzhak Mizrahi

Host Genetic Determinants of the Microbiome Across Animals:

From *Caenorhabditis elegans* to Cattle

Erica P. Ryu and Emily R. Davenport

Chagas Disease Ecology in the United States: Recent Advances in Understanding *Trypanosoma cruzi* Transmission Among Triatomines, Wildlife, and Domestic Animals and a Quantitative Synthesis of Vector–Host Interactions

Rachel E. Busselman and Sarah A. Hamer

From the *Annual Review of Genetics*, Volume 56 (2022)

The Genetics of Autophagy in Multicellular Organisms

Hong Zhang

From the *Annual Review of Microbiology*, Volume 76 (2022)

Division and Transmission: Malaria Parasite Development in the Mosquito

David S. Guttery, Mohammad Zeeshan, David J.P. Ferguson, Anthony A. Holder, and Rita Tewari

From the *Annual Review of Phytopathology*, Volume 60 (2022)

Yellow Dwarf Viruses of Cereals: Taxonomy and Molecular Mechanisms

W. Allen Miller and Zachary Lozier

Future of Bacterial Disease Management in Crop Production

Anuj Sharma, Peter Abrahamian, Renato Carvalho, Manoj Choudhary, Mathews L. Paret, Gary E. Vallad, and Jeffrey B. Jones

Ecology of Yellow Dwarf Viruses in Crops and Grasslands: Interactions in the Context of Climate Change

Jasmine S. Peters, Beatriz A. Aguirre, Anna DiPaola, and Alison G. Power

From the *Annual Review of Virology*, Volume 9 (2022)

Citrus Tristeza Virus: From Pathogen to Panacea

Svetlana Y. Folimonova and Yong-Duo Sun

Advances in Understanding Neuropathogenesis of Rift Valley Fever Virus

Kaleigh A. Connors and Amy L. Hartman