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The Resilience of Plant–Pollinator Networks

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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

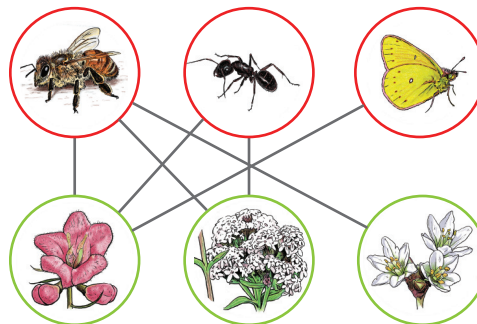


Figure 1

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.

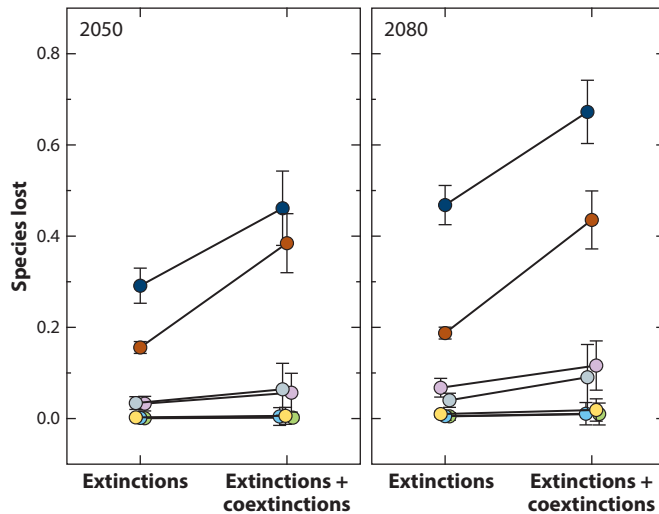


Figure 2

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

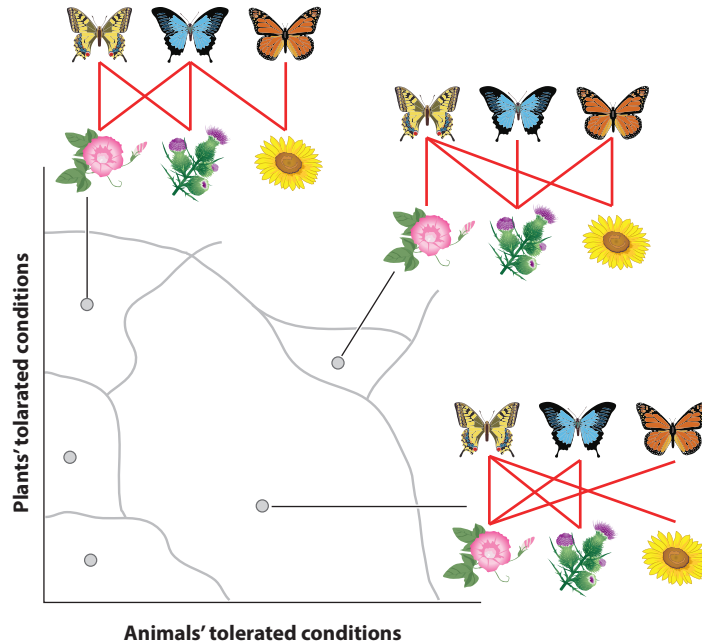


Figure 3

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

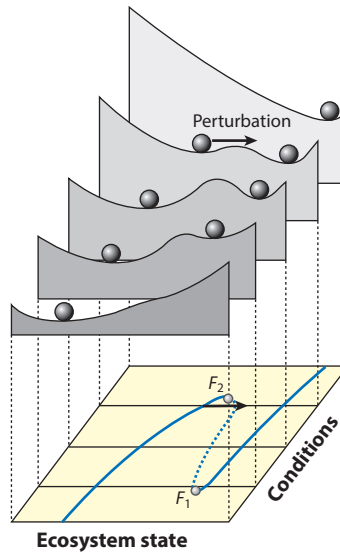


Figure 4

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.

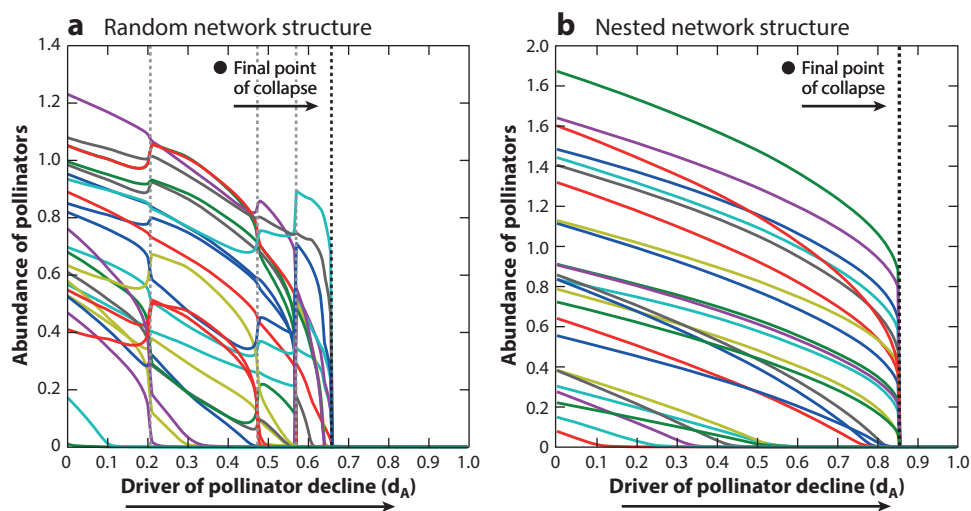


Figure 5

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

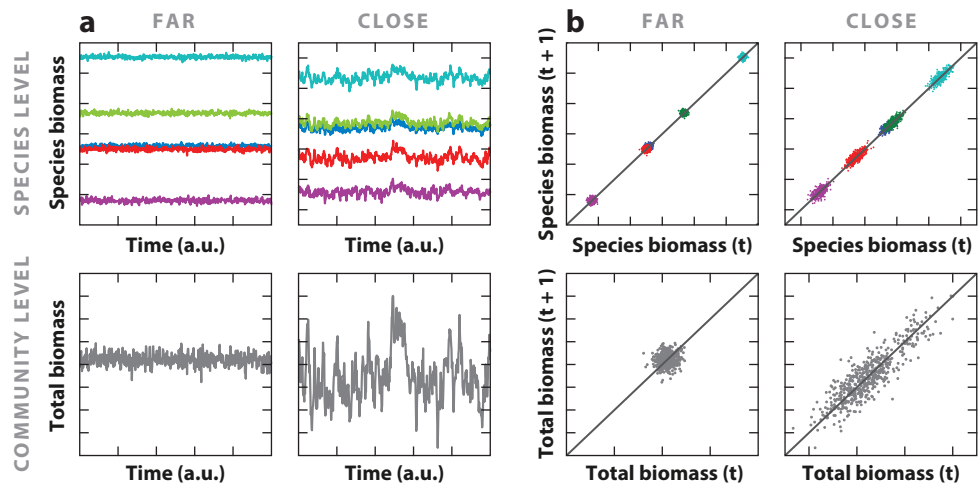


Figure 6

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.

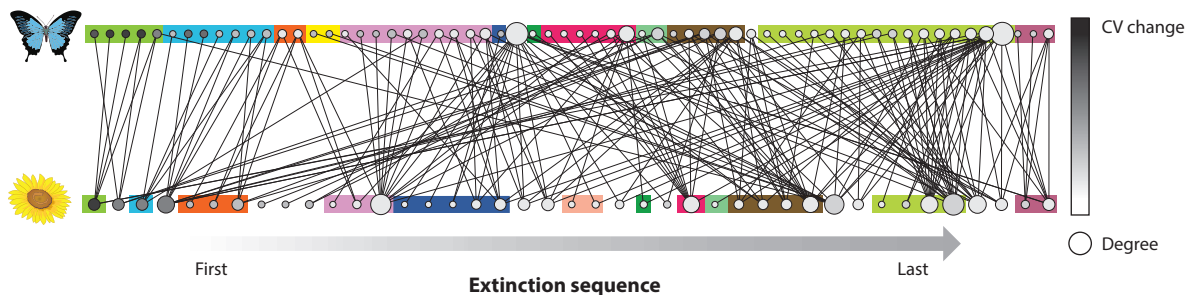


Figure 7

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.

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