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The fundamental benefits of multiplexity in ecological networks

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A tipping point presents perhaps the single most significant threat to an ecological system as it can lead to abrupt species extinction on a massive scale. Climate changes leading to the species decay parameter drifts can drive various ecological systems towards a tipping point. We investigate the tipping-point dynamics in multilayer ecological networks supported by mutualism. We unveil a natural mechanism by which the occurrence of tipping points can be delayed by multiplexity that broadly describes the diversity of the species abundances, the complexity of the interspecific relationships, and the topology of linkages in ecological networks. For a double-layer system of pollinators and plants, coupling between the network layers occurs when there is dispersal of pollinator species. Multiplexity emerges as the dispersing species establish their presence in the destination layer and have a simultaneous presence in both. We demonstrate that the new mutualistic links induced by the dispersing species with the residence species have fundamental benefits to the well being of the ecosystem in delaying the tipping point and facilitating species recovery. Articulating and implementing control mechanisms to induce multiplexity can thus help sustain certain types of ecosystems that are in danger of extinction as the result of environmental changes.

Key words: tipping point, mutualistic networks, multiplexity, species extinction, species dispersal, nonlinear dynamics, complex networks

Introduction

Complex networked systems in the real world are often dependent upon each other. Such interdependent, multilayer networks are also referred to as networks-of-networks [1]. One of the best known examples of such systems is urban infrastructure systems [2] consisting of transportation, communication, electric power, and water supply networks, which are heavily dependent upon each other. For instance, the operation of electric power grids is controlled by the communication network, but the former provides electricity that is essential to the latter. Another example is brain networks, where the necessity to use multilayer modeling and analysis to understand the structure and function of the human brain has begun to be appreciated [3–7]. In recent years, the concept of multilayer networks has also been adopted to ecology [8–12].

The dynamics and robustness of multilayer networks have been an area of active research in network science and engineering [13–27]. Most previous studies of dynamical processes on multilayer networks focused on cascading failures [1,14,15,28,29], percolation [13,21,24,25,30–36], and disease spreading [22,23,26,27]. Take the urban infrastructure systems as an example. Because of the sharing of services among these systems, the loss of a single service such as mobility can impact others including electric power and clean water supplies. From a dynamical point of view, when a node or a link in one infrastructure network fails, because of the interdependencies, the failure can propagate to other infrastructure networks [37]. To understand the ways by which interdependencies in multilayer networks affect robustness is essential to making resilience recommendations and developing control strategies.

Multiplexity is a basic notion in complex multilayer networks, where a subset of nodes belong simultaneously to different network layers. An example is virus or disease spreading in the human society, where an individual is simultaneously a node in the physical contact layer that actually spreads the virus and a node in the virtual layer that diffuses all kinds of real information or disinformation about the virus [22]. In such a case, multiplexity arises naturally and is intrinsic to the dynamical processes in both the physical and virtual layers. As to be explained, *the main point of this paper is that multiplexity can also arise in multilayer ecological networks and, more importantly, it has the fundamental benefits to sustaining the whole networked system and keeping it in a healthy state by delaying, often significantly, the occurrence of a catastrophic tipping point that would otherwise lead to extinction on a massive scale.*

In complex ecological networks, tipping point is a fundamental dynamical phenomenon [38–59]. A tipping point is a point of "no return" in the parameter space where, as the bifurcation parameter of the system passes through a critical value, the whole system collapses. In a physical network, such a collapse can manifest itself as a catastrophic breakdown of the system. In an ecological network, the collapse can result in massive species extinction. From a dynamical point of view, a tipping point is the result of the systems passing through a bifurcation point, typically a forward or a backward saddle-node bifurcation. A typical scenario is that, in a parameter regime of interest, there are two coexisting stable fixed-point attractors: one corresponding to the normal or "healthy" state of the system but the other to a catastrophic behavior, e.g., extinction. Suppose that, as the parameter value increases, a backward saddle-node bifurcation occurs, after which the healthy fixed point together with its basin of attraction is destroyed, leaving the catastrophic fixed point as the only attractor in the system. The critical parameter value at which the saddle-node bifurcation occurs is the tipping point.

Given the ubiquity of multilayer networks in natural and engineering systems, a concerning issue of considerable interest is the interplay among the tipping-point dynamics in different network layers. For example, if the network in one layer has experienced a tipping point, would a tipping-point transition occur in another layer because of the interdependence between the two layers? A related issue is whether the processes of recovery in the aftermath of a tipping point in different network layers would promote or impede each other. In spite of the large literature on multilayer networks and on tipping-point dynamics, the interplay between the two has not been studied. This represents a gap in our knowledge about complex dynamical systems. The aim of this paper is to fill this gap.

For simplicity, we consider an interdependent networked system of two layers that are coupled together through some physical flow or flux between them. We assume that each layer has a mutualistic network of plants and pollinators [51,54,60–62], so the whole system models the situation of interaction and interdependence of two ecological networks that are respectively located in two adjacent geographical regions. The coupling between the two network layers is due to the dispersal of pollinator species. Depending on the specific networks in the two layers, there are two different scenarios of coupling. In the first scenario, the two networks share a subset of identical pollinator species, which are the common nodes in the two layers so the double-layer configuration is intrinsically a duplex networked system. In this case, the common species can disperse from one layer to another without establishing new nodes and new mutualistic relationships with the existing species in the latter. While the coupling changes the overall species abundances in both layers, the network structures remain intact. For convenience, we call this type of interaction between the two layers that results in no change in the network structure as *type-I coupling*. In the second scenario, prior to the occurrence of any species dispersal, there are no common species between the two layers. That is, in the absence of coupling, the double-layer system does *not* have a duplex structure. In this case, the dispersing species from one layer can establish new nodes and new mutualistic relationships with the resident species in the other layer. The coupling thus not only changes the structure of the mutualistic network in the latter, but more importantly, *induces* multiplexity. This is denoted as *type-II coupling*. We note that type-II coupling can be understood as a species turnover and rewiring. In particular, the migration rates are randomly selected and the migrating species may survive at a low abundance or even disappear in the original layer, but could survive and rewire in the new sublayer. When migrating species reach the new sublayer, they wire new links over the original network structure, resulting in a new structure. This can occur, for example, when certain pollinator species migrate to a different region. A key observation is that, regardless of the coupling type, there is multiplexity in the double-layer interdependent network system.

The main findings are the following. Type-I coupling can result in a slight delay in the occurrence of a tipping point in the network layer into which the species disperse, and the coupling has little effect on the resilience of the whole double-layer system. However, type-II coupling has a much more significant effect on delaying the tipping point than type-I coupling, and the tipping point can be suppressed when the coupling is sufficiently strong. In particular, by establishing new mutualistic relationships there, mutualism is strengthened, leading to stronger connections among the species. As the number of established mutualistic relationships increases, there is a substantial delay in the occurrence of the collapsing tipping point. That is, *induced multiplexity can make the whole system significantly more resilient*. (In Supplementary Information, we develop a heuristic theoretical understanding of these findings through an effective dimension-reduced model and obtain solutions of the delay of the tipping point as the result of the induced multiplexity.)

It is worth noting that mutualistic networks are ubiquitous in ecosystems, providing coexisting symbiotic relationships by which species depend on and benefit from each other [51,60–73]. Examples include the coral polyps that make up the giant coral reefs [74] and bacteria in human intestinal flora [75]. The pollinator-plant network is one such example, being highly important because flowering plants rely on pollinators for reproduction and survival, and the pollinators rely on plants to sustain themselves. Habitat destruction, parasites, diseases, and pesticides leading to environmental changes are linked to large-scale population extinctions of wild bees, possibly through the dynamical mechanism of a tipping point transition. At the same time, many of the still surviving species are in danger of extinction. The extinction and decline of pollinator species are damaging to both ecosystems and agriculture, rendering important and critical to devise strategies to preserve pollinator diversity [56,76]. Our finding and understanding of how the tipping points of two interdependent mutualistic networks are affected by their coupling and the uncovered beneficial role of multiplexity provide insights into developing methods to mitigate or control the tipping point.

Double-layer mutualistic network model and coupling types

Our double-layer system is constructed from the bipartite mutualistic network model [51,54,60–62] with the Holling type of dynamics [77], where the two layers are coupled through species dispersal, as schematically illustrated in Fig. 1. For a single mutualistic network, a generic model must include the following processes: intrinsic growth, intraspecific and interspecific competitions, and mutualistic interactions among the plant and pollinator species. These effects were considered by

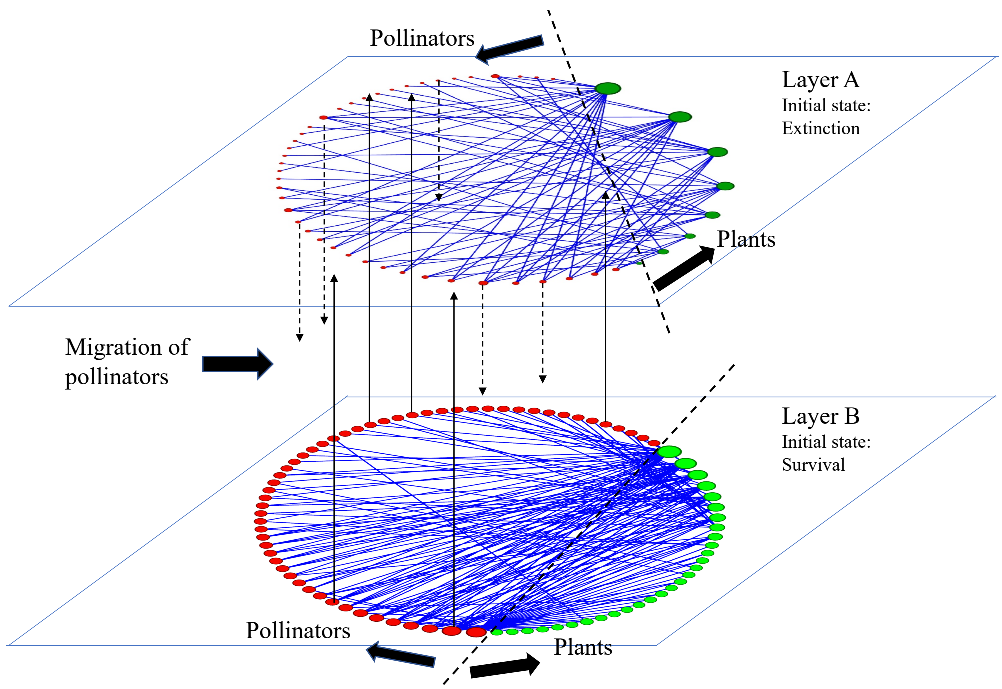

Figure 1: Schematic illustration of a double-layer mutualistic network system and simulation setting. The layers are denoted as A and B. Each layer hosts a mutualistic network, where the filled circles represent pollinator and plant species, and interactions occur only between the pollinator and plant species. In layer A, a tipping point has already occurred so its network is in the extinction state. In layer B, the network has not experienced a tipping point so it is in the survival state. Pollinator dispersal occurs both ways but initially, the dominant flux is from B to A (the solid arrows), because the species abundances in B are much larger than those in layer A, enabling recovery of the species abundances in in A. During the recovery process, the flux from A to B gradually increases (dashed arrows), preventing a tipping point from occurring in layer B.

Lever et al. and Rohr et al. in their pioneering work to derive a comprehensive model of differential equations [51,60], with all detailed reasoning and derivation steps therein. Here, we adopt their single-layer differential equation model to our double-layer system. In particular, mathematically, a double-layer network dynamics model is described by the following set of differential equations:

$$\frac{dX_i^{(a)}}{dt} = X_i^{(a)}\left(\alpha_i^{X^{(a)}} - \kappa_i^{X^{(a)}} - \sum_{j=1}^{S_X^{(a)}} \beta_{ij}^{(X^{(a)})} X_j^{(a)} + \frac{\sum_{k=1}^{S_Y^{(a)}} \gamma_{ik}^{(X^{(a)})} Y_k^{(a)}}{1 + h\sum_{k=1}^{S_Y^{(a)}} \gamma_{ik}^{(X^{(a)})} Y_k^{(a)}}\right) + \mu_{in}^{(a)} X_i^{(b)} - \mu_{out}^{(a)} X_i^{(a)}, \tag{1}$$

$$\frac{dY_i^{(a)}}{dt} = Y_i^{(a)}\left(\alpha_i^{Y^{(a)}} - \sum_{j=1}^{S_Y^{(a)}} \beta_{ij}^{(Y^{(a)})} Y_j^{(a)} + \frac{\sum_{k=1}^{S_X^{(a)}} \gamma_{ik}^{(Y^{(a)})} X_k^{(a)}}{1 + h\sum_{k=1}^{S_X^{(a)}} \gamma_{ik}^{(Y^{(a)})} X_k^{(a)}}\right), \tag{2}$$

$$\frac{dX_i^{(b)}}{dt} = X_i^{(b)}\left(\alpha_i^{X^{(b)}} - \kappa_i^{X^{(b)}} - \sum_{j=1}^{S_X^{(b)}} \beta_{ij}^{(X^{(b)})} X_j^{(b)} + \frac{\sum_{k=1}^{S_Y^{(b)}} \gamma_{ik}^{(X^{(b)})} Y_k^{(b)}}{1 + h\sum_{k=1}^{S_Y^{(b)}} \gamma_{ik}^{(X^{(b)})} Y_k^{(b)}}\right) + \mu_{in}^{(b)} X_i^{(a)} - \mu_{out}^{(b)} X_i^{(b)}, \tag{3}$$

$$\frac{dY_i^{(b)}}{dt} = Y_i^{(b)}\left(\alpha_i^{Y^{(b)}} - \sum_{j=1}^{S_Y^{(b)}} \beta_{ij}^{(Y^{(b)})} Y_j^{(b)} + \frac{\sum_{k=1}^{S_X^{(b)}} \gamma_{ik}^{(Y^{(b)})} X_k^{(b)}}{1 + h\sum_{k=1}^{S_X^{(b)}} \gamma_{ik}^{(Y^{(b)})} X_k^{(b)}}\right), \tag{4}$$

where the superscripts $(\cdot)^{(a)}$ and $(\cdot)^{(b)}$ denote layers A and B, and the capital letters X and Y represent the abundances of the pollinator and plant species, respectively. For example, $X_i^{(l)}$ and $Y_j^{(l)}$ are the abundances of the ith pollinator and the jth plant in layer l for $l = A$ or $l = B$, respectively, $S_X^{(l)}$ and $S_Y^{(l)}$ are the numbers of pollinators and plants in layer l. The parameters $\alpha_i^{X^{(l)}}$ and $\alpha_i^{Y^{(l)}}$ are the intrinsic growth rates of the pollinator and plant species, respectively, $\kappa_i^{X^{(l)}}$ is the rate of pollinator decay. In layer l, the intraspecific competitions within an individual pollinator species and interspecific competitions among the different pollinator species are characterized by the parameters $\beta_{ii}^{X^{(l)}}$ and $\beta_{ij}^{X^{(l)}}$, respectively. In the pollinator-plant mutualistic system, typically intraspecific competitions are stronger than interspecific competitions [51,60], so we have $\beta_{ii}^{X^{(a)}} \gg \beta_{ij}^{X^{(a)}}$, $\beta_{ii}^{Y^{(a)}} \gg \beta_{ij}^{Y^{(a)}}$, $\beta_{ii}^{X^{(b)}} \gg \beta_{ij}^{X^{(b)}}$, and $\beta_{ii}^{Y^{(b)}} \gg \beta_{ij}^{Y^{(b)}}$. The saturation effect is quantified by the half-saturation constant h of the Holling type-II functional response [77]. In Eqs. (1-4), the fractional terms represent the various mutualistic interactions with the strength γ. For example, in Eq. (1), $\gamma_{ik}^{X^{(a)}}$ is the strength of the mutualistic interaction from the kth plant to the ith pollinator in layer A. The coupling between the two layers is characterized by the following four parameters: $\mu_{in}^{(a)}$, $\mu_{out}^{(a)}$, $\mu_{in}^{(b)}$ and $\mu_{out}^{(b)}$, where $\mu_{in}^{(l)}$ and $\mu_{out}^{(l)}$ are the dispersal rates of species dispersing into and out of layer l, respectively, for $l = A, B$. There is no dispersal term for any plant species.

The inward dispersal rate terms $\mu_{in}^{(a)} X_i^{(b)}$ in Eq. (1) and $\mu_{in}^{(b)} X_i^{(a)}$ in Eq. (3) can be justified, as follows. In a real ecological system there are many species and the number of dispersing species is determined by their abundances and the ability to disperse that depends on the environmental conditions. For all the pollinator species in the same layer, the environmental conditions are approximately identical but their abundances can be drastically different. It is thus reasonable to choose the rate parameters $\mu_{in}^{(a)}$ and $\mu_{in}^{(b)}$ to be layer dependent but not species dependent. For a given pollinator species X_i, the effective dispersal rate as characterized by the term $\mu_{in}^{(a)} X_i^{(b)}$ or $\mu_{in}^{(b)} X_i^{(a)}$ does depend on the species abundance. The dispersal follows a two-way pattern: the species in both layers not only disperse into each other, but their own abundances are affected by the dispersal. The size of the outward dispersal is determined by the species abundance in the layer: the richer the species, the greater is the probability that dispersal occurs.

Intuitively, a single layer hosting species with high abundances may not have the sufficient habitat capacity, so more species are likely to disperse in order to find a new habitat. The increase in the probability represents a dispersal "tendency" for the species to explore other habitats. In fact, as our simulations will show, the dispersal probability does not have any significant effect on the steady state abundances, even though the probability of dispersal becomes larger as the species abundance increases.

To study the interplay between the tipping-point dynamics in the two layers in a concrete way, we focus on the setting where the network in layer A has gone through a tipping point transition and is in the extinction state, but no tipping point has occurred in layer B so its network is in the survival state. Through coupling, layer B keeps feeding dispersing species into layer A. A question is whether, because of the species dispersing from layer B, the species populations in layer A can be recovered. If so, during the process of recovering the abundances of species in layer A, dispersal to layer B can also occur. It is worth noting that, before species recover in A, effectively there is no dispersal from A to B as the species abundances in layer A are near zero. As in previous work [54,56], we choose the pollinator decay rates $\kappa_i^{X^{(l)}}$ $(l = A, B)$ as the bifurcation parameters whose increase can lead to a tipping point. Specifically, in an isolated layer, the mutualistic network can experience a tipping point transition as the decay rate increases through a critical value. This choice of the bifurcation parameter is based on the hypothesis that there is a correspondence between the species apoptosis rate κ and the state of the environment for species survival, i.e., a deterioration in the environment corresponds to an increase in κ and vice versa. Species extinction occurs as the apoptotic κ value increases. The tipping point of the system is defined as the threshold value of κ at which all species become extinct.

For type-I coupling, multiplexity is intrinsic and the abundances of the pollinator species in both layers are disturbed in a dynamical way, but the network structures are unaffected. In particular, every pollinator species in layer B has a probability to disperse to layer A but, when some individuals from this species arrive at their destination, they simply use the existing mutualistic connections there and do not establish any new mutualistic connections with the plant species in layer A. That is, only the total abundance of species in layer A is increased due to the inter-layer coupling. The dispersal rate for each species in layer B depends linearly on the abundance. Note that dispersal of a species does not mean that the the corresponding node in layer B disappears, as the species disperses at a finite rate. That is, in spite of the dispersal and certain loss of abundance, the species in layer B continue to survive according to their own mutualistic dynamics. In this case, the inter-layer coupling can be understood as the action of feeding individuals of the pollinator species from layer B into A. As the species abundances in layer A increase from near zero, they also disperse.

For type-II coupling, multiplexity is induced by dispersal. The network structures of the two layers are modified in the sense that the quantities characterising the network structure such as the numbers of the nodes and of the connected edges are changed. For example, the dispersal of a pollinator species from layer B into layer A can establish a new mutualistic connection with one or more plant species in layer A, and similarly from A to B. To be concrete, in our simulations, we choose the number of dispersing species to be one, five, or $S_X^{(a)}$ and $S_X^{(b)}$ (the total number of pollinator species). In the first two cases, the species engaged in dispersal are chosen randomly, so are the plant species in a given layer that get the mutualistic connections with the dispersing species from the other layer. As with type-I coupling, the species in one layer dispersing to another do not disappear at the destination layer or change their original mutualistic interactions during or after the dispersal. However, the abundances of species decrease due to the outward dispersal. Taken together, the quantities that have an impact on the network structure are: (1) the number and the set of species in one layer that randomly disperse to another layer, (2) the number of new nodes created by the dispersing species, and (3) the number of new mutualistic connections that the dispersing species randomly establish. Type-II coupling thus takes into account the change in the topological structure in both networks due to the inward dispersing species.

Results

We construct two mutualistic networks, one for each layer. Before dispersal occurs (i.e., when the networks are uncoupled), each network has 30 pollinator and 10 plant species, but their connecting structures are random and differ in detail. With the pollinator species decay rate chosen as the bifurcation parameter, without coupling the collapse tipping point $\kappa_{c0}^{X^{(a)}}$ of the network in layer A is $\kappa_{c0}^{X^{(a)}} \approx 1.0$ while that in B is $\kappa_{c0}^{X^{(b)}} \approx 1.3$. Suppose the network in layer A has gone through a tipping-point transition and is in the extinction state, but the layer B network remains in the survival state. At $t = 0$, layer B begins to feed dispersing species to layer A.

Type-I coupling. We demonstrate that type-I coupling can lead to species recovery in the network in layer A. Before coupling is turned on, we set $\kappa^{X^{(a)}} = 1.12 > \kappa_{c0}^{X^{(a)}}$ so the original species

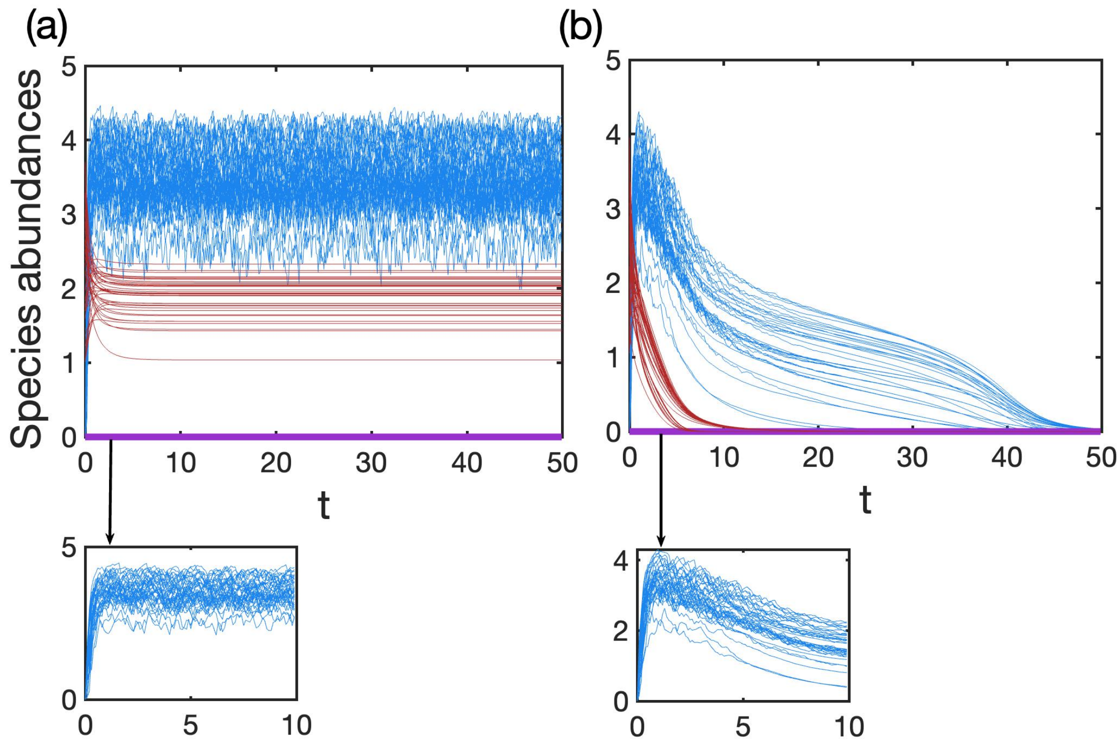

Figure 2: Interlayer coupling induced species recovery. (a) Time series of species abundances of both layers for $\kappa^{X^{(a)}} = 1.12 > \kappa_{c0}^{X^{(a)}}$, where the blue and red curves represent the abundances in layers A and B, respectively. The horizontal purple line on the abscissa indicates the collapse state of the layer A network in the post-tipping-point regime. Due to interlayer coupling, the abundances in both layers reach a healthy steady state. (b) A case of unsustainable recovery. The legends are the same as in (a), except that the network in layer B is also in the post tipping-point regime, even if initially it is in a survival state with its initial abundances chosen randomly between 1 and 4. The parameter values are $\alpha^{X^{(a)}} = \alpha^{Y^{(a)}} = \alpha^{X^{(b)}} = \alpha^{Y^{(b)}} = -0.3$, $\beta_{ii}^{X^{(a)}} = \beta_{ii}^{Y^{(a)}} = \beta_{ii}^{X^{(b)}} = \beta_{ii}^{Y^{(b)}} = 1$, and $h = 0.2$. The parameters $\gamma^{(X^{(a)})}$, $\gamma^{(Y^{(a)})}$, $\gamma^{(X^{(b)})}$, and $\gamma^{(Y^{(b)})}$ are normalized by the degree of the network in the layer and are set as one in the simulations. The dispersal parameters $\mu_{in}^{(a)}$ and $\mu_{out}^{(a)}$ are chosen randomly from the interval $[0, 0.3]$ while $\mu_{in}^{(b)}$ and $\mu_{out}^{(b)}$ are chosen randomly from the unit interval. The two insets show the recovery time series of layer A over a short initial period of time.

in layer A were extinct, and $\kappa^{X^{(b)}} = 1.0 < \kappa_{c0}^{X^{(b)}}$ so that the network in layer B is in a steady survival state. Without coupling, the species abundances in layer A are taken to be near zero, as indicated by the thick horizontal purple line in Fig. 2(a). With coupling, the abundances in layer A can recover quickly, as shown by the blue curves in Fig. 2(a) and its inset. In fact, the recovery process begins immediately after dispersal from layer B starts. Due to the dispersal, the species abundances in layer B decrease initially but quickly approach a steady survival state, as shown by the red curves in Fig. 2(a). The end result is that, due to interlayer coupling, the networks in both layers now remain in the survival state, although the steady state abundances levels are different.

If the layer B network is also in the post tipping-point regime, even when it was in a survival state initially, eventually the species abundances in both layers collapse. When the network in layer B collapses so that the source of dispersal disappears, the recovery process in layer A will stop and the abundances of its species will approach zero. This is demonstrated in Fig. 2(b) and its inset, where we set $\kappa^{X^{(b)}} = 2.0 > \kappa_{c0}^{X^{(b)}}$. Because the network in layer B is in the collapse regime, its species abundances decrease from the initial values to zero, as shown by the red curves in Fig. 2(b). The inset in Fig. 2(b) reveals that the recovery process in layer A starts initially but quickly reverses course as the abundances in layer B begin to collapse. After certain time, the species abundances in both layers are zero and the entire double-layer system collapses.

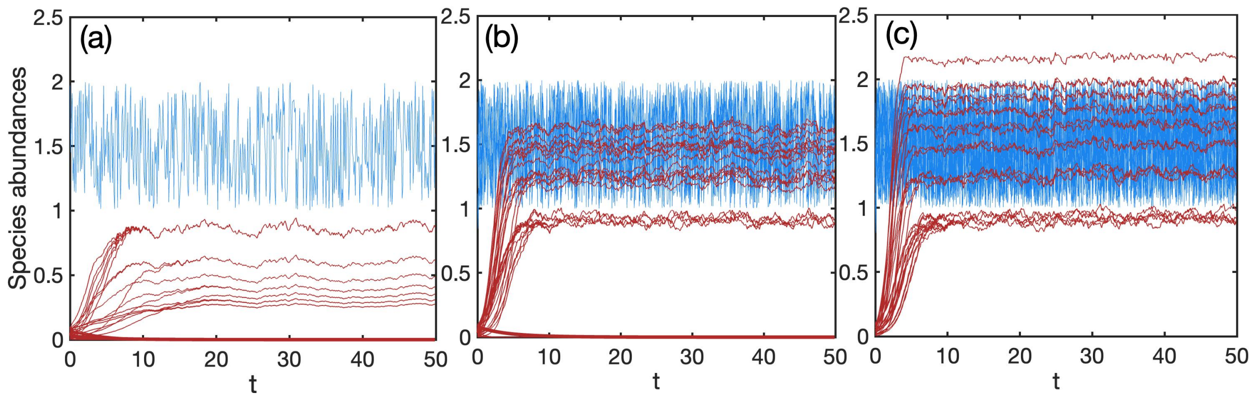

Figure 3: Recovery process with only one dispersing species. (a-c) The recovery process of layer A represented by the time series of the species abundances when there is only one dispersing species from layer B and the number of new mutualistic connections in layer A is one, five, and ten. For all three cases, the number of dispersing species from layer A to layer B is fixed to be five, and the number of new mutualistic connections established in layer B is 25. The blue and red curves are the abundance time series of the dispersing species from layer B and the species abundances in layer A, respectively. The growth and decay rates of the dispersing species from layer B are set to zero, and their competition and mutualistic interaction strengths are the same as the species in layer A. The initial species abundances in layer A are chosen randomly from the small interval $[0.1, 0.5]$, signifying that the network was in a state of collapse. The pollinator species decay rates are $\kappa^{X^{(a)}} = 1.12$ and $\kappa^{X^{(b)}} = 1.3$. Other parameter values are the same as those in Fig. 2.

Type-II coupling. We assume three cases in which one, five, or all species in layer B disperse to the collapsed layer A, and that each dispersing species randomly establishes mutualistic connections with the species in layer A. With the exception that all species in layer B disperse, the species engaged in dispersal are selected randomly. The variations in the dispersed species abundances are influenced by intraspecific competitions and mutualistic connections with the resident species in layer A. As the m dispersing species are indirectly connected through mutualistic interactions in layer A, they have the same competitive and mutualistic advantages as those that were already in layer A. For this type of dispersing coupling, the issue is what the impacts of the newly created connections on the tipping point in layer A would be. We fix the species dispersal rate from layer B at a specific value to guarantee that layer B provides a constant source of dispersal. For outward dispersal, the tacit assumption is that the extinction of the species in the original network is not the result of dispersal, so the outward dispersal rates of both layers are set between 0.1 and 0.3.

We first consider the case where only one random species from layer B disperses to layer A and establishes one mutualistic connection with one of the species in layer A. The number of species that migrants from layer A to layer B is five, and the number of new mutualistic connections established in layer B is 25. Figure 3(a) shows that the best recovered species in layer A is the one that establishes mutualistic connections with the dispersing species from layer B. However, there are species in layer A that are unable to recover, as indicated by the red lines on the abscissa in Fig. 3(a). The results from the case where the dispersing species establish mutualistic connections with five random species in layer A are shown in Fig. 3(b). Compared with the case in Fig. 3(a), more species recover due to the presence of more newly established mutualism, despite some species's failure to recover. Figure 3(c) shows the results from the setting where the dispersing species from layer B establish 10 mutualistic connections in layer A. In this case, all the species in layer A are able to fully recover from the extinction state. These results indicate that, the more mutualistic connections are established between the dispersing species and the original species in layer A, the more the collapsed species are able to recover. Figures 4(a) and 4(b) show the abundances in A for the two cases where each of the five dispersing species establishes mutualistic connections with one and all species, respectively. When each new dispersing species only establishes one new mutualistic connections, even if all species in layer B can disperse to layer A as in Fig. 4, the species in layer A are unable to achieve full recovery.

Our simulations reveal that, when one species disperses to layer A and establishes a mutualistic connection, 31 species in layer A are unable to recover. When five species disperse, each establishing a mutualistic connection, seven species in layer A cannot be fully recovered. When all species in layer B disperse with each establishing a new mutualistic connection, the number of species in layer A that are unable to fully recover is reduced to three. These results indicate that, while only one new mutualistic connection is unable to lead to the recovery of all species, a larger number of dispersing species can make the network dynamics evolve towards a full recovery. More dispersing species can also expedite the recovery process, as shown in Figs. 4(b) and 4(d), where all species in layer B disperse to layer A.

The results in Figs. 3 and 4 indicate that the keys to changing the tipping point in layer A are not only the number of species dispersing from layer B, but also the number of mutualistic connections established by the dispersing species with the resident species in layer A. For example,

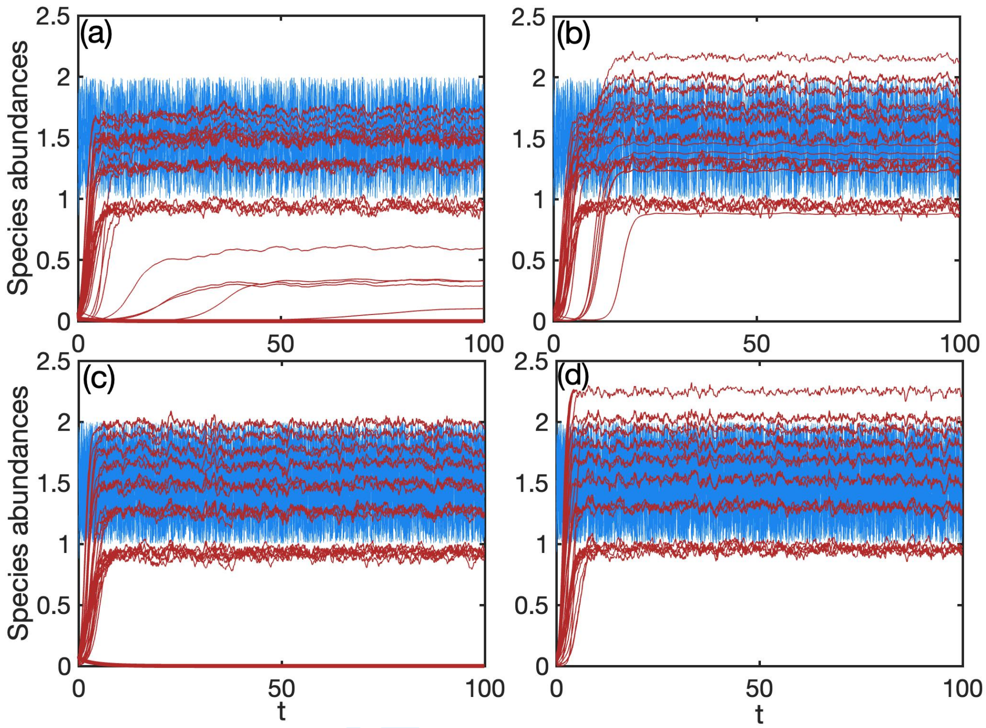

Figure 4: Recovery process with more than one dispersing species. Shown are the time series of species abundances in layer A for the following four cases: (a) five dispersing species from B, each establishing one mutualistic connection, (b) five v species from B, each establishing mutualistic connections with all plant species in A, (c) all species in B dispersing, each establishing one mutualistic connection, (d) all species in B dispersing, each establishing mutualistic connections with all plant species in A. The blue curves represent the dispersing species from layer B, and the red curves are for the species in layer A. For all the four cases, the number of dispersing species from layer A to layer B is five and the number of new mutualistic connections established in layer B is 25. The initial states and parameter values are the same as those in Fig. 3.

as shown in Fig. 3(c), even if only one species disperses and if it establishes mutualistic connection with ten species in layer A, a full recovery of the species abundances in A can be achieved. Likewise, Fig. 4(a) shows that, with five species dispersing and each establishing a mutualistic connection in layer A with only one plant species, the recovery process is quite similar to that in Fig. 3(c), since the total numbers of the new mutualistic connections in both cases are sufficiently large. This is a feature of mutualistic networks, where even if only one species in the network is not extinct, the species connected to it can survive due to the mutualistic connections. Depending on the structure of the mutualistic network A, even if the dispersing species generate the same number of mutualistic connections in layer A, a different number of the dispersing species can result in a different tipping point. For example, if 50 new mutualistic connections are generated, the tipping point for layer A is about 1.13 with five dispersing species, 1.41 with ten dispersing

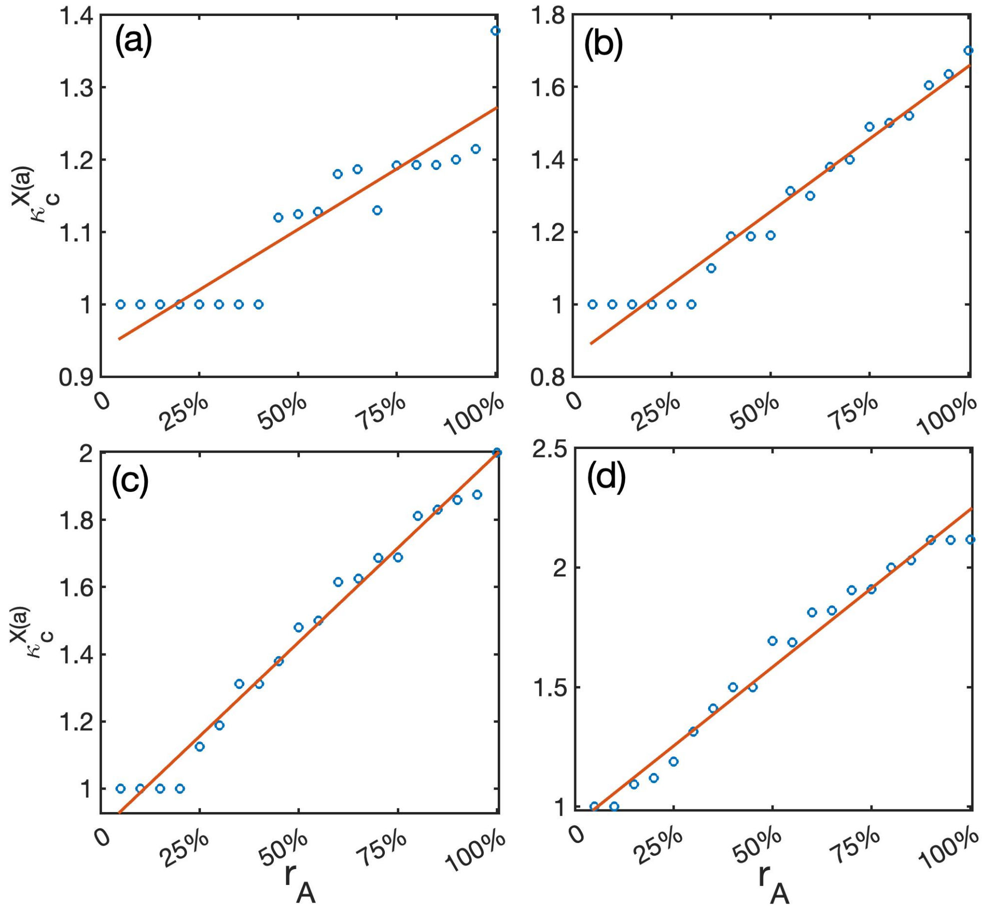

Figure 5: Tipping point $\kappa_c^{X(a)}$ versus the density r_A of new mutualistic connections. Shown is the correlation between the tipping point and r_A in layer A for (a) five, (b) ten, (c) 20, and (d) 30 dispersing species from B with the fixed number of dispersing species and fixed r_B in layer B. Each data point represents the tipping point position for the corresponding density of new mutualistic connections in layer A. The straight lines are for guiding the eyes. The initial states and parameter values are the same as those in Fig. 3.

species, 1.50 with twenty dispersing species, and 1.59 with thirty dispersing species. Likewise, the same number of dispersing species can establish different numbers of mutualistic connections, leading to different tipping points. Simultaneously, since dispersal between the two layers occurs in both directions, new mutualistic connections generated in layer B also affect the tipping point of layer A. For instance, the layer A tipping points in situations where ten dispersing species establish one, 50 and 100 mutualistic connections in layer B are about 1.09, 1.41 and 1.82, respectively.

To characterize the interplay among the number of dispersing species, the new mutualistic connections and the tipping points, we introduce the densities r_A and r_B of new mutualistic connections in layer A and layer B, respectively, defined as the ratio of the number of randomly

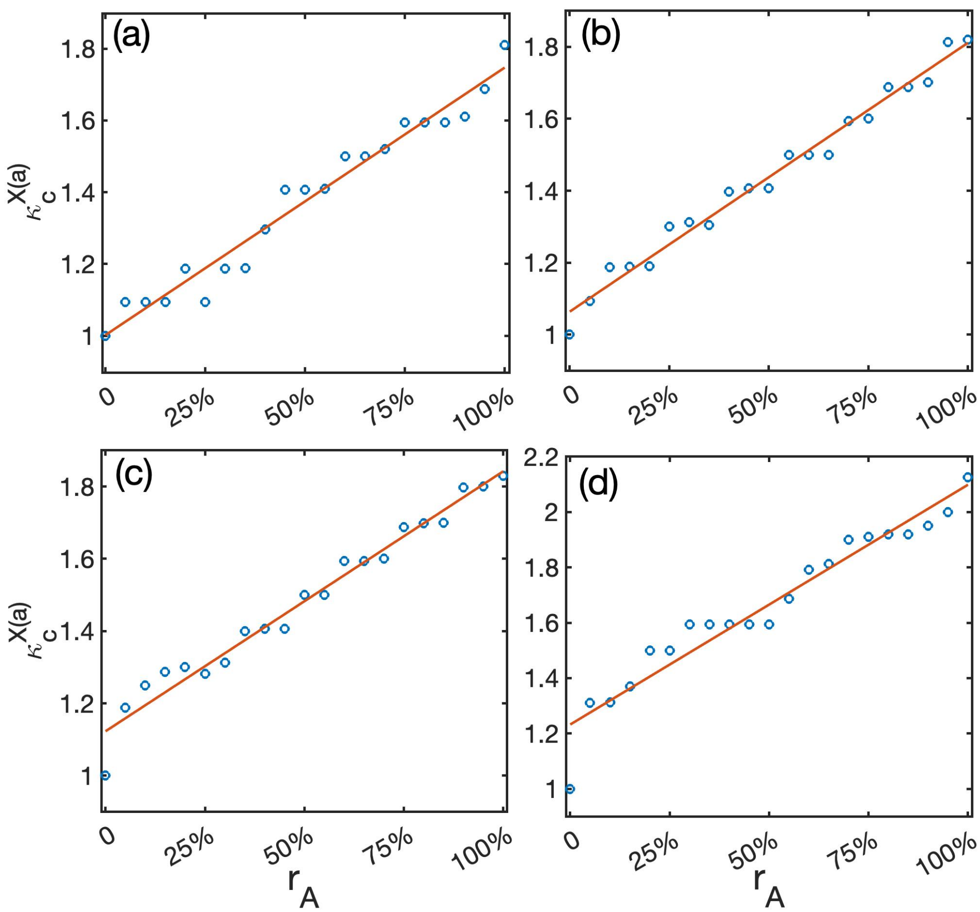

Figure 6: Tipping point $\kappa_c^{X^{(a)}}$ versus the density r_A of new mutualistic connections. (a-d) Coupling-induced delay of the tipping point in A when the density of new mutualistic connections r_B in layer B is 5%, 25%, 50% and 75%, respectively. The pollinator decay rate in layer B is set to be $\kappa^{X^{(b)}} = 1.297$. Other parameter values are the same as those in Fig. 2.

generated new mutualistic connections to the maximum number of mutualistic connections that can be generated for a fixed number of dispersing species. Figure 5 shows a positive correlation between the tipping point and r_A for five, ten, 20, and 30 dispersing species, where a higher number of dispersing species leads to a stronger correlation. Figure 6 shows that, with an increase in the density of new mutualistic connections in layer B, the strong correlation in Fig. 5 still persists as the densities of newly established mutualistic connections r_B in layer B vary.

Figure 7 shows the difference between layer A as a single network and as a layer in a double-layer network. As shown by the purple line in Fig. 3(a), layer A in a collapse condition without the benefit of layer B dispersal is unable to recover. In fact, layer A has a tipping point at one as a single network and a tipping point at 1.8 as a single layer in a double-layer network, as shown

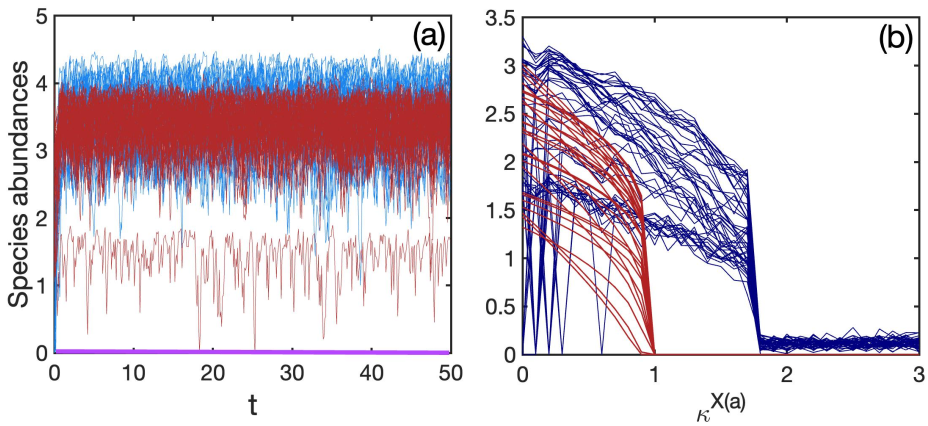

Figure 7: Delay in the tipping point due to interlayer coupling. (a) Time series of species abundances recovery of both layers with Type-II coupling, where the blue and red curves represent the abundances in layers A and B, respectively. The horizontal purple line on the abscissa indicates that layer A remains in the collapsed state without dispersal. (b) Comparison of the collapse process for layer A in a single layer and a double-layer networks. The initial abundance of layer A is between 0.1 and 0.5, i.e., it is in a collapsed state, and the initial abundance of layer B is between 1 and 4, i.e., in a survival state. The dispersal terms for layers A and B are randomly chosen from $[0, 0.3]$ and from $[0, 1]$, respectively. The larger the species abundance, the higher the dispersal rate. The red lines are the species abundances in layer A as an uncoupled single layer, while the blue lines are the abundance as part of the double-layer network.

in Fig. 3(b). The dispersal-induced duplexity can not only help the recovery of the species but also significantly delays the tipping point in the single layer network. Figure 8 summarizes the benefits of type-II coupling induced multiplexity to delaying the collapse tipping point in layer A with different structures of layer B. Recall that the tipping point of the network in the absence of coupling is at $\kappa_{c0}^{X(a)} \approx 1.0$. We define N_{m_A} and N_{m_B} as the numbers of species dispersing into layer A and B, respectively, and N_{c_A} and N_{c_B} as the respective numbers of original species in layer A and B which can establish new mutualistic connections with the dispersing species. With the dispersing conditions in layer A set as $(N_{m_A}, N_{c_A}) = (10, 10)$, if ten species disperse ($N_{m_B} = 10$), each establishing mutualistic connections with one species in layer B ($N_{c_B} = 1$), layer A's collapse tipping point becomes $\kappa_c^{X(a)} \approx 1.4$, as shown in Fig. 8(a). If ten species disperse ($N_{m_B} = 10$), each establishes mutualistic connections with five species in layer B ($N_{c_B} = 5$), layer A's collapse tipping point becomes $\kappa_c^{X(a)} \approx 1.6$, as shown in Fig. 8(b). With the dispersing conditions in layer A set as $(N_{m_A}, N_{c_A}) = (5, 10)$, when five dispersing species establish mutualistic connections with one species in layer B [$(N_{m_B}, N_{c_B}) = (5, 1)$], layer A's collapse tipping point is $\kappa_c^{X(a)} \approx 1.35$, as shown in Fig. 8(d). When five dispersing species in layer B establish mutualistic connections with the 5 plant species in layer B [$(N_{m_A}, N_{c_A}) = (10, 5)$], the collapse tipping point is $\kappa_c^{X(a)} \approx 1.35$, as shown in Fig. 8(d). As a two-way dispersing network, the change in the tipping point of layer A is not only related to the modification of its own network structure, but also to the structure of

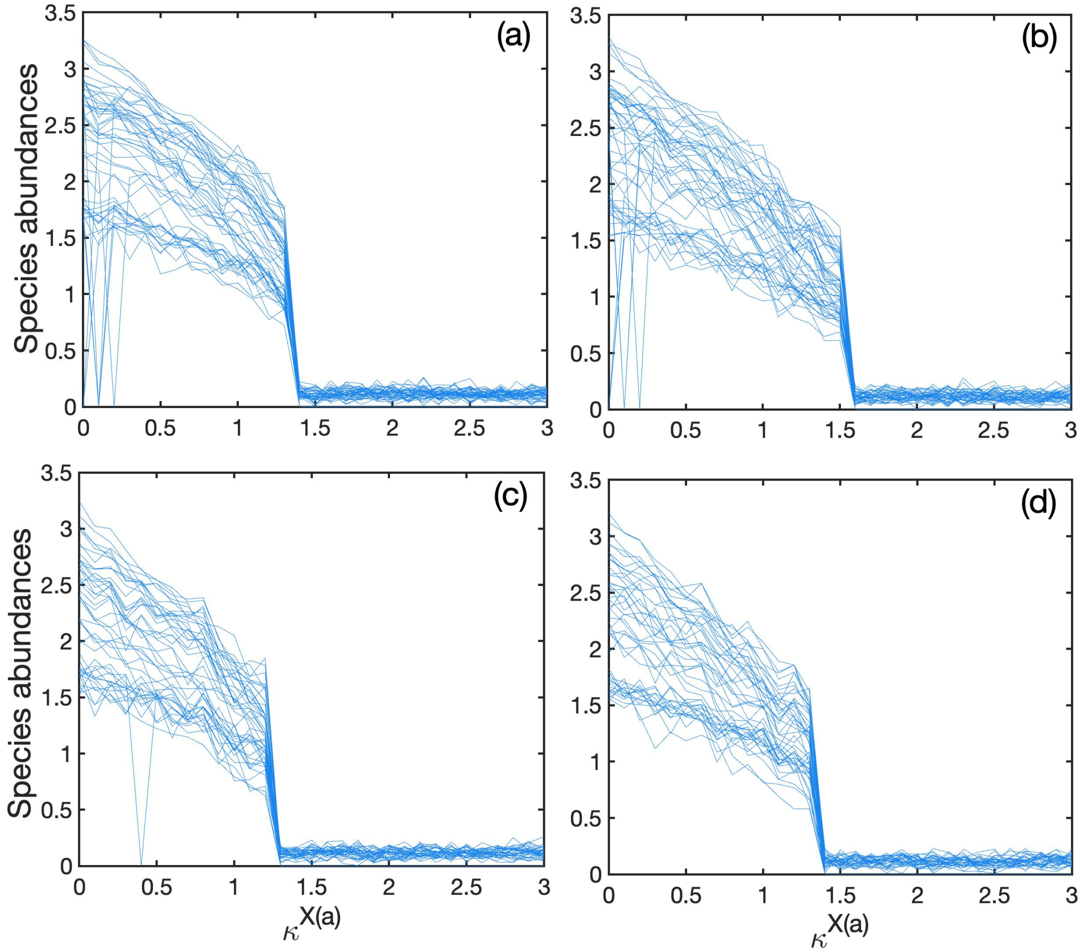

Figure 8: Delay of the tipping point due to type-II interlayer coupling. (a,b) Coupling-induced delay of tipping point in A for $(N_{m_A}, N_{c_A}) = (10, 10)$ for layer A, and $(N_{m_B}, N_{c_B}) = (10, 1)$ and $(N_{m_B}, N_{c_B}) = (10, 5)$ for layer B, respectively. (c,d) Coupling-induced delay of tipping point in A with $(N_{m_A}, N_{c_A}) = (5, 10)$ for layer A, and $(N_{m_B}, N_{c_B})) = (10, 1)$ and $(N_{m_B}, N_{c_B})) = (10, 5)$ for layer B, respectively. The tipping point in (a,b) occurs at $\kappa_{c0}^{X^{(a)}} \approx 1.4$ and 1.6, respectively. In (c,d), the tipping points are $\kappa^{X^{(a)}} \approx 1.35$, and 1.4, respectively. The pollinator decay rate for layer B is set to be $\kappa^{X^{(b)}} = 1.297$. Other parameter values are the same as those in Fig. 2.

layer B due to the coupling.

Suppression of the tipping point. So far we have studied the phenomenon of tipping-point delay with enhanced density of network connections for relatively low mutualistic connection density. Here we show that, as the numbers of dispersing species in and out of both layers as well as the densities r_A and r_B of the newly created mutualistic connections increase, the collapse tipping

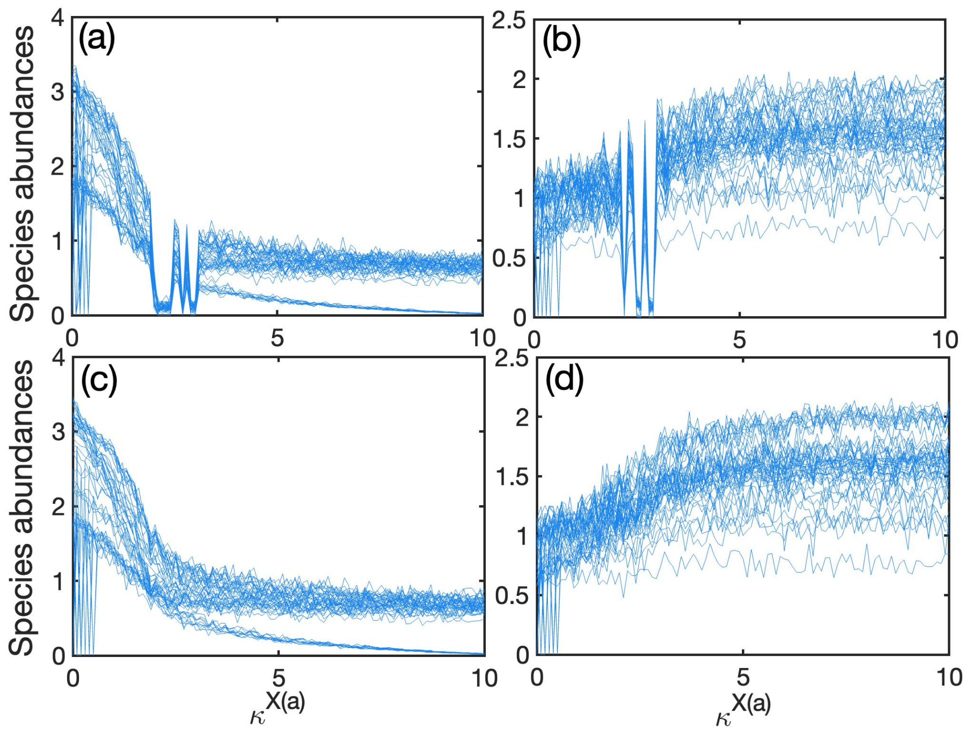

Figure 9: Multiplexity induced delay of tipping point transition. (a,b) Evolution of species abundances in layers A and B, respectively, with 80% new mutualistic connections in layer B. (c,d) The same as in (a,b) but with 85% new mutualistic connections in layer B. Other parameter values are the same as in Fig. 2. In both cases, the density of new mutualistic links in layer A is 80%.

points in both layers can be completely suppressed. As shown in Fig. 9, when the density of layer B increases to 80%, there is a sudden decrease in the abundance of species in both layers as the decay rate $\kappa^{X(a)}$ increases, but they still remain in the survival state. While there are individual species that go extinct at high decay rates, the whole double-layer network is still in a survival state. As the density of the mutualistic connections in the double-layer network increases, almost every new dispersing species is provided with a species for creating a mutualistic partnership. Species that have established mutualistic connections depend on each other for survival even under difficult conditions, insofar as the species with which they have mutualistic connection are still surviving. In a normal survival environment, species that have established mutualistic connections can depend on each other's abundances for stable survival. For the double-layer network, even if a small number of individual species are extinct as the result of an increase in the decay rate, the entire network does not become extinct under hostile environmental conditions (e.g., unusually high decay rates). We find that, in general, increasing the magnitude and density of dispersal within the double-layer network can suppress the onset of the global collapse tipping point.

Discussion

Complex ecological networks are nonlinear dynamical systems exhibiting multistability [78–80]. From a coarse-grained perspective, an ecological system has two distinct stable steady states: survival and extinction, so multistability in fact manifests itself as bistability. From the dynamical point of view, the bistability in complex mutualistic networks is created by an inverse saddle-node bifurcation as a control parameter, e.g., the species decay rate κ, decreases through a critical point [56,58]. In the forward direction, i.e., as κ increases, a tipping point arises: when κ is below the inverse saddle-node bifurcation point, there are two coexisting states: survival and extinction. In this case, if the system is already in the survival state, its stability guarantees that small perturbations are incapable of driving the system to extinction so that it remains in the healthy state. However, as κ increases through the tipping point, the survival state disappears, leaving extinction the only stable state in the system and leading to the inevitable collapse of the system. Stochastic disturbances, however, can affect the tipping point and facilitate species recovery in the aftermath of a tipping-point transition [57–59]. At the present, parameter variations as the result of climate change which can potentially lead to a tipping point are no longer exceptions. To sustain various ecosystems into the future, it is of great interest to uncover mechanisms in the natural world that can delay the tipping point.

This paper reports such potential behaviors and mechanisms in mutualistic systems. When coupling between two mutualistic networks is enabled, e.g., by species dispersal, the occurrence of a tipping point can be delayed, where the amount of delay depends on the extent of dispersal and a significant delay would not be infeasible. This finding, in addition to its fundamental importance, has implications to ecosystem management: seeking to enhance mutual coupling between ecosystems with mutualistic interactions can in general be beneficial. Our computation and analysis have revealed that, not only is the coupling able to delay the tipping point, but even when one ecosystem has already experienced a tipping point, the coupling can lead to a recovery through the restoration of species abundances. Articulating and implementing natural or engineered mechanisms to induce coupling, e.g., in the form of species dispersal, can be of significant value to sustaining mutualistic ecosystems that are or will be in danger of extinction as the result of environmental changes.

We have studied two types of dispersal coupling to form the double-layer mutualistic system, where one layer is responsible for supplying species to the other that is in the extinct state. The first type of dispersal coupling does not change the number of nodes, but only changes the species abundances levels. The double-layer system in this case can be seen as a higher-dimensional stochastic complex network, where the dynamics of the two layers are identical with intrinsic random coupling between them. The second type of coupling allows variations in the number of nodes in a layer, where the dispersing species can establish new links in the destination layer, thereby changing its network structure. In this case, multiplexity in the system is established as the result of the coupling. The new nodes and links allow the original resident species to recover in response to mutualistic effects of the dispersing species. As the importance of the species in the destination layer increases due to the new links, more species achieve recovery as a result of mutualism. As species within the two layers can disperse to each other and establish mutualistic interactions in their respective new layers, the change in network structure is not a change in a single destination layer, but one in the destination of both layers. With the benefit of new dispersing species and new mutualistic relationships, each layer can maintain a well-functioning survival state. Our analysis has revealed that the ability to achieve a total recovery requires a focus on increasing the number of new mutualistic interactions. This is consistent with the effect of the importance of nodes on controlling the global network [56,59].

The establishment of multiplexity through dispersal, as studied in this work, is able to largely delay the tipping point. Increasing the mutualistic strength through active dispersal of species or artificial addition of new species can be an effective means of controlling tipping points and avoiding widespread extinction. In real networks, complications can arise. For example, in the absence of artificial selection, foreign pollinators establishing mutualistic interactions with local plants is one aspect, but dispersal can also induce invasive competition between the foreign and local species, which can cause habitat displacement with consequent extensive loss of plants. The changes in a layer can also lead to a number of related changes to the structural properties and dynamical behaviors of the network such as the resilience and robustness [21,81–83]. Further studies of these effects are worthy.

Author Contributions All conceived the project. YM performed computations and analysis. All analysed data. All wrote the paper.

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Data Accessibility All data and computer codes are available from the authors upon request.

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1. D. S. Reis, S. *et al.* Avoiding catastrophic failure in correlated networks of networks. *Nat. Phys.* **10**, 762–767 (2014).

2. Ouyang, M. Review on modeling and simulation of interdependent critical infrastructure systems. *Relia. Eng. Sys. Safety* **121**, 43–60 (2014).

3. Domenico, M. D. Multilayer modeling and analysis of human brain networks. *Gigascience* **6**, 1–8 (2017).

4. Battiston, F., Nicosia, V., Chavez, M. & Latora, V. Multilayer motif analysis of brain networks. *Chaos* **27**, 047404 (2017).

5. Kang, l., Tian, C., Huo, S. & Liu, Z. A two-layered brain network model and its chimera state. *Sci. Rep.* **9**, 14389 (2019).

6. Zhao, D., Zeng, Y., Zhang, T., Shi, M. & Zhao, F. GLSNN: A multi-layer spiking neural network based on global feedback alignment and local STDP plasticity. *Front. Comput. Neurosci.* **14**, 101 (2020).

7. Simpson-Kent, I. L. *et al.* Bridging brain and cognition: A multilayer network analysis of brain structural covariance and general intelligence in a developmental sample of struggling learners. *J. Intelligence* **9** (2021).

8. Baggio, J. A. *et al.* Multiplex social ecological network analysis reveals how social changes affect community robustness more than resource depletion. *Proc. Nat. Acad. Sci. (USA)* **113**, 13708–13713 (2016).

9. Pilosof, S., Porter, M. A., Pascual, M. & Kéfi, S. The multilayer nature of ecological networks. *Nat. Ecol. Evol.* **1**, 0101 (2017).

10. Hutchinson, M. C. *et al.* Seeing the forest for the trees: Putting multilayer networks to work for community ecology. *Func. Ecol.* **33**, 206–217 (2019).

11. Kundu, S., Majhi, S. & Ghosh, D. Persistence in multilayer ecological network consisting of harvested patches. *Chaos* **31**, 033154 (2021).

12. Fortin, M.-J., Dale, M. R. T. & Brimacombe, C. Network ecology in dynamic landscapes. *Proc. R. Soc. B* **288**, 20201889 (2021).

13. Parshani, R., Buldyrev, S. V. & Havlin, S. Interdependent networks: reducing the coupling strength leads to a change from a first to second order percolation transition. *Phys. Rev. Lett.* **105**, 048701 (2010).

14. Buldyrev, S. V., Parshani, R., Paul, G., Stanley, H. E. & Havlin, S. Catastrophic cascade of failures in interdependent networks. *Nature* **464**, 1025–1028 (2010).

15. Parshani, R., Buldyrev, S. V. & Havlin, S. Critical effect of dependency groups on the function of networks. *Proc. Nat. Acad. Sci. (USA)* **108**, 1007–1010 (2011).

16. Gao, J., Buldyrev, S. V., Havlin, S. & Stanley, H. E. Robustness of a network of networks. *Phys. Rev. Lett.* **107**, 195701 (2011).

17. Gao, J., Buldyrev, S. V., Stanley, H. E. & Havlin, S. Networks formed from interdependent networks. *Nat. Phys.* **8**, 40–48 (2012).

18. De Domenico, M. *et al.* Mathematical formulation of multilayer networks. *Phys. Rev. X* **3**, 041022 (2013).

19. Kivelä, M. *et al.* Multilayer networks. *J. Complex Net.* **2**, 203–271 (2014).

20. Radicchi, F. & Bianconi, G. Redundant interdependencies boost the robustness of multiplex networks. *Phys. Rev. X* **7**, 011013 (2017).

21. Liu, R.-R., Eisenberg, D. A., Seager, T. P. & Lai, Y.-C. The ”weak” interdependence of infrastructure systems produces mixed percolation transitions in multilayer networks. *Sci. Rep.* **8**, 2111 (2018).

22. Liu, Q.-H., Wang, W., Cai, S.-M., Tang, M. & Lai, Y.-C. Synergistic interactions promote behavior spreading and alter phase transitions on multiplex networks. *Phys. Rev. E* **97**, 022311 (2018).

23. Yang, H., Gu, C., Tang, M. T., Cai, S.-M. & Lai, Y.-C. Suppression of epidemic spreading in time-varying multiplex networks. *Appl. Math. Model.* **75**, 806–818 (2019).

24. Liu, R.-R., Jia, C.-X. & Lai, Y.-C. Remote control of cascading dynamics on complex multilayer networks. *New J. Phys.* **21**, 045002 (2019).

25. Liu, R.-R., Jia, C.-X. & Lai, Y.-C. Asymmetry in interdependence makes a multilayer system more robust against cascading failures. *Phys. Rev. E* **100**, 052306 (2019).

26. Wu, D., Tang, M., Liu, Z. & Lai, Y.-C. Impact of inter-layer hopping on epidemic spreading in a multilayer network. *Commun. Nonlinear Sci. Numer. Simulat.* **90**, 105403 (2020).

27. Wang, X. *et al.* Anomalous role of information diffusion in epidemic spreading. *Phys. Rev. Research* **3**, 013157 (2021).

28. Min, B., Yi, S. D., Lee, K.-M. & Goh, K.-I. Network robustness of multiplex networks with interlayer degree correlations. *Phys. Rev. E* **89**, 042811 (2014).

29. Liu, R.-R., Li, M. & Jia, C.-X. Cascading failures in coupled networks: The critical role of node-coupling strength across networks. *Sci. Rep.* **6**, 35352 (2016).

30. Hu, Y. *et al.* Percolation of interdependent networks with intersimilarity. *Phys. Rev. E* **88**, 052805 (2013).

31. Cellai, D., López, E., Zhou, J., Gleeson, J. P. & Bianconi, G. Percolation in multiplex networks with overlap. *Phys. Rev. E* **88**, 052811 (2013).

32. Bianconi, G. & Dorogovtsev, S. N. Multiple percolation transitions in a configuration model of network of networks. *Phys. Rev. E* **89**, 062814 (2014).

33. Azimi-Tafreshi, N., Gómez-Gardeñes, J. & Dorogovtsev, S. N. k-core percolation on multiplex networks. *Phys. Rev. E* **90**, 032816 (2014).

34. Baxter, G. J., Dorogovtsev, S. N., Mendes, J. F. F. & Cellai, D. Weak percolation on multiplex networks. *Phys. Rev. E* **89**, 042801 (2014).

35. Zhou, D. *et al.* Simultaneous first- and second-order percolation transitions in interdependent networks. *Phys. Rev. E* **90**, 012803 (2014).

36. Wang, Z., Zhou, D. & Hu, Y. Group percolation in interdependent networks. *Phys. Rev. E* **97**, 032306 (2018).

37. Rinaldi, S. M., Peerenboom, J. P. & Kelly, T. K. Identifying, understanding, and analyzing critical infrastructure interdependencies. *IEEE Cont. Sys.* **21**, 11–25 (2001).

38. Scheffer, M. *Ecology of Shallow Lakes* (Springer Science & Business Media, 2004).

39. Scheffer, M. *et al.* Early-warning signals for critical transitions. *Nature* **461**, 53–59 (2009).

40. Scheffer, M. Complex systems: foreseeing tipping points. *Nature* **467**, 411–412 (2010).

41. Wysham, D. B. & Hastings, A. Regime shifts in ecological systems can occur with no warning. *Ecol. Lett.* **13**, 464–472 (2010).

42. Drake, J. M. & Griffen, B. D. Early warning signals of extinction in deteriorating environments. *Nature* **467**, 456–459 (2010).

43. Chen, L., Liu, R., Liu, Z.-P., Li, M. & Aihara, K. Detecting early-warning signals for sudden deterioration of complex diseases by dynamical network biomarkers. *Sci. Rep.* **2**, 342 (2012).

44. Boettiger, C. & Hastings, A. Quantifying limits to detection of early warning for critical transitions. *J. R. Soc. Interface* **9**, 2527–2539 (2012).

45. Dai, L., Vorselen, D., Korolev, K. S. & Gore, J. Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* **336**, 1175–1177 (2012).

46. Ashwin, P., Wieczorek, S., Vitolo, R. & Cox, P. Tipping points in open systems: bifurcation, noise-induced and rate-dependent examples in the climate system. *Phil. Trans. Roy. Soc. A* **370**, 1166–1184 (2012).

47. Lenton, T. M., Livina, V. N., Dakos, V., van Nes, E. H. & Scheffer, M. Early warning of climate tipping points from critical slowing down: comparing methods to improve robustness. *Phil. Trans. Roy. Soc. A* **370**, 1185–1204 (2012).

48. Barnosky, A. D. *et al.* Approaching a state shift in earths biosphere. *Nature* **486**, 52–58 (2012).

49. Boettiger, C. & Hastings, A. Tipping points: From patterns to predictions. *Nature* **493**, 157–158 (2013).

50. Tylianakis, J. M. & Coux, C. Tipping points in ecological networks. *Trends. Plant. Sci.* **19**, 281–283 (2014).

51. Lever, J. J., Nes, E. H., Scheffer, M. & Bascompte, J. The sudden collapse of pollinator communities. *Ecol. Lett.* **17**, 350–359 (2014).

52. Lontzek, T. S., Cai, Y.-Y., Judd, K. L. & Lenton, T. M. Stochastic integrated assessment of climate tipping points indicates the need for strict climate policy. *Nat. Clim. Change* **5**, 441–444 (2015).

53. Gualdia, S., Tarziaa, M., Zamponic, F. & Bouchaudd, J.-P. Tipping points in macroeconomic agent-based models. *J. Econ. Dyn. Contr.* **50**, 29–61 (2015).

54. Jiang, J. *et al.* Predicting tipping points in mutualistic networks through dimension reduction. *Proc. Nat. Acad. Sci. (UsA)* **115**, E639–E647 (2018).

55. Yang, B. *et al.* Dynamic network biomarker indicates pulmonary metastasis at the tipping point of hepatocellular carcinoma. *Nat. Commun.* **9**, 678 (2018).

56. Jiang, J., Hastings, A. & Lai, Y.-C. Harnessing tipping points in complex ecological networks. *J. R. Soc. Interface* **16**, 20190345 (2019).

57. Meng, Y., Jiang, J., Grebogi, C. & Lai, Y.-C. Noise-enabled species recovery in the aftermath of a tipping point. *Phys. Rev. E* **101**, 012206 (2020).

58. Meng, Y., Lai, Y.-C. & Grebogi, C. Tipping point and noise-induced transients in ecological networks. *J. R. Soc. Interface* **17**, 20200645 (2020).

59. Meng, Y. & Grebogi, C. Control of tipping points in stochastic mutualistic complex networks. *Chaos* **31**, 023118 (2021).

60. Rohr, R. P., Saavedra, S. & Bascompte, J. On the structural stability of mutualistic systems. *Science* **345**, 1253497 (2014).

61. Dakos, V. & Bascompte, J. Critical slowing down as early warning for the onset of collapse in mutualistic communities. *Proc. Natl. Acad. Sci. (USA)* **111**, 17546–17551 (2014).

62. Guimaraes, P. R., Pires, M. M., Jordano, P., Bascompte, J. & Thompson, J. N. Indirect effects drive coevolution in mutualistic networks. *Nature* **550**, 511–514 (2017).

63. Koh, L. P. *et al.* Species coextinctions and the biodiversity crisis. *Science* **305**, 1632–1634 (2004).

64. Colwell, R. K., Dunn, R. R. & Harris, N. C. Coextinction and persistence of dependent species in a changing world. *Ann. Rev. Ecol. Evol. Syst.* **43**, 2012 (2012).

65. Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P. & Sodhi, N. S. The sixth mass coextinction: are most endangered species parasites and mutualists? *Proc. R. Soc. B London Biol. Sci.* **276**, 3037–3045 (2009).

66. Brodie, J. F. *et al.* Secondary extinctions of biodiversity. *Trends Ecol. Evol.* **29**, 664–672 (2014).

67. Memmott, J., Waser, N. M. & Price, M. V. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B London Biol. Sci.* **271**, 2605–2611 (2004).

68. Kaiser-Bunbury, C. N., Muff, S., Memmott, J., Müller, C. B. & Caflisch, A. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Lett.* **13**, 442–452 (2010).

69. Fricke, E. C., Tewksbury, J. J., Wandrag, E. M. & Rogers, H. S. Mutualistic strategies minimize coextinction in plant–disperser networks. *Proc. R. Soc. B London Biol. Sci.* **284**, 20162302 (2017).

70. Valdovinos, F. S. Mutualistic networks: moving closer to a predictive theory. *Ecol. Lett.* **22**, 1517–1534 (2019).

71. Valdovinos, F. S. & Marsland III, R. Niche theory for mutualism: A graphical approach to plant-pollinator network dynamics. *Ame. Naturalist* **197**, 393–404 (2021).

72. Bascompte, J., Jordano, P. & Olesen, J. M. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431–433 (2006).

73. Bastolla, U. *et al.* The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**, 1018–1020 (2009).

74. Green, A. L. *et al.* Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biol. Rev.* **90**, 1215–1247 (2015).

75. Han, S. *et al.* Role of intestinal flora in colorectal cancer from the metabolite perspective: a systematic review. *Cancer Manag. Res.* **10**, 199 (2018).

76. Ollerton, J. Pollinator diversity: distribution, ecological function, and conservation. *Ann. Rev. Ecol. Evol. Syst.* **48**, 353–376 (2017).

77. Holling, C. S. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**, 385–398 (1959).

78. Feudel, U. & Grebogi, C. Multistability and the control of complexity. *Chaos* **7**, 597–604 (1997).

79. Kraut, S., Feudel, U. & Grebogi, C. Preference of attractors in noisy multistable systems. *Phys. Rev. E* **59**, 5253–5260 (1999).

80. Lai, Y.-C. & Grebogi, C. Quasiperiodicity and suppression of multistability in nonlinear dynamical systems. *Euro. Phys. J. Spec. Top.* **226**, 1703–1719 (2017).

81. Vázquez, A. & Moreno, Y. Resilience to damage of graphs with degree correlations. *Phys. Rev. E* **67**, 015101 (2003).

82. Vespignani, A. The fragility of interdependency. *Nature* **464**, 984–985 (2010).

83. Son, S.-W., Grassberger, P. & Paczuski, M. Percolation transitions are not always sharpened by making networks interdependent. *Phys. Rev. Lett.* **107**, 195702 (2011).