

# The multilayer nature of ecological networks

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**Although networks provide a powerful approach to study a large variety of ecological systems, their formulation does not typically account for multiple interaction types, interactions that vary in space and time, and interconnected systems such as networks of networks. The emergent field of ‘multilayer networks’ provides a natural framework for extending analyses of ecological systems to include such multiple layers of complexity, as it specifically allows one to differentiate and model ‘intralayer’ and ‘interlayer’ connectivity. The framework provides a set of concepts and tools that can be adapted and applied to ecology, facilitating research on high-dimensional, heterogeneous systems in nature. Here, we formally define ecological multilayer networks based on a review of previous, related approaches; illustrate their application and potential with analyses of existing data; and discuss limitations, challenges, and future applications. The integration of multilayer network theory into ecology offers largely untapped potential to investigate ecological complexity and provide new theoretical and empirical insights into the architecture and dynamics of ecological systems.**

Networks give a powerful way to explore ecological complexity and have generated numerous insights into the understanding of the structure, function, and dynamics of ecological systems<sup>1–7</sup>. Although ecological networks have become fundamental to ecological theory, they have for the most part been studied as disconnected from other networks, defined at a single point in space and time, and/or aggregated over multiple spatial locations and times. However, natural systems typically exhibit multiple facets of complexity, such as pollinators interacting with flowers in one season but not in another<sup>8</sup> and the same plant species interacting with both pollinators and herbivores<sup>9,10</sup>. Despite the recognized need to generalize investigations of ‘monolayer’ networks<sup>10,11</sup>, there are challenges to doing so explicitly and within a unified framework. Specific examples include the detection of community structure in networks with edges representing different interaction types<sup>10,12</sup> and the analyses of resource flows in temporal networks<sup>13</sup>.

Recent advances in the theory of ‘multilayer’ networks<sup>14,15</sup> provide a promising approach. A mathematical framework for the analysis of multilayer networks has been developed only recently, although multilayer network structures, which encode different types of interactions and/or entities as a single mathematical object, have a long history in subjects like sociology and engineering<sup>14,16</sup>. These recent advances, in concert with the growing availability of large ecological data sets, provide an exciting opportunity for their theoretical and practical integration into network ecology. In this Perspective, we define ecological multilayer networks, give examples of the kinds of insights that they can enable, and discuss challenges and future applications.

## Ecological multilayer networks

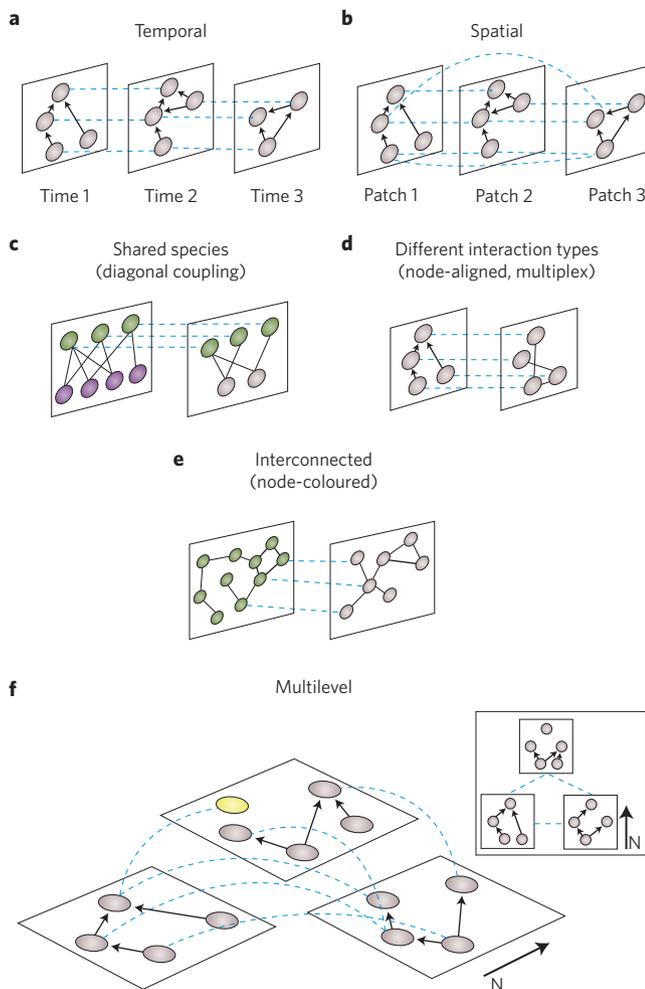
Multilayer networks have two or more ‘layers’, which can represent different types of interactions, different communities of species, different points in time, and so on (Fig. 1). Dependencies across layers result from ecological processes that affect multiple layers. For example, dispersal of individuals between two patches affects the network structure of both patches<sup>17</sup>. A multilayer network consists

of (i) a set of ‘physical nodes’ representing entities (for example, species); (ii) a set of layers, which can include multiple ‘aspects’ of layering (for example, both time-dependence and multiple types of relationships); (iii) a set of ‘state nodes’, each of which corresponds to the manifestation of a given physical node on a specific layer; and (iv) a set of (weighted or unweighted) edges to connect the state nodes to each other in a pairwise fashion. The edge set includes both the familiar ‘intralayer’ edges and ‘interlayer’ ones, which connect state nodes across layers. We provide a formal definition with a detailed example in Box 1.

Previous studies of ecological multilayer networks (Supplementary Table 1) have predominantly used multiple but independent networks of the same system, with interlayer edges formally absent. In such cases, network diagnostics are calculated independently for each layer. For instance, Olesen *et al.*<sup>8</sup> reported—using a plant–pollinator system sampled over 12 years and represented with 12 individual networks—that connectance (that is, edge density) exhibits little variation over time despite significant turnover of species and interactions. By contrast, networks with explicit interlayer connectivity enable one to address questions about interactions between the processes that operate within and between layers. To set the stage for ecological development, we identify the major types of layering that are relevant for ecological systems (Fig. 1 and Supplementary Table 1).

**Layers defined across space or time.** Early work on spatial and temporal networks focused primarily on how the composition of species changes in time (for example, across seasons) or over environmental gradients, especially in food webs<sup>18–23</sup>. More recent studies have focused on studying spatial and temporal dissimilarities in species and interactions<sup>24–26</sup>. This variability has a natural representation using multilayer networks: one can define a monolayer network at each point in space or time, and one can then use interlayer edges to connect each node to its counterparts in different layers. Layers in temporal multilayer networks are typically ordered (‘ordinal coupling’; Fig. 1a), but the order of the layers is not important for

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**Figure 1 | Multilayer networks in ecology.** In these toy examples, layers are squares, solid black lines are intralayer interactions, and dashed blue arcs are interlayer edges. **a**, Temporal food webs. Nodes are connected to themselves across layers in an ordinal way (one layer follows another). **b**, Spatial food webs. Nodes are connected to themselves across all layers (via categorical interconnections). In panels **a,b**, it is permissible for species or intralayer interactions to appear in one layer but not in another. **c**, Networks with different interaction types that are connected through shared species. Layers are ‘diagonally coupled’, so interlayer edges occur only between shared species. **d**, One can represent different interaction types between species (for example, trophic and facilitative) using a node-aligned multiplex network, in which all nodes appear in all layers and each layer corresponds to a different interaction type. Nodes are connected to all of their counterparts across layers. **e**, Two interacting populations of different hosts. Nodes are individuals, and intralayer and interlayer edges are, respectively, social ties within and between populations. In this example, each node appears in one layer. **f**, A multilevel network representing a metacommunity. Layers are communities, and nodes are species. Intralayer edges are trophic interactions, and interlayer edges represent species dispersal between communities. A species can also disperse to a new community (represented by the yellow node). Communities are often associated with some space (for example, with different habitats or patches). In the inset, we illustrate that such networks are sometimes represented without explicit specification of interlayer edges. Interactions between species at a lower level automatically impose interactions between the communities.

spatial networks (‘categorical coupling’; Fig. 1b). Another approach is to use a network of networks. For example, Gilarranz *et al.*<sup>17</sup> defined a spatial network of plant–pollinator networks in which each community of plants and pollinators is a layer and in which

interlayer edges represent species extinction and colonization. By considering a network of layers (see the inset of Fig. 1f), in which each layer is construed as a node, the authors demonstrated an association between the importance of communities (quantified with a measure of node betweenness centrality) and their architecture: communities with higher betweenness in the network of layers are also more nested, with potential consequences for the local stability of the communities<sup>27,28</sup>.

**Layers defined by interaction type.** Because the stability and function of ecological networks can depend on the way in which different interaction types are combined in communities, considering only a single interaction type can give an incomplete picture of system properties<sup>10–12,28–32</sup>. For instance, Bastolla *et al.*<sup>29</sup> illustrated that both the structure of mutualistic networks and competition for common resources can determine the number of co-existing species in a system. In another example, incorporating facilitative interactions to a resource–consumer model affects total system biomass and hence the way that an ecosystem functions<sup>11,33</sup>. Finally, Rudolf and Lafferty<sup>34</sup> showed that food webs that include edges representing ontogenetic shifts in addition to trophic interactions can change the robustness of systems to extinctions.

Ideally, one should simultaneously consider the structure of multiple interaction types, and this is achievable with multilayer networks. Some ecological networks have a common set of species (for example, a set of plants connected to their pollinators and herbivores<sup>9</sup>). One can represent such data<sup>9,35,36</sup> in a multilayer formalism using a ‘diagonally coupled’ multilayer network (Fig. 1c). Each ecological interaction occurs in a different layer, and interlayer edges connect common species to their counterparts in other layers.

Another approach is to examine different interaction types between all species in a system using ‘node-aligned’ multilayer networks, in which all entities exist on all layers<sup>12,32,37,38</sup> (Fig. 1d). Kéfi *et al.*<sup>12,32</sup> used a highly resolved ecological community from the central intertidal coast of Chile to construct a multilayer network in which each layer includes all species of the community but represents different interaction types: trophic, non-trophic positive (for example, refuge provisioning), and non-trophic negative (for example, predator interference). They found that the distribution of non-trophic edges throughout the food web was different from what would be expected by chance (by shuffling the non-trophic edges while fixing the trophic web), suggesting that there is a strong association between the different layers of the network<sup>32</sup>. Such structural patterns suggest the possibility of important dynamic constraints on the combined architecture of trophic and non-trophic interactions<sup>12,32</sup>.

**Layers defined by different group identity.** An intuitive way to describe and examine variation in individual-based interactions between populations of the same or different species is with an interconnected network in which each node appears only in one layer (Fig. 1e). In disease ecology, this representation can model interpopulation or interspecific disease transmission (when each layer is a population of a different species) at the same time that it considers underlying social networks<sup>39</sup>. For example, intralayer edges can represent the social structure of bat groups, and interlayer edges can represent transmission of a vector-borne disease between these populations. Moreover, interconnected networks are not limited to individual organisms. For example, one can define a multilayer network in which each layer represents a food web (with its own trophic interactions) and interlayer edges represent trophic interactions between species from different food webs<sup>40,41</sup>.

**Layers defined by levels of organization.** Biological processes at any given level of organization (for example, genes, individuals,

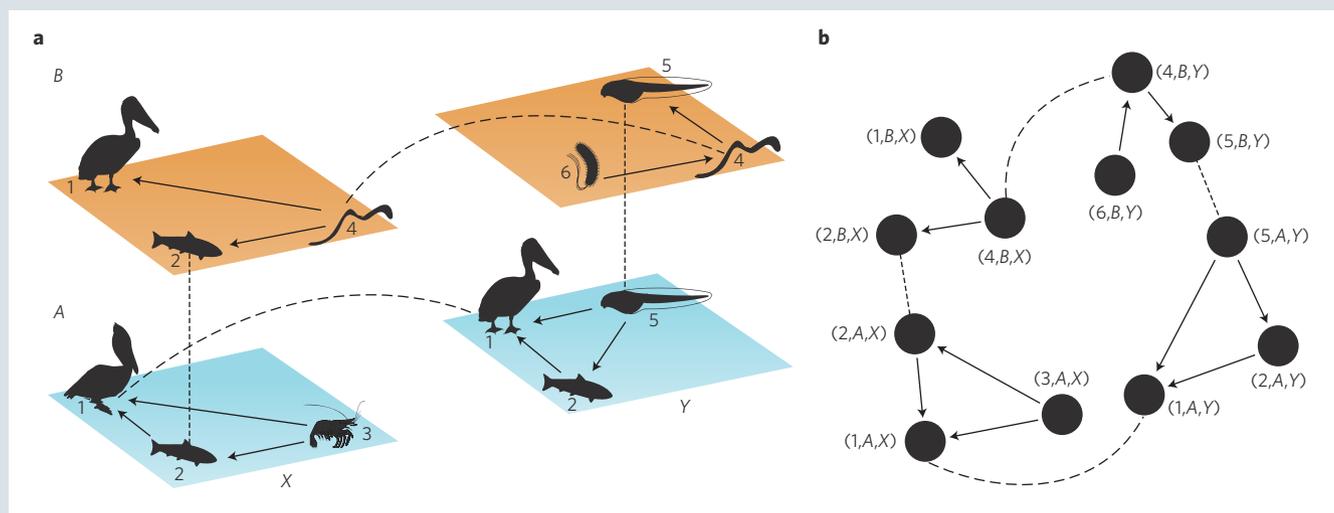
**Box 1 | Definition of multilayer networks.**

A ‘multilayer network’ is a quadruplet  $M = (V_M, E_M, V, L)$ . Multilayer networks can have several ‘aspects’ of layering, and an ‘elementary layer’ is a single element in one aspect of layering. A ‘layer’ encompasses one choice of elementary layer for each type of aspect (see the figure for an example). We include such relationships using sequences  $\mathbf{L} = \{L_a\}_{a=1}^d$  of sets  $L_a$  of elementary layers, where  $a$  indexes the  $d$  different aspects. Note that  $d = 0$  for a monolayer network,  $d = 1$  when there is one type of layering, and  $d = 2$  when there are two types of layering (as in the figure). The set of entities (that is, physical nodes) is  $V$ . The set  $V_M \subseteq V \times L_1 \times \dots \times L_d$  of node-layer tuples (that is, state nodes) encodes the manifestations of an entity  $v \in V$  on a particular layer  $l \in \hat{L} = L_1 \times \dots \times L_d$ .

The edge set  $E_M \subseteq V_M \times V_M$ , which includes both intralayer and interlayer edges, encodes the connections between pairs of state nodes. In a given layer, the intralayer edges encode connections of a specified type (for example, a certain type of interaction at a

given point in time). A function  $w : E_M \rightarrow \mathbb{R}$  encodes weights on edges. A pair of node-layer tuples,  $(u, \alpha)$  and  $(v, \beta)$ , are ‘adjacent’ if and only if there is an edge between them. One places a 1 in the associated entry in an adjacency tensor (a generalization of a matrix that consists of a higher-dimensional array of numbers)<sup>14,16</sup> if and only if  $((u, \alpha), (v, \beta)) = 1$ . Otherwise, one places a 0 in the corresponding entry. One can ‘flatten’ such an adjacency tensor into a matrix, called a ‘supra-adjacency matrix’, with intralayer edges on the diagonal blocks and interlayer edges on the off-diagonal blocks (see Supplementary Fig. 1b).

Constraints on the above general definition restrict the structure of a multilayer network<sup>14</sup>. For example, ‘diagonal coupling’ (see Fig. 1c) is a constraint in which the only permissible type of interlayer edge is one between counterpart entities on different layers. See ref.<sup>14</sup> for additional definitions and important types of constraints on  $M$  that produce common types of multilayer networks.



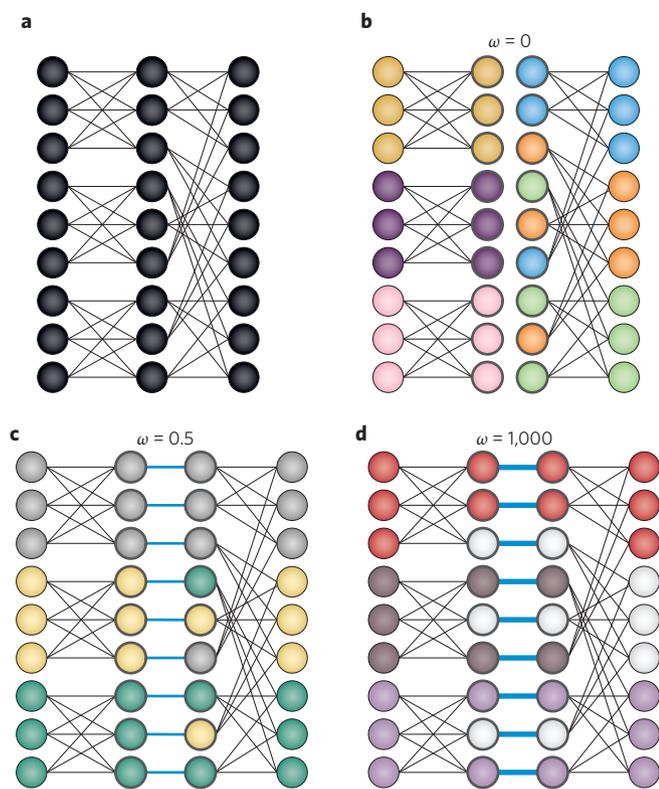
**Toy example of a multilayer network. a.** The network has  $d = 2$  aspects: (i) different types of ecological interactions (trophic interactions are in the blue layer (A), and host-parasite interactions are in the orange layer (B)); and (ii) space (X and Y represent different patches). The elementary-layer set for ecological interaction types is  $L_1 = \{A, B\}$ , and the one for patches is  $L_2 = \{X, Y\}$ . A layer consists of a tuple of elementary layers. For example, the layer (A,X) encodes trophic interactions in patch X. We show intralayer edges using solid arrows. We depict diagonal interlayer edges (for example, between node 2 on layer (A,X) and node 2 on layer (B,X)) with dotted lines; such edges encode the extent to which a parasitized species is more susceptible to predation than a non-parasitized one. Interlayer edges between patches represent dispersal; we show them with dashed arcs. **b.** The ‘supra-graph’ that corresponds to the multilayer network in panel **a**. Each node in this graph is a node-layer tuple (that is, a state node) in the corresponding multilayer network. See Supplementary Fig. 1 for an example of how to represent a similar multilayer network as a supra-adjacency matrix. Figure adapted with permission from ref.<sup>14</sup>, Oxford Univ. Press.

populations, etc.) can depend on processes at other levels<sup>42</sup>. For example, changes in species’ biomass can affect the stability of food webs in dynamical models based on allometry<sup>43</sup>. When the layers in a multilayer network represent different levels of organization, one has a ‘multilevel’ network, and interactions between nodes at a lower level automatically entail interactions at upper levels<sup>14</sup>. For example, a trophic interaction between two species from two different patches implies that there is an interaction between the patches. The simplest example is a two-level multilevel network, which can also be construed as a network of networks (Fig. 1f). In an analysis of a three-level multilevel network (population, community, and metacommunity), Scotti *et al.*<sup>44</sup> illustrated that the metacommunity was sensitive to population-level processes (for example, social dynamics) that cascaded through different levels. The identification of such dependencies is one of the values of a multilayer approach.

**Analyses of ecological multilayer networks**

To illustrate the kinds of insights that one can gain by taking a multilayer approach, we analyse examples of ecological multilayer networks in which layers are connected explicitly. We consider (i) maximum modularity, a structural property that is commonly studied in monolayer networks; and (ii) extinction cascades, a consequence of structure that is common in robustness analyses of networks. We use both synthetic networks and networks constructed from empirical data.

**Modularity.** In monolayer networks, maximizing modularity can help quantify the extent to which a network is organized into groups (modules) of species that interact more strongly with each other than with other species<sup>45,46</sup>. To illustrate the distinction between studying a multilayer network and studying a collection of networks, we start with a synthetic example from Fontaine *et al.*<sup>10</sup>. In



**Figure 2 | Modularity maximization in a diagonally coupled multilayer network.** **a**, An example network (from ref. <sup>10</sup>) that does not have interlayer edges. **b–d**, Network with two layers, which interconnect via a common set of nodes (indicated with thick borders in the central column). Interlayer edges (in blue) connect the two instances of a node. In panels **b–d**, we test three different scenarios. In each panel, nodes of the same colour belong to the same module. We construe the left set of nodes as the root-parasite guild, the middle set with thick borders as plants, and the right set as herbivores. For our calculations, we use  $\omega = 1,000$  to approximate interlayer edge weights of  $\infty$ . In panel **b** we obtain a maximum modularity of  $\bar{Q}_b \approx 0.667$ , each layer has three modules, and no plant state nodes appear in the same module. In panel **c**,  $\bar{Q}_b \approx 0.651$  and the network is partitioned into a mean of  $n \approx 3.04$  modules. On average, 4.6 (that is, approximately 51%) of the plants are assigned to more than one module. In panel **d**,  $\bar{Q}_b \approx 0.99$ , we obtain a mean of  $\bar{n}_b \approx 3.38$  modules, and state nodes of each plant belong exclusively to a single module. See Supplementary Notes 1 and 2 for the details of our calculations. Panel **a** adapted with permission from ref. <sup>10</sup>, Wiley-Blackwell.

this example, a plant–herbivore network and a plant–root–parasite network (so there are two layers) interconnect via a common set of species, which are the plants (Fig. 2a). Interlayer edges connect each plant species to its counterpart in the other layer (Figs 1c and 2c,d) and represent the extent to which parasitism affects herbivory. Thus, each plant appears in both layers and has two instances corresponding to different ‘state nodes’, which can be assigned to different modules. See Supplementary Note 1 for details on how we calculate multilayer modularity and assign state nodes to modules.

The propensity of a state node to belong to distinct modules depends on the relative weights of interlayer and intralayer edges<sup>47,48</sup>. Ecologically, it depends on the extent to which processes in one layer affect those in other layers. Consider the three conceptual scenarios that follow.

(1) When the interlayer edge weights are 0, the two networks in this example are independent entities. The instances of plants in different layers must belong to different modules, and modules are defined separately for herbivory and parasitism. Hence, herbivory

has no effect on parasitism (and vice versa), and no perturbation can pass from one layer to another (Fig. 2b).

(2) At the other extreme, interlayer edge weights are much larger than intralayer ones. (They are infinite in the limiting case.) In this scenario, herbivory and parasitism always affect each other, implying that herbivory always renders plants more susceptible to parasites, and vice versa. (Note that it does not imply that each plant is always parasitized and preyed upon.) Consequently, each of the two instances of a plant always belongs to the same module. Note that modules can contain species from any of the three guilds and from either interaction type (Fig. 2d).

(3) Interlayer and intralayer edge weights have comparable values (that is, they are on similar scales). In this scenario, herbivory has some effect on the propensity of a plant to be parasitized, and vice versa. A plant can therefore interact strongly with a given set of herbivores in one layer and with a given set of parasites in another layer. Each of the two instances of a plant can belong to different modules. Modules can contain species from any of the three guilds and either interaction type, but the identity of the modules can be rather different from those in the previous two cases (Fig. 2c).

This example illustrates that defining community organization in multilayer networks depends strongly on the extent to which the ecological processes that operate in the different layers affect each other (in our example, the relationship between parasitism and herbivory). Another insight is that considering intermediate values of interlayer edge weights provides a possible means to identify the plants that can buffer perturbations: the two instances of such plants may be assigned to different modules (Fig. 2c).

One challenge is to quantify the weights of interlayer edges. In this example, one way to measure the extent to which herbivory and parasitism affect each other is to conduct a series of experiments in which one group of plants of a given species is exposed to herbivores while a second group of the same species (control) is not. For example, if a plant exposed to a given herbivore species is infected by twice the number of parasites compared with the control plant, a reasonable choice for the value of the interlayer edge is 2.

Several studies outside of ecology have illustrated that modular (and other mesoscale) network structures can change over time<sup>47,49,50</sup>. In ecology, such network variation was considered in a study based on the analysis of multiple disconnected networks<sup>51</sup>. Time-dependent modular structure, including changes in module composition over time, can also be examined by studying a multilayer network. As an example, consider a network representing the infection of 22 small mammalian host species by 56 ectoparasite species during 6 consecutive summers in Siberia (1982–1987)<sup>52,53</sup>, yielding a multilayer network with 6 layers. We quantify intralayer edge weights as the prevalence of a given parasite on a given host. Interlayer edges connect instances of the same species across consecutive time points (Fig. 1a), representing the relative changes in abundance between two consecutive summers. For example, if a host has an abundance of 10 in one year and 5 in the next, then the value of the interlayer edge is  $5/10 = 0.5$  (Supplementary Note 3). The idea behind this way of determining interlayer edge values is that temporal fluctuations in abundance affect the availability of hosts to parasites and parasite pressure on hosts, and these factors in turn affect host–parasite interactions at any given time. (That is, they affect the intralayer edges; see equation (3) in Supplementary Note 3.)

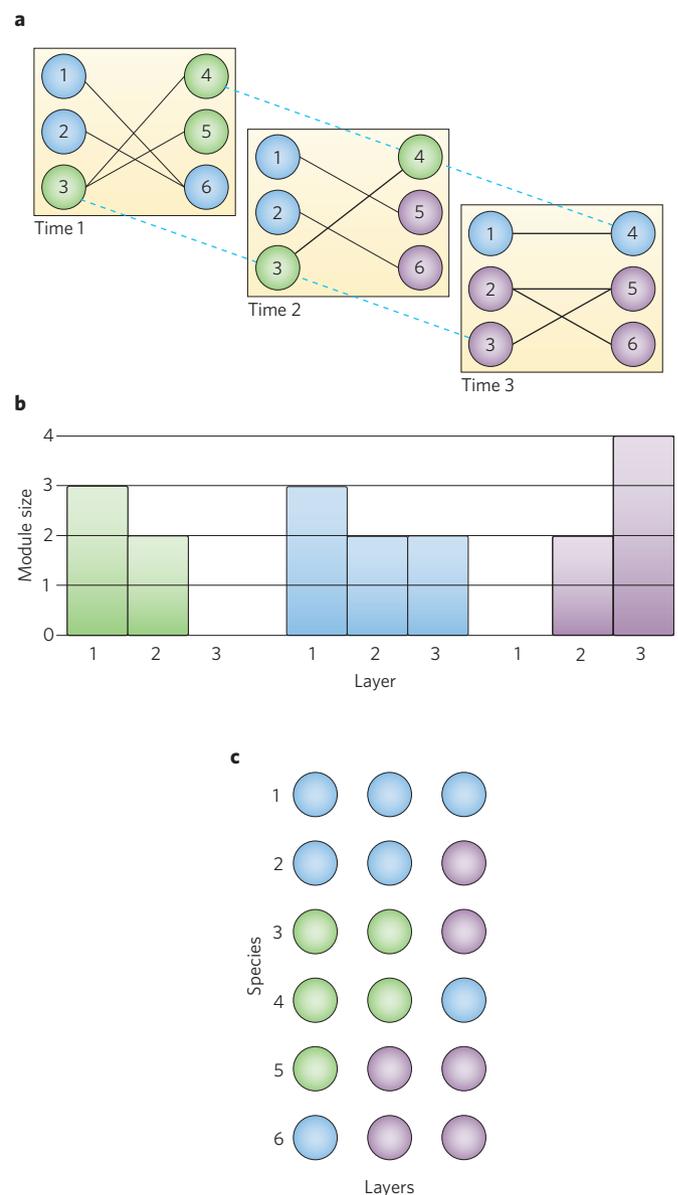
In a temporal network, a given species can interact strongly with some species at one time and with other species at other times. Consequently, each state node can belong to a different module at different times, and modules can vary in size over time<sup>47,48</sup> (Fig. 3). We define ‘host adjustability’ and ‘parasite adjustability’ as the proportion of hosts and parasites, respectively, that change module affiliation at least once. We observe non-negligible values of this measure: about 47% of the hosts and about 35% of the parasites

change their module affiliation at least once, and a module's size also changes over time (Supplementary Figs 2,3). One interpretation of this pattern is that the same species is functionally different at different times. For example, one ecological characteristic of a host is the extent to which it supports populations of different parasite species in a community. Fluctuations in the abundance of different host species (encoded in the interlayer edges) can lead to fluctuations in the availability of hosts to parasites. Additionally, there are temporal changes in interaction patterns of other species in the network (encoded in the intralayer edges). These mechanisms lead to a time-dependent distribution of parasites in hosts, in which the same host species supports populations of different parasites at different times. This variation is expressed as the assignment of the same host species to different modules in different layers.

Constructing and analysing a temporal network also allows one to consider hypotheses on the effect of intralayer and/or interlayer connectivity on community structure. This approach dominates studies of monolayer ecological networks. In such studies, one often compares the structure of an observed network to those of networks in an ensemble that has been generated from shuffling the network in particular ways<sup>4,54</sup> (or to networks constructed using a generative random-graph model<sup>45,46</sup>). The added value of the generalization of this approach to multilayer networks is that it allows one to test hypotheses that relate directly to the temporal structure of a community. For example, one can shuffle the interlayer edges between each pair of consecutive layers (separately for hosts and parasites) to test the hypothesis that the modular structure is a result of random temporal changes in species abundances (Supplementary Note 3). The observed network has higher maximum modularity than the shuffled networks ( $\bar{Q}_B^{\text{observed}} \approx 0.55$  versus  $\bar{Q}_B^{\text{shuffled}} \approx 0.21$ ;  $P < 0.001$ ). Additionally, it has about 6 (respectively, 15) times fewer modules than in networks in which the interlayer host edges (respectively, parasite edges) have been shuffled. All hosts and parasites change modules at least once in the shuffled networks. These observations lead us to reject the above hypothesis. One can also hypothesize that the modular structure of the community is (i) a result of random associations between hosts and parasites in any given layer and (ii) independent of the temporal order in which hosts and parasites are observed (Supplementary Note 3). We reject these hypotheses as well (Supplementary Tables 4,5). The rejection of the three hypotheses improves understanding of the functional groupings of species by demonstrating that host–parasite interactions are structured non-randomly in time and depend both on how species interact in a given time period and on their persistence in time (as measured by changes in species abundance). Consequently, altering host–parasite interactions or the survival probability of species (for example, by applying parasite control programs) can strongly affect temporal community organization.

Any assessment of such questions by studying each layer separately would necessarily be incomplete. Modules in individual layers of multilayer networks without interlayer edges are disconnected from (and thus independent of) each other. Hence, one cannot directly address the effect of interlayer phenomena on modular structures (Supplementary Notes 1,3). In the host–parasite network without interlayer edges, species assignment to modules in any given layer contains, on average, only about 35% of the information on species assignment to modules in the interconnected temporal network (Supplementary Note 3.3).

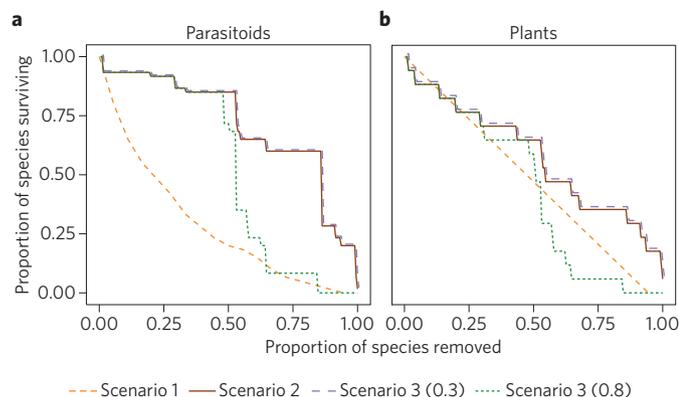
As an alternative to using a multilayer network, ecologists can aggregate species and interactions (for example, across space or time). Aggregation may be necessary when species interactions (intralayer edges) are sampled sparsely in time. However, data aggregation entails a set of (usually implicit) assumptions<sup>14,55</sup>, and different aggregation methods can lead to qualitatively different conclusions. By calculating ‘reducibility’<sup>56</sup> (Supplementary Table 2) in the host–parasite network, one can quantify whether some layers



**Figure 3 | A toy example of temporal modularity maximization.** The figure illustrates that species can change their module affiliation across time points. We represent six species with numbers and indicate three different modules using different colours. **a**, The toy temporal network has three layers, and each layer has a bipartite structure. All species occur in all layers. For clarity, we represent interlayer edges using blue dashed lines for two species. **b**, Modules can change in size (that is, the number of species that they include) across layers. For example, the green module does not exist at time point 3, and the purple module does not exist at time point 1. **c**, Representation of the module affiliation of each species in different layers. For example, species 1 does not change modules, whereas each of the other changes switches once.

contain overlapping information and can therefore be aggregated. We find that all 6 layers are necessary to describe the complexity of the system. Consistent with this finding, the affiliation of species to modules in the aggregated network provides only about 52% of the information on their affiliation to modules in the multilayer network (Supplementary Note 3.3).

Taken together, our computations illustrate that multilayer networks are natural for asking questions about time-dependent phenomena<sup>13,47–49</sup>. Temporal variations in the size and composition of



**Figure 4 | Network robustness to species removal in a multilayer network of plant-flower-visitors and plant-leaf-miner parasitoids. a, b.** The proportion of surviving (a) leaf-miner parasitoids and (b) plants as a function of the proportion of species removed in three scenarios. Scenario 1 simulates a monolayer case, where we remove plants from the plant-leaf-miner parasitoid layer (orange curves). This results in a linear decrease in the proportion of plants surviving (in panel b). In scenario 2, we remove flower visitors and quantify secondary extinctions (the proportion of surviving species) in plants and concomitant tertiary extinctions of leaf-miner parasitoids (brown curves). Scenario 3 is the same as 2, but with additional plant removal (which is independent of the secondary plant extinctions) with probability 0.3 (purple curves) or 0.8 (green curves). We detail the algorithms for each of the removal scenarios in Supplementary Table 6. There is an overlap between the curves for scenarios 2 and 3 with low probability, so we separated them slightly for clarity. In panel a, we note a ‘transition’ in the proportion of species that survive in scenario 3. Although discerning whether this is a general feature of extinction processes in ecological multilayer networks requires further research, a plausible explanation is that when there is a high probability of random independent extinctions of plants, the system reaches a threshold in which too many plants have become extinct and thus can no longer sustain the community.

modules may be relevant to phenomena such as species coevolution, coexistence, and community stability<sup>4,10,57</sup>. For instance, hosts assigned to more than one module may provide important bridges for transmission of ectoparasites across years and/or groups of strongly connected hosts. These hosts can change their ecological function in a system<sup>53</sup>, and such flexibility in community structure may contribute to system robustness in the face of perturbations.

**Robustness to perturbations.** Network structure can affect the stability of ecological communities<sup>7,27,28</sup>. To illustrate how multilayer networks can contribute to studies of stability, we use a network with two layers, plant–flower-visitors and plant–leaf-miner parasitoids<sup>35</sup>, that are interconnected via the same set of plants (Fig. 1c, Supplementary Note 4). We investigate the patterns of parasitoid extinctions in two scenarios: (i) direct secondary extinctions due to plant removal (that is, a monolayer scenario) and (ii) tertiary extinctions due to the removal of pollinators, which causes plant secondary extinctions that, in turn, result in parasitoid tertiary extinctions (that is, a multilayer scenario) (Supplementary Table 6). A plant (respectively, a parasitoid) goes extinct when it becomes completely disconnected from flower visitors (respectively, flowers). We find that parasitoid extinctions occur more slowly in the multilayer network than when separately examining the plant–parasitoid layer as a monolayer network. Additionally, allowing plant extinctions in addition to flower visitors extinctions in scenario (ii) leads to nontrivial extinction patterns (Fig. 4). Therefore, considering the multilayer nature of the network changes the qualitative conclusions about the robustness of parasitoids to extinctions. This kind of analysis can be extended in many ways (see Supplementary Note 4)

and is valuable for understanding the interplay between different interaction types and their effect on system robustness.

### Limitations and challenges

Whether a multilayer approach is more appropriate than a monolayer one obviously depends on the specific research question. Collecting the necessary data for questions requiring multilayer networks can be resource-intensive, as the data needs to be gathered from multiple places, at multiple times, and/or with different observational methods to capture different types of interactions. Measuring interlayer edge weights may require additional sampling efforts that are different from those used for collecting data on intralayer edges. Fortunately, data sets are already becoming available (Supplementary Table 1), but they are scattered in the literature and need to be curated.

One challenge is to define the meaning (and measure the values) of interlayer edges, and the choice of definition can itself play a significant role in analyses. For example, interlayer edges that connect species in two different communities may relate to species dispersal or changes in a species’ state (for example, abundance). Furthermore, intralayer and interlayer edges can represent ecological processes at different scales, and it is not always clear how to define the relative weight(s) of interlayer edges with respect to intralayer edges. How to choose appropriate values for interlayer edges remains a topic of active research in the study of multilayer networks. For some applications (for example, transportation), there already exist principled ways to choose values. In ecology, this issue is uncharted territory. Where possible, it is best to measure interlayer edges directly<sup>58</sup>. An *ad hoc* approach, which has been very insightful for several applications outside of ecology<sup>48–50,59</sup>, is to systematically sweep through a set of values. For example, one can ask how the relative relationship between two interaction types affects the dynamics of an ecological system. For this theoretical question, one would measure a quantity of interest (for example, some network diagnostic) for different interlayer edge weights. We also note that different types of interactions can also involve different ‘currencies’. For example, pollination is measured differently than dispersal, and it is important to consider discrepancies in the scales of the two edge types.

Just as prior advances in network ecology<sup>2,4,60</sup> used (and adapted) methods from monolayer network theory<sup>61</sup>, one can borrow and adapt techniques from applications of multilayer networks to other disciplines<sup>14,15</sup> (Supplementary Table 2). It is important, however, to determine which existing methods are best suited for ecological applications and to develop methods and diagnostics with ecology specifically in mind. These methods include multilayer versions of common network diagnostics (for example, vulnerability and generality), null models to test hypotheses about network structure<sup>59,62</sup>, and mathematical models for dynamical processes. Availability of software<sup>57,63,64</sup> has played an important role in the accessibility of monolayer network analyses, and it is important for the same to become the norm for the analysis and visualization of multilayer networks (by developing well-described and easy-to-use tools). Several software packages are already available (Supplementary Table 3), although these are not yet as mature as those for monolayer ecological networks.

### Future directions and applications

We have argued that multilayer networks provide a versatile and powerful framework for investigations of community ecology. This is also true for biogeography, where networks that include species dispersal or colonization/extinction dynamics as interlayer edges can help one understand how spatial dynamics affect community structure and stability<sup>17</sup>. A multilayer formalism can address not only correlations between geographic distance and beta diversity of species and interactions (which to date have been studied using multiple disconnected networks; see, for example, ref. 26), but

also the mechanisms behind such correlations. Another open area concerns the effect of space on the stability of ecological communities<sup>65</sup>. One could use a multilayer network that explicitly incorporates different instances of the same species at different locations instead of a matrix of interactions for a single community in space. Habitat alteration is a growing concern, and it would be interesting to explore the stability of ecological networks with different spatial connectivity patterns (encoded in the interlayer edges).

The framework of ecological multilayer networks is new, and it would benefit from the development of theoretical models to help provide a basis for comparisons with data. The framework provides a way to consider, for example, multiple interaction types when modelling the dynamics of interacting populations, which are typically modelled in networks with a single interaction type<sup>29,31</sup>. Interlayer edges in such models encode coupling between different dynamical processes and provide a way to describe the relative importances of different interaction types in processes such as species' population dynamics. For example, a key question in disease ecology is assessing the roles that different types of host–parasite interactions play in disease transmission (for example, the contact patterns of individuals<sup>66</sup> or the trophic web within which parasites and hosts are embedded<sup>67</sup>). Using a multilayer network with three layers—contact network, trophic web, and host–vector interactions—Stella *et al.*<sup>38</sup> modelled the relative importance of vectors for diseases that can be transmitted both via trophic interactions and via vectors by varying the coupling between the trophic and the vector layers. They reported that transmission that spreads only on the trophic layer hinders the infection of host populations.

Multilayer networks can also advance metacommunity theory, where interlayer edges provide a way to develop spatially-explicit models to investigate how species move between local communities, thereby creating spatial structure in the regional species' pool. For example, one can study spatial structure in resource and species flow in interconnected food webs, such as those of lakes or ponds that are interconnected via common sets of animals. In such examples, interlayer edge values can represent dispersal<sup>17</sup> or biomass flows between patches. One can also use a temporal food web to explore bioenergetic flows across food webs—an area that remains largely unexplored<sup>13</sup>. Layers can represent temporal instances of a given food web, and interlayer edges can represent changes in species biomass with time.

Another key question in food-web theory is the effect of parasitism on food-web structure and stability<sup>67–69</sup>. For example, parasitism may have different effects than trophic interactions on a given species. Parasitized hosts can be more susceptible to predation, but it is unclear how the structure of host–parasite networks affects the trophic interactions between hosts. One way to model such systems is by coupling a host–parasite network and a food web (Box 1 and Supplementary Fig. 1). Multilayer networks also provide a possible approach for analysing disease transmission when there are multiple hosts and parasites<sup>39,70</sup>, which to date has been difficult to study.

In animal behaviour, one can explore networks in which intralayer edges between individuals represent reproduction and interlayer edges represent movement (and hence gene flow) to study genetic relatedness between individuals as a function of both dispersal and intra-group social behaviour. In movement ecology, multilayer networks can help model relationships between a network of social interactions and a network of movement patterns to examine moving decisions. Understanding movement has consequences for conservation biology, where one can represent different connectivity scenarios using a multilayer network in which each layer describes the movement patterns of a different species. Such models should be helpful for informing decision-makers on which land-use designs are best-suited for the movement of a diverse set of species. Multilayer networks can also help improve the identification of keystone species. A simple notion of a keystone species

arises from calculating a 'centrality' measure of species in a food web (where keystone species have the highest values of that centrality)<sup>71</sup>, but more nuanced definitions of centralities—and hence of keystone species—can incorporate participation in several interaction types<sup>58</sup>, as well as temporal and spatial dependencies.

Finally, multilayer networks can be used to study reciprocal effects between ecological and non-ecological systems. For example, Baggio *et al.*<sup>72</sup> represented three indigenous Alaskan communities using a multiplex network in which each layer is a unique combination of ecological resources and social relations. They reported that changes to the social relations have a larger impact on the robustness of the networks (and hence on the human communities) than depletion of ecological resources (for example, removal of marine species that are used as food).

## Conclusions

The simultaneous expansion in the availability of ecological data and the tools to analyse multilayer networks<sup>14,15,70,73–75</sup> provides a timely and valuable opportunity for ecologists to explore the multilayer nature of ecological networks. The strength of a multilayer approach lies in its ability to formulate and analyse complex systems in a way that explicitly incorporates processes operating both within and across layers (as well as interactions between these processes). Formulating systems as multilayer networks also allows one to address questions that are not feasible using monolayer networks. Working within the same framework facilitates comparisons of results across ecological systems and network types because of consistency in technical terms and methodology. A unified framework should also further encourage collaboration with scientists from other disciplines. Other fields of study, in turn, will benefit from methodology and theory developed for ecological multilayer networks, as has been the case for monolayer ecological networks<sup>76</sup>. In closing, the integration of multilayer network theory into ecology offers novel perspectives, with the potential to provide new theoretical and empirical insights, into the architecture and dynamics of ecological systems.

**Data availability.** The raw data for the example temporal network are in Supplementary Data 1 and deposited in Figshare (<https://dx.doi.org/10.6084/m9.figshare.3472646.v2>). The code for general procedures to prepare data, manipulate networks, post-process modularity-maximization calculations, and analyse network robustness are written in R, and they are available at <https://dx.doi.org/10.6084/m9.figshare.3472664.v1>. The code for examination of modular structure is written in MATLAB and available at <https://dx.doi.org/10.6084/m9.figshare.3472679.v1>.

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### Author contributions

S.P. conceived the idea, performed numerical simulations, and analysed the data; M.A.P. contributed insights about the mathematics of multilayer networks and data analysis; M.P. and S.K. contributed insights on the use of multilayer networks in ecology and the interpretation of results; S.P., M.A.P., M.P., and S.K. wrote the manuscript.

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### Competing interests

The authors declare no competing financial interests.