

Ecological Multilayer Networks: A New Frontier for Network Ecology

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Abstract

Networks provide a powerful approach to address myriad phenomena across ecology. Ecological systems are inherently ‘multilayered’. For instance, species interact with one another in different ways and those interactions vary spatiotemporally. However, ecological networks are typically studied as ordinary (i.e., monolayer) networks. ‘Multilayer networks’ are currently at the forefront of network science, but ecological multilayer network studies have been sporadic and have not taken advantage of rapidly developing theory. Here we present the latest concepts and tools of multilayer network theory and discuss their application to ecology. This novel framework for the study of ecological multilayer networks encourages ecologists to move beyond monolayer network studies and facilitates ways for doing so. It thereby paves the way for novel, exciting research directions in network ecology.

Key words: Ecological networks, Metacommunity, Multiplex, Multilayer networks, Network ecology, Network of networks

In a nutshell

- The use of networks has led to novel insights in ecological theory. However, the field of network ecology has been hindered because descriptions of ecological systems are typically monolayered—for example, addressing one interaction type (e.g., trophic or competitive) at a time.
- The need to study ecological networks with multiple layers of complexity (e.g., networks that change in time or space or networks with several interaction types) has been acknowledged and a few attempts have begun to emerge. However, such studies are still sporadic, and lack an overarching mathematical framework.
- The theory and tools to decipher structure and dynamics in multilayer networks are now booming in other scientific fields, and data sets of ecological networks become readily available. This presents an exciting opportunity for ecologists to move beyond studies of monolayer networks.
- A framework for the study of *ecological multilayer networks*, which is based on the sound mathematical framework of multilayer networks can stimulate both theoretical and empirical studies to solve open problems in ecology.

Ecological Networks and Network Ecology

Ecologists use networks to explore a multitude of ecological and evolutionary processes—including community structure and robustness [1], trophic interactions [2], patterns of co-evolution [3], genetic variation [4], and disease dynamics [5]. In an ecological network, nodes can represent individuals, species, patches or other entities. Edges, which encode interactions between pairs of nodes, are used to represent numerous different types of ecological relationships. The vast majority of ecological networks are defined by trophic, parasitic, or mutualistic interactions between species [6], although there are also other types of interactions—including non-trophic interactions such as competition, facilitation, or dispersal [7–9]. The most commonly studied networks are unipartite (see Glossary) food webs and bipartite networks of two interacting guilds—such as mutualistic (e.g., plant–pollinator) or antagonistic (e.g., host–parasite) networks. [6]. Networks provide a powerful representation and associated tools to explore ecological complexity; and they repeatedly have led to valuable insights into understanding the structure and function of ecological systems [6, 10–13]. Indeed, network architecture can have crucial consequences for the stability and diversity of complex, multi-species communities [14–16].

Although ecological networks are fundamental to the development of ecological theory, they have usually been studied in isolation, in the sense that either the studied network represents a particular community at a single point in space and time or that it is not connected to other networks. In nature, however, networks usually vary in both space and time, and they are also interconnected. For example, animal movement connects different communities with each other [17, 18], and a pollinator can interact with flowers in one season but not in another, entailing temporal variations in network structure [19]. Ecologists recognize the need to move beyond the investigation of ‘isolated’ networks [7, 17, 18, 20–22], and recent years have witnessed a growing number of studies that involve analysis of what we will call *ecological multilayer networks* (see Table 1). For example, Olesen *et al.* [20] advocated the investigation of networks that are interconnected in space and time, Fontaine *et al.* [21] discussed the importance of simultaneously considering different interaction types, and Bauer & Høye [18] suggested examining networks that are connected to each other by migrating animals. However, these ideas are still preliminary, and they lack an overarching theoretical framework. Ecologists also still lack a set of tools dedicated to multilayer networks, and enormous variation in jargon across studies hinders collaboration with scientists from other disciplines.

Recent advances in the theory of multilayer networks [23, 24], in concert

with a growing set of publicly available tools, now provide an exciting opportunity for ecologists to move beyond the prototypical studies of isolated, ‘monolayer’ networks. Adequate ecological data, appropriate statistics and null models, and network diagnostics are emerging simultaneously. Here we synthesize these ideas to advance theoretical and practical integration between multilayer network theory and network ecology. Our aim is to give an overview of the various types of ecological multilayer networks and of the available theory and tools to analyze such networks. We argue that by adopting approaches from multilayer network science, ecologists can significantly improve their understanding of complex ecological systems.

Introduction to Multilayer Networks

A *multilayer network* provides a way to encode different types of entities and/or interactions as a single mathematical object (see Box 1). Layers can represent different types of interactions, different communities of species, different points in time, and so on. A multilayer network is a quadruplet that consists of the following:

1. A set of entities (the nodes).
2. A set of layers to represent different types of entities, different types of interactions, and so on. These layers can include multiple types (i.e., ‘aspects’) of layering (see below and Box 1).
3. A set of node-layer tuples that each correspond to the manifestation of a given entity on a specific layer.
4. A set of edges to connect the node-layer tuples to each other in a pairwise fashion. The edge set can be divided into *intralayer* edges (i.e., the ‘usual’ type of edge) and *interlayer* edges. The latter can connect the same node either to one of its counterparts on a different layer through a so-called ‘diagonal’ edge or to a different node on a different layer. Both interlayer and intralayer edges can be either unweighted or weighted.

Multilayer network structures are ubiquitous and have a long history in subjects like sociology [25, 26] and engineering [27], although an explicit framework for the investigation of multilayer networks was developed only very recently [23, 28]. Amidst this rapid development, there have been investigations of an increasingly diverse set of applications—including multimodal

transportation networks [29], coupled infection processes [30], and examination of changes in network structure that relate causally to the learning of a simple motor task [31].

Multilayer networks can provide important new insights as compared to monolayer networks or multiple networks without interlayer edges [23, 24]. For example, they provide a natural way to examine the allegiance of nodes to different modules at different points in time and to belong to multiple modules through their different types of interactions [31, 32]. They also allow the analysis of new effects, such as interlayer correlations, that arise from multilayer structures. For example, De Domenico *et al.* [33] expanded the idea of node importance, usually quantified with ‘centrality’ measures in monolayer networks, to node ‘versatility’, which explicitly considers the importance of a node both within and across layers. Additionally, Taylor *et al.* [34] developed a way to measure time-dependent centralities using multilayer networks. In Table 2, we present several examples of multilayer network diagnostics, and we suggest possible applications in ecology.

What are Ecological Multilayer Networks?

In this section, we identify and present major types of layering that are relevant for ecological networks, and we discuss how layers interconnect to form ecological multilayer networks (see Fig. 1). We provide examples and context based on a thorough review of the ecological literature (see Table 1), and we give an example analysis of an ecological multilayer network in Box 2.

Layers Defined Over Space or Time

The study of community dynamics over space or time has a long history in ecology. Early work on spatial and temporal networks focused primarily on how the composition of species changes over environmental gradients or time (e.g., seasons), especially in food webs [35–38]. For example, Schoenly & Cohen [35] compared time-specific instances of food webs to an aggregated food web—in which all of the species and interactions between them were considered regardless of the time when they were collected—to explore species composition at different trophic levels. Now, however, there is intensifying interest in understanding spatial and temporal dissimilarities between communities not only with respect to species but also with respect to interactions [22, 39, 40].

In most existing studies (see Table 1), a set of multiple networks are not defined as a single multilayer network, as interlayer edges are not explicitly

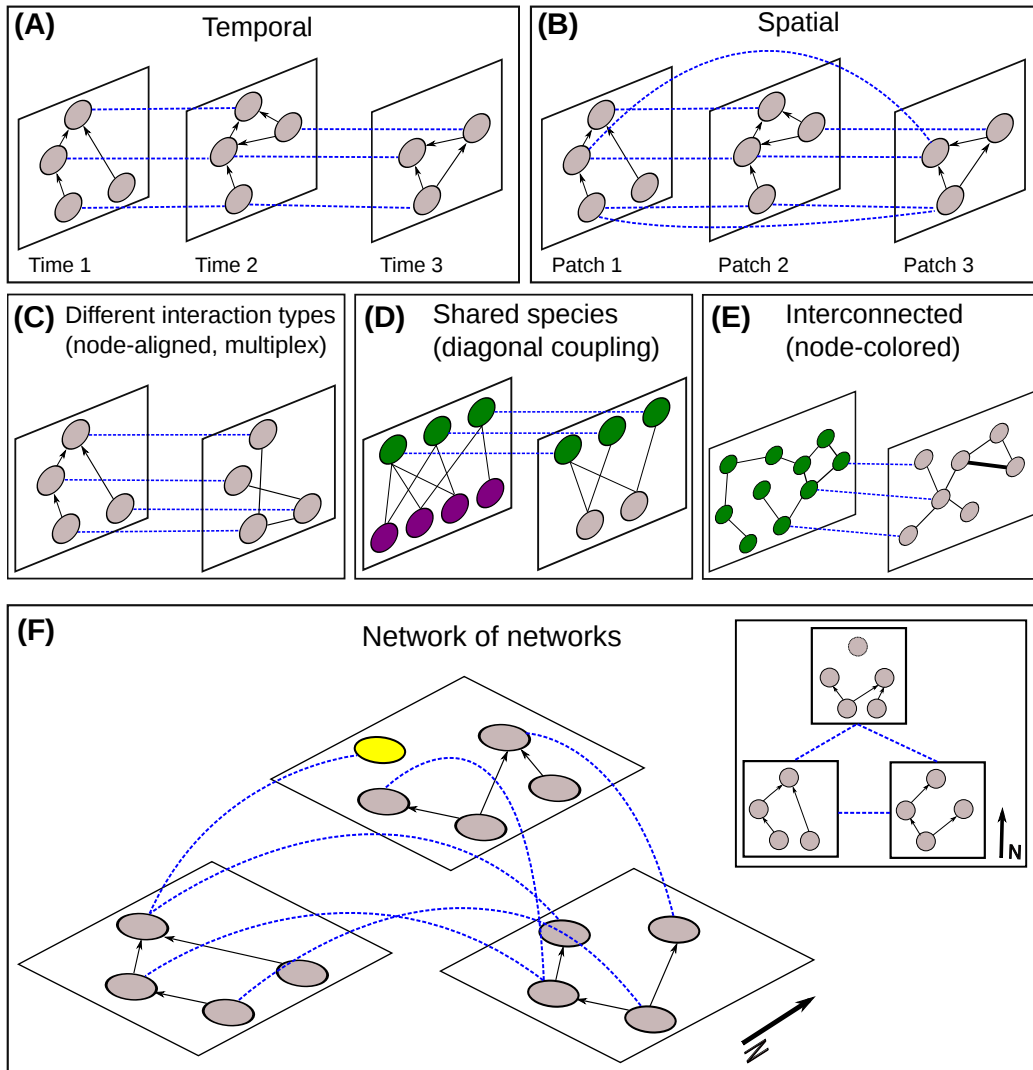


Figure 1. **Multilayer networks in ecology.** In these toy examples, layers are squares, solid black lines are intralayer interactions, and dotted blue arcs are interlayer edges. **(A)** Temporal food webs. Species or intralayer interactions can appear in one time step and not in another. Nodes are connected to themselves across layers in an ordinal way (i.e., one layer follows another). **(B)** Spatial food webs. Species or intralayer interactions can appear in one patch and not in another. Nodes are connected to themselves across all layers (i.e., categorical interconnections). **(C)** Different interaction types among a given set of species (e.g., trophic and facilitative) can be represented with node-aligned multiplex networks, 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. **(D)** Networks with different interaction types that are connected through shared species. We show an example with mutualistic interactions between purple and green nodes and antagonistic interactions between green and gray nodes. One can represent such networks using multilayer networks with diagonal coupling; interlayer edges occur only between shared species. **(E)** Two interacting populations of different hosts. Nodes are individuals, and intralayer and interlayer edges are, respectively, social ties within and between populations. Each node appears in one layer. **(F)** A network of networks representing a meta-community. Layers are communities, and nodes are species. Intralayer edges are trophic interactions, and interlayer edges represent species dispersal among communities. A species can also disperse to a new community (represented by the yellow node). Communities are often embedded in space (e.g., different habitats or patches). In the inset, we illustrate that such networks are sometimes represented without explicit specification of interlayer edges.

included. Instead, the general approach has been to independently calculate diagnostics for each network separately and to subsequently compare the values of such diagnostics (see, e.g., [20, 41, 42]). Using this approach, Olesen *et al.* [19] reported using a plant–pollinator system sampled over 12 years, represented using 12 individual networks, that connectance (i.e., edge density) exhibits little variation over time despite significant turnover of species and interactions.

Intuitively, one defines a layer in a spatial or temporal multilayer network as a monolayer network at a given point in space or time. One then constructs a multilayer spatial or temporal network by using interlayer edges to connect each node to itself in other layers. Layers in temporal multilayer networks are typically ordered (‘ordinal coupling’; see Fig. 1A), but the order of the layers is not important for spatial networks (‘categorical coupling’; see Fig. 1B). This helps illustrate the most obvious use of multilayer networks: they can help us understand how species and interactions diversity or how structures change over space and/or time. By defining layers in different ways, multilayer networks also allow us to answer new types of questions. For example, Gilarranz *et al.* [8] defined a network of plant–pollinator networks in which each community of plants and pollinators is a layer and in which interlayer edges represent extinction and colonization processes. The layers are also embedded in space (see Fig. 1F). By considering a network of layers (see inset of Fig. 1F), whereby each layer was considered a node, it was possible to analyze the importance of communities themselves. Using empirical data, the authors reported that communities that are more central (using betweenness centrality) in the network of layers are more nested and hence more resilient.

Layers Defined by Interaction Type

The stability and function of ecological networks can depend on the way in which different interaction types are combined in communities [7, 21, 43, 44]. Because species can interact in multiple ways in nature, trying to understand ecological networks while limiting edge definitions to a single interaction type hinders a holistic understanding of ecological systems. For example, plants can simultaneously be pollinated by bees (mutualistic interactions) and consumed by caterpillars (antagonistic interactions) [21, 45]. Pioneering studies by Lafferty *et al.* [46, 47] explored food webs with both trophic and parasitic interactions. These studies revealed that food webs that also take parasites into account have substantial structural differences (e.g., increased connectance and longer food chains) from those that do not [46, 47].

Thus far, the primary way in which the problem of different interaction

types has been tackled is by merging networks with different interaction types through a common set of species [45, 48, 49]. For example, Melián *et al.* [45] compiled an ecological network that combines two mutualistic (plant–pollinators and plant–seed dispersers) networks and one antagonistic (plant–herbivores) network, where plants serve as the nodes to enable the amalgamation of the three networks. They observed that the ratio of mutualistic to antagonistic interactions is not distributed uniformly across species. Instead, strong interactions are concentrated in a few plant species with high mutualistic-to-antagonistic ratios (which is a structure that increases species diversity).

One can represent an ecological multilayer network that uses a set of shared species using a diagonally coupled multilayer network (see Table 1 and Fig. 1D). For example, in the networks of Melián *et al.* [45], the set of nodes includes plants, herbivores, pollinators, and seed dispersers. These nodes are connected using edges of different types: herbivory, pollination, and dispersal. The same data can be represented as a multilayer network in which each ecological interaction occurs in a different layer and interlayer edges connect plants to their counterparts in the different 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 (see Fig. 1C). Bauer & Hoyer [18] suggested using a node-aligned ‘multiplex’ network, in which intralayer edges correspond to different interaction types and interlayer edges connect each node to its counterparts in other layers, to simultaneously model trophic, mutualistic, and antagonistic interactions. To the best of our knowledge, the first study that explicitly used an ecological node-aligned multilayer network is the one by Kéfi *et al.* [9]. The authors used a highly-resolved ecological community from the central intertidal coast of Chile to construct a multilayer network in which each layer consists of all 104 species but represents different interaction types—trophic, non-trophic positive (e.g., refuge provisioning), and non-trophic negative (e.g., predator interference). They found that the distribution of non-trophic edges throughout the food web was different than expected by chance (by randomizing the non-trophic edges while keeping the trophic web fixed), suggesting that there is a strong association between the different layers of the network. Their findings, which could not have been achieved by using a monolayer network, open new research directions to understand how the multilayer complexity of natural communities affects species coexistence and the resilience of ecological communities to perturbations.

Layers Defined by Levels of Organization

In biology, it is well-known that processes at any given organizational level (e.g., genes, individuals, populations, etc.) depend on processes at other levels [50]. For example, colonization–extinction dynamics in a metapopulation affect community structure [51]. Exploring interdependence among organizational levels is challenging because interconnecting processes from different levels encompass the complexity of each level in concert with interactions among processes from different levels. One way to represent such systems is with a multilayer network [23]. When the layers in a multilayer network represent different levels of organization, one has a ‘multilevel’ network, and interactions among nodes at a lower level automatically impose interactions at upper levels. For example, a trophic interaction between two species from two different patches entails an interaction between the patches. The simplest example is a 2-level multilevel network, which can also be construed as a network of networks (see Fig. 1F). For example, Melián *et al.* [52] studied metacommunity dynamics at local and regional scales using a Caribbean food web and reported that dispersal affected inter-community variance in the abundance differently for tri-trophic and omnivore food chains.

Scotti *et al.* [53] made the most thorough attempt to examine multiple processes at different organizational levels using a multilayer network approach. The authors constructed a multilayer network with three layers: population, community (food web), and metacommunity (patches in a landscape). They modeled a multitude of ecological processes—including the formation of social ties, trophic interactions, and migration. They illustrated that the metacommunity was sensitive to processes (e.g., social dynamics) of a single species that cascaded through the different levels. Their results uncovered nontrivial dependencies among different organizational levels in ecological systems. Much remains to be done in this arena, which is limited primarily by lack of data.

Layers Defined by Different Group Identity

Many ecological interactions arise from interactions that occur among individuals. For example, pollination is an interaction between an individual pollinator and an individual plant. Individual-based interactions can also occur within species in the form of cannibalism, social contacts that lead to disease transmission, and other scenarios. Unlike species, which can occur in more than one ecological community (and thereby in more than one network layer), individuals can only belong to one community. Individual-based networks have rarely been studied in ecology [6], but they are now becoming

more common (e.g., [54, 55]).

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 (see Fig. 1E) in which each node appears only in one layer. Each layer represents a set of interactions within a population, and interlayer edges represent interpopulation interactions. Both intralayer and interlayer edges can represent a variety of interactions (including competitive, mutualistic, or social contacts). When layers represent populations of different species, interlayer edges correspond to interspecific interactions. A multilayer representation provides an intuitive framework to model interspecific disease transmission while considering an underlying social network, similar to the modeling of disease spread between populations in other studies [23, 24, 30].

Interconnected networks are not limited to individual organisms, as nodes can also represent other types of entities. For example, one can define a multilayer network in which each layer can represent a food web (with its own trophic interactions), and interlayer edges represent inter-food-web trophic interactions. Nakano & Murakami [56] studied a system composed of a stream food web and a terrestrial food web that are interconnected through common aquatic and terrestrial prey species. They found that common prey species are crucial for maintaining food-web dynamics in both habitats.

Challenges and Future Directions

The application of network theory to ecology has led to improved understanding of the structure, dynamics, stability, and function of ecological systems. We believe that multilayer networks likewise constitute a new frontier in network ecology. Many challenges lie ahead, and we will touch upon several of these. We are confident that they will be overcome and that multilayer networks will lead to exciting new avenues for theoretical and applied ecology (see Outstanding Questions).

Data

Collecting multilayer data for ecological networks involves considerable effort. First, data have to be gathered in multiple places, at multiple times, or involving different observational methods to capture different types of interactions. Additionally, ecological systems can have several network aspects. For example, communities can have different interaction types, which can also change in space and/or time. Collecting good multilayer data dramatically

increases logistical challenges and requires the investment of many resources. Designing studies specifically for multilayer networks will aid in optimally focusing such efforts. For instance, it may be more beneficial to create a high-resolution temporal network than to sample several low-resolution temporal networks in different patches. It may also be necessary to standardize collection methods to perform optimal comparative investigations (e.g., across space). Fortunately, many data sets already exist—especially in the context of temporal networks (see Table 1). Using a multilayer network framework, existing data sets can be explored explicitly as multilayer networks rather than as multiple but independent networks. Such investigations should not only provide new insights (see Box 2), but they can also be used as a starting point to verify theoretical predictions and thereby guide future efforts in data collection.

It is important to collect, curate, and standardize the data that is currently scattered in the literature (see Table 1). Several recent projects such as Web of Life (<http://www.web-of-life.es/> and mangal (<http://mangal.uqar.ca/>) aim to provide convenient repositories and formats to store ecological network data. It is also necessary to upgrade these platforms (or create new ones) to accommodate multilayer data. Consistency across repositories will facilitate the combination and comparison of data sets. Such efforts will require developing a standard data format and convenient visualization tools. Some software and data formats are already available (Table 3)—for example from the PLEXMATH project (http://www.plexmath.eu/?page_id=327), but new techniques and data sets need to be incorporated into such resources as they become available.

Analyzing multilayer data also presents several challenges. For instance, the most common method to aggregate network data is to simply include all of the species and interactions observed in a system across all time points (or patches). However, there are many ways to aggregate data, and each entails its own underlying assumptions [23, 57], which usually tend to be implicit rather than explicit. Different aggregation methods can lead to qualitatively different (or wrong) conclusions, but studying more complicated, non-aggregated, structures—such as multilayer networks—requires one to generalize existing tools in ways that are context-dependent and are not necessarily obvious. (It also requires a larger set of situations, such as interlayer interactions, for which one needs to collect reliable data [23].) For example, there are many more types of multilayer clustering coefficients than monolayer clustering coefficients [58]. In general, one is faced with the difficult choice of an inappropriate simplification of a network to use better-understood tools versus using a richer and more appropriate network structure but with tools that are potentially poorly understood.

Theory

In network ecology, many theoretical aspects were borrowed or adapted from the more general science of networks. For example, network diagnostics such as ‘centrality’ measures of node and edge importance [59] and nestedness [60], algorithms for community detection [61, 62] and associated null models for shuffling bipartite networks (see, e.g., [63]), and algorithms that simulate species extinction cascades [14]. Ecological multilayer networks are a new development in network ecology, and we now face the challenge of developing tools that are appropriate for ecology.

One natural step is to adopt (and adapt) diagnostics and algorithms from the many that are available in other disciplines. Many of the structural diagnostics that have been developed thus far are reviewed in [23, 24]. In Table 2, we briefly present some of them and their potential use for ecological networks. It is crucial to determine which existing notions are best suited to ecological problems, and it is even more important to develop methods and diagnostics with ecology particularly in mind. Major challenges include:

1. Developing diagnostics and methods that consider the multilayer nature of ecological networks—for example, by incorporating multiple interaction types in the calculation of diagnostics such as generality/vulnerability, specificity, and nestedness. Importantly, this needs to include advances in studying multilayer networks that have two or more aspects (e.g., that are both time-dependent and multiplex).
2. Developing null models to help consider appropriately shuffled species and interactions. As with ecological monolayer networks, null models are used to test hypotheses about the structure of a network—for example, to examine if a network is more modular than expected by some random process of generating species interactions [63, 64] (see Box 2).
3. Development of mathematical models for dynamical processes such as animal movement, colonization–extinction dynamics, population demography, and species interdependency.

Tools

It is also essential to develop easy-to-use tools to visualize ecological multilayer networks and quantify their structural properties. The availability of user-friendly software packages, such as ‘bipartite’ and ‘igraph’ for the R environment or dedicated software discussed in ecological context—as the case for modularity maximization [62]—has played an important role in boosting

the accessibility of network analysis to many ecologists. Similar efforts would greatly benefit future scholars of ecological multilayer networks. Several algorithms and packages are already available (see Table 3), but it is necessary to develop accessible tools for ecologists from diverse backgrounds.

Concluding remarks

Ecological systems inherently have multiple layers of complexity, but they are not usually analyzed as multilayer networks. Exploring ecological networks using a multilayer representation (as opposed, e.g., to using multiple independent networks) makes it possible to advance network ecology and to gain new insights into the complexity of ecological systems. As the data and tools to decipher structure and dynamics in multilayer networks are now booming in several scientific fields, we are witnessing an exciting opportunity for ecologists to move beyond the studies of monolayer networks. Additionally, many of the challenges that we have outlined can be overcome by strengthening collaborations with mathematicians, physicists, and computer scientists. Such collaborative efforts are necessary for a rapid and successful advancement of multilayer network ecology. We believe that the novel integration of multilayer network theory into ecology offers a fresh and encouraging perspective to tackling ecological complexity that will stimulate both theoretical and empirical studies.

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Box 1. Mathematical Definition of a Multilayer Network

A *multilayer network* is a quadruplet $M = (V_M, E_M, V, \mathbf{L})$, where V is the set of entities (i.e., ‘nodes’), $E_M \subseteq V_M \times V_M$ is the set of (both intralayer and interlayer) edges, V_M is the set of ‘node-layer tuples’ that represent an entity on a particular layer, and $\mathbf{L} = \{L_a\}_{a=1}^d$ is a set of elementary layers. The quantity d gives the number of types (so-called ‘aspects’) of layering, and an ‘elementary layer’ refers to a single element in one aspect of layering (Figure 1). For example, $d = 0$ for an ordinary network, $d = 1$ when there is one type of layering (e.g., as in multiplex networks), and $d = 2$ when there are two types of layering (e.g., a network that is both multiplex and time-dependent).

Let’s consider a time-dependent multiplex network to illustrate a multilayer network with $d = 2$ aspects. In such a network, one aspect is multiplexity, and the other is time-dependence. A single type of relation (e.g., A or B) or a single point in time (e.g., X or Y) constitutes an elementary layer, and a layer consists of a tuple of elementary layers. For example, the intralayer edge between nodes 2 and 3 in layer (B, X) refers to a relationship of type B at time X between these two nodes. A function $w : E_M \rightarrow \mathbb{R}$ yields weights on edges. The set E_M includes both intralayer edges and interlayer edges. A pair of node-layer tuples, (u, α) and (v, β) , are adjacent if and only if there is an edge between them. Thus, 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) if and only if $((u, \alpha), (v, \beta)) = 1$ [23, 28]. Otherwise, one places a 0 in the corresponding entry. Note that 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. The graph that corresponds to a supra-adjacency matrix is called a ‘supra-graph’.

See Kivela *et al.* [23] for additional definitions, discussions of relevant concepts, and important types of constraints on M that produce common types of multilayer networks. Constraints restrict the structure of a multilayer network. For example, enforcing that every node exists on all layers yields a ‘node-aligned’ multilayer network (see Fig. 1C), and it is common to assume node-alignment as a convenient simplification (especially in the study of multiplex networks). Another common constraint is ‘diagonal coupling’ (see Fig. 1D), in which the only permissible type of interlayer edge is

one between counterpart entities on different layers.

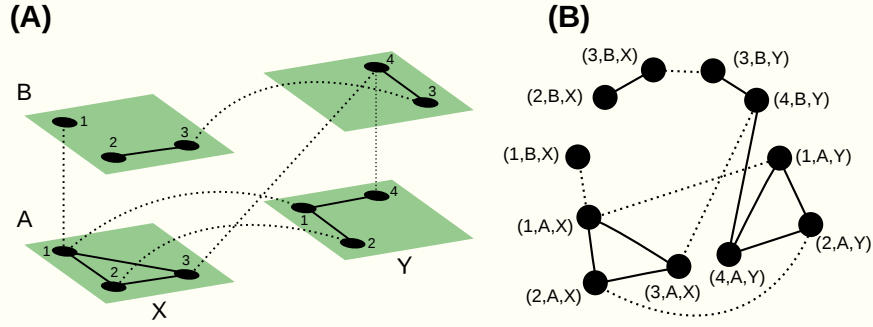


Figure 1. Toy example of a multilayer network. (a) This multilayer network has two aspects: one with elementary layers A and B and the other with elementary layers X and Y . The layers are (A, X) , (B, X) , (A, Y) , and (B, Y) . An example of a diagonal interlayer edge is the edge between node 1 on layer (A, X) and node 1 on layer (B, X) . (b) The graph (a so-called ‘supra-graph’) that corresponds to the multilayer network in panel (a). Each node in this graph is a node-layer tuple in the corresponding multilayer network. For example, the aforementioned diagonal interlayer edge is the edge $((1, A, X), (1, B, X))$, and the intralayer edge between nodes 2 and 3 is $((2, B, X), (3, B, X))$. Intralayer edges and interlayer edges are given, respectively, by solid and dashed arcs. [This figure is modeled after Fig. 2 of Kivelä *et al.* [23].]

Box 2. Example Analysis of an Ecological Multilayer Network

To demonstrate the novel insights that are possible by using a multilayer approach, we analyze a time-dependent ecological network (see [42] for details and data availability). We use an undirected and unweighted version of the network, in which intralayer edges represent infection of small mammalian hosts by fleas and mites. The data were collected in Siberia during six consecutive summers (1982–1987). Each species is connected to itself (i.e., interlayer edges) in an ordinal fashion across six layers as in Fig. 1A. Not all species occur in all years.

Monolayer host–parasite networks are commonly reported to have a modular structure—that is, they consist of groups (modules) of hosts and parasites that interact more strongly within the groups than with other hosts or parasites in the network [21]. A modular structure can also be time-dependent [32, 65]. For example, hosts can interact strongly with given parasites in one year but with other parasites in another year. Consequently, such hosts can belong to different modules in different years, and modules can vary in size across years.

We test for a time-dependent modular structure using the multilayer modularity quality function [32], which we adjust for bipartite networks [see the Supplemental Information (SI)] and denote by Q_B . We compare the maximized modularity (i.e., the value of Q_B) of the observed network to that obtained from 1000 reshuffled networks. (See the SI for details on the null model.) We calculate the significance of the observed modularity, Q_B^{obs} , as the proportion of reshuffled networks with a lower maximized modularity than that of the observed network. We also calculate the mean $\overline{Q_B^{\text{null}}}$ of the maximized modularity of the shuffled networks and the maximized modularity Q_B^{agg} of the fully aggregated network.

The host–parasite network was significantly modular ($Q_B^{\text{obs}} \approx 0.77$ and $\overline{Q_B^{\text{null}}} \approx 0.73$; the p-value is $P < 0.001$). These close values (0.73 vs. 0.77) indicate that a closer inspection regarding the nature of the modular structure is necessary [66]. More importantly, this observed modularity is larger than that of the aggregated network, which was $Q_B^{\text{agg}} \approx 0.6$. The network has 5 time-dependent modules across the six years. The number of species in the modules varies across years (see Figure 1). We also observe that about 28% of hosts and about 30% of parasites change their module affiliation at least once (see Fig. S1 in the SI).

These results point to strong temporal effects in the organization of the ecological community. For example, hosts affiliated with more than one module may be important bridges for transmission of ectoparasites across years. Such insights into the temporal structure of a network are discarded by examining modularity in an aggregated network (which lacks a temporal

structure). Also, if each layer is treated individually we assume layers are independent, which can lead to qualitatively incorrect conclusions and the inability to study questions about time-dependent phenomena [31, 32, 65]).

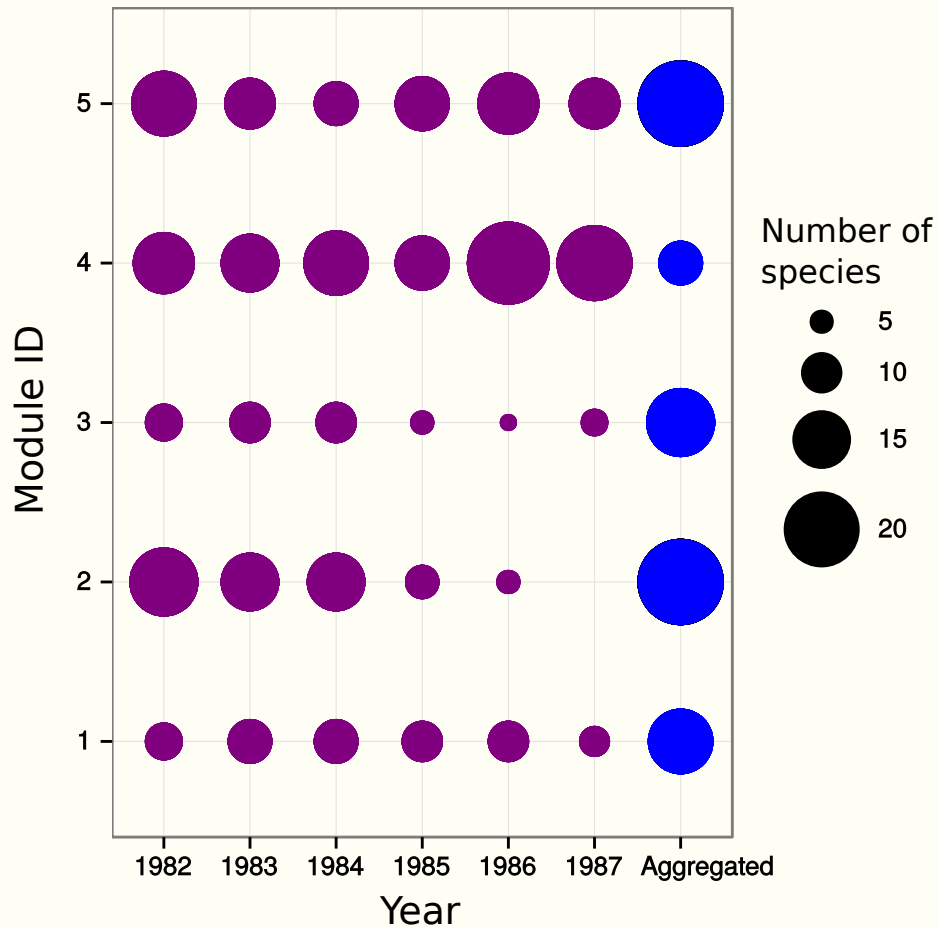


Figure 1. Modules across six years in a host–parasite network. Larger disks indicate modules with more species. The size of the modules changes over time. The aggregated network (i.e., a network that contains all of the species and interactions that were observed during the six years) also has 5 modules (in blue), though their size distribution is rather different.

Outstanding Questions

Species Level

1. Are some species more important (e.g., as quantified using a measure of node centrality) than others in bridging connections across layers (e.g., across patches)?
2. Do species roles (e.g., quantified by their connectivity properties) change across layers (e.g., through time or space)?
3. How does one characterize key species in a system across space and time or when considering different interaction types?

Community Level

1. Do structural patterns (e.g., nestedness and community structure) vary when considering additional layers of complexity, such as space, time, or different interaction types?
2. How does the multilayer character of ecological networks change understanding of basic ecological phenomena such as species coexistence and stability–complexity relationships?
3. How does the multilayer character of ecological networks affect network responses to perturbations?
4. Can a multilayer network help us understand the potential effect of the movement of organisms on food-web structure and function?

Ecosystem Level

1. What are the drivers of network variability across environmental gradients?
2. How do species diversity and species interactions vary as a function of geographic distance?
3. How do interaction effects scale up from the species to the ecosystem level?

Glossary

- **Aspect:** characterizes the type of layering that a multilayer network can have (e.g., one aspect can be space and another can be time, so a multilayer network can have several layers corresponding to different time points and different locations in space). Another example for an aspect is interaction type.
- **Bipartite network:** a network in which the nodes are split into two disjoint groups (e.g., plants and pollinators). Edges can occur between nodes of the two groups (e.g., between a plant and a pollinator) but not within a group (e.g., between two plants).
- **Diagonal interlayer edge:** an edge that connects a node to one of its counterparts on a different layer.
- **Diagonally coupled:** a type of multilayer network in which the only interlayer edges are diagonal ones.
- **Ecological network:** a network in which nodes represent ecologically-relevant entities such as individuals, species or patches. The edges between the nodes can represent numerous different types of ecological relationships such as predation, parasitism, mutualism or dispersal.
- **Elementary layer:** one layer of a multilayer network from a single type of aspect. For example, one point in time or one type of interaction constitutes an elementary layer.
- **Interlayer edge:** an edge that occurs between a pair of nodes in two different layers of a multilayer network.
- **Intralayer edge:** an edge that occurs between a pair of nodes within a layer of a multilayer network (e.g., at one spatial location of a multilayer network in which the layers represent different locations in space).
- **Modularity:** a network-level property that quantifies the extent to which a network is modular; that is, characterized by groups of species that are highly interconnected and that are poorly connected to species of other groups.
- **Multilayer network:** a network characterized by several layers that can represent, e.g., different points in time, different points in space, different types of ecological interactions, and so on. In this case, time, space, and interaction type are different *aspects* of the multilayer network.

- **Nestedness:** a network-level property that quantifies the extent to which species with few connections share their interaction partners with more highly-connected species.
- **Unipartite network:** a network in which interactions can occur between any pair of nodes. (Contrast it with the definition of a bipartite network.)
- **Unweighted network:** a network in which all edges in a network have a value of 1.
- **Weighted network:** a network in which different values (representing different strengths of interaction) can be associated with edges between species.

Table 1. Ecological Multilayer Networks.

Layer	Nodes	Interlayer edges	Intralayer edges	Structural characteristics	Primary research themes/questions	Reference	Figure
Time	S	Each node to itself (ordinal)	M, A, T	A set of networks defined separately at different time points.	Temporal variation in network or node diagnostics (e.g., centrality, connectance). Species or interaction turnover. Network assembly dynamics. Temporal variation in beta-diversity of species and/or interactions.	[19, 20, 35, 42, 67–79]	Fig. 1A
Space	S	Each node to itself (categorical)	M, A	A set of networks defined separately at different sites.	Spatial variation in network or node diagnostics (e.g., number of species, connectance). Spatial variation in beta-diversity of species and their interactions as a function of geographic distance.	[39–41]	Fig. 1B
Interaction type	S	Each node to itself	T, NT+, NT–	Layers with the same set of species and different interaction types (e.g., trophic, facilitation, mutualism).	Quantify architecture of trophic and non-trophic interactions, and quantify the association between these different interaction types. How does including different interaction types affect functional diversity?	[9]	Fig. 1C
Interaction type	S, FA	Each node to itself	M, A, G	Networks interconnected via shared species (diagonal coupling).	How does considering different interaction types change our understanding of ecological and evolutionary dynamics? How do different interaction types affect the stability and robustness of a system?	[21, 45, 48, 49, 80]	Fig. 1D
Community	S	Each node to itself	T	Food webs connected via common species.	How does interaction between food webs (via common species) affect the dynamics of each food web separately?	[38, 56]	Fig. 1D
Community	S	Dispersal	M, T	Networks of communities (e.g., food webs, mutualistic bipartite networks) connected by species dispersal. The communities can be spatially embedded.	How are dispersal and colonization–extinction dynamics associated with network architecture in each community?	[8, 17, 52, 81]	Fig. 1F
Population	I	Each node to itself	Sc	Network layers defined separately for each behavioral interaction.	The function and dynamics of social networks are defined by different behaviors.	[82]	Fig. 1C
Population	I	Among nodes from different layers	Sc	Layers interconnected through one or more nodes.	Disease dynamics in populations of different hosts	[Pilosof et al., in prep]	Fig. 1E

Nodes: Species (S), Individuals (I), Communities (C), Metacommunities (MC), Functional alleles (FA), Intra-layer edges: Antagonistic (A), Mutualistic (M), Trophic (T), Non-trophic positive (NT+), Non-trophic negative (NT–), Genetic (G), Dispersal (D), Social (Sc). References are to studies which explored either networks with multiple (but independent) layers or multilayer networks.

Table 2. Diagnostics for and other features of multilayer networks and their application for ecological multilayer networks (EMLNs).

Index	Definition (words)	Example application(s) in EMLNs	Reference
Multiedge	A vector (whose length is equal to the number of layers) that consists of the set of edges that connect a given pair of nodes in different layers of a multiplex network.	Represent a set of ecological interactions between two species	[83]
Multidegree	Total number of multiedges incident to a given node	Quantify generality and/or vulnerability of a species across different interaction types, different places, etc.	[83]
Versatility	A generalization of centrality measures that considers a node's importance across multiple layers	Identify species that are important (i.e., versatile) because they also bridge different interaction types, communities, and/or locations	[33]
Clustering coefficients	Measure extent to which nodes in a network tend to form transitive triples.	Evaluate the tendency of species to form interaction triples, including when there are multiple types of interactions	[58]
Network community structure	Sets of nodes (in the same or different layers) that are connected to each other more densely than to other nodes in a network; network communities (i.e., modules) are usually identified as the output of algorithms	Identify modular structure across multiple times, spatial locations, and/or interaction types	[32, 84, 85]
Stochastic block models	Generative statistical models to which one fits network data to find mesoscale features (such as modular structure or others)	Identify sets of species across multiple times, spatial locations, and/or interaction types	[86, 87]
Node degree correlation across layers	Indicates relationship between intralayer degrees in different layers (e.g., are high-degree nodes in one layer typically also high-degree nodes in other layers?)	Are species generalists or specialists with respect to various interaction types or in various patches?	[88]
Reducibility	How many layers are needed to represent an ecological system in a way that would be distinguishable from an aggregated graph?	(1) Guide for temporal and/or spatial resolution at which data should be collected. (2) In a network in which each layer is a different community, indicates which of the communities contain unique species and/or interactions (3) Informs researchers about aggregation of data.	[89]
Node/interaction turnover	mean proportion of node appearance and disappearance in different layers	Understand species/interaction temporal dynamics	[19]
Measures of beta-diversity	Similarity between a pair of network layers due to differences in species and/or interactions		[22]

See the references for explicit mathematical definitions.

Table 3. Available software for analyzing multilayer networks

Software	Interface	Uses	Link
MuxViz	GUI (but may require some knowledge of R and OCTAVE)	Visualization, basic calculations (e.g., versatility and community detection)	muxviz.net
Multilayer Networks Library	PYTHON	Provides data structures for general multilayer networks and basic methods for analyzing them	http://www.plexmath.eu/wp-content/uploads/2013/11/multilayer-networks-library_html_documentation/
GenLouvain	MATLAB	Code for determining network community structure in multilayer networks.	http://netwiki.amath.unc.edu/GenLouvain/GenLouvain ; code for the case when layers are bipartite networks is in the SI.
LocalCommunity	MATLAB	Local community-detection method used in [90]	https://github.com/LJeub/LocalCommunities
Betalink package	R	Quantify dissimilarity between ecological networks	https://github.com/PoisotLab/betalink
Multiplex package	R	Algebraic procedures for the analysis of multiplex networks. Create and manipulate multivariate network data with different formats	http://cran.r-project.org/web/packages/multiplex/index.html

We specify relevant websites to download the software.

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Supplementary Material

Ecological Multilayer Networks: A New Frontier for Network Ecology

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S1 Additional Details on Modularity Maximization

S1.1 Modularity Function

We use the multilayer modularity quality function $Q_{\text{multislice}}$ from [32]. For an unweighted unipartite multilayer network with diagonal interlayer edges only and the standard (Newman–Girvan) null model, multilayer modularity is

$$Q_{\text{multislice}} = \frac{1}{2\mu} \sum_{ijsr} \left[\left(A_{ijs} - \gamma_s \frac{k_{is}k_{js}}{2m_s} \right) \delta_{sr} + \delta_{ij} C_{jsr} \right] + \delta(g_{is}, g_{jr}), \quad (1)$$

where A_{ijs} is the weight of the intralayer edge between nodes i and j on layer s (for an unweighted network, the weight is exactly 1 if there is an edge), the tensor element C_{jsr} gives the weight of the interlayer edge between node j on layer r and node j on layer s , the resolution-parameter value on layer s is γ_s , the quantity k_{is} is the intralayer degree of node i on layer s (and k_{js} is defined analogously), $2m_s$ is the total edge weight in layer s , the set g_{is} is the community that contains node-layer (i, s) (and g_{js} is defined analogously), we denote the Kronecker delta between indices x and y by δ_{xy} (which is equal to 1 for $x = y$ and equal to 0 for $x \neq y$), and $2\mu = \sum_{ijs} A_{ijs}$ [32]. Because we are considering an ordinal network, C_{jsr} is nonzero only when

s and r are consecutive layers. For simplicity, we suppose that all nonzero $C_{j_{sr}} = \omega \in [0, \infty)$ have the same value.

For our calculations, we need to adjust the null-model contribution $P_{ijs} = \gamma_s \frac{k_{is}k_{js}}{2m_s}$, which gives the expected number of interactions between nodes i and j in layer s , to consider the bipartite structure of a host–parasite network. That is, hosts are only allowed to be adjacent to parasites, and parasites are only allowed to be adjacent to hosts.¹ To do this, we use Eq. 15 from [92] and thereby write a bipartite multilayer modularity as

$$Q_B = \frac{1}{2\mu} \sum_{ijsr} \left[\left(A_{ijs} - \gamma_s \frac{k_{is}d_{js}}{m_s} \right) \delta_{sr} + \delta_{ij} C_{j_{sr}} \right] + \delta(g_{is}, g_{jr}), \quad (2)$$

where k_i is the degree of host i on layer s and d_j is the degree of parasite j on layer s . We thus modify the code from <http://netwiki.amath.unc.edu/GenLouvain/GenLouvain> (see Table 3 and Matlab code below) by changing the employed null model P_{ijs} .

We use the default resolution-parameter value of $\gamma = 1$. (See [32, 65] for details.) We also need to specify the value of the parameter ω , which determines the strength of the interlayer edges. There is no ‘correct’ value ω and investigating the effect of ω values on the results of modularity maximization is an active research area [65]. As one considers larger values of ω , instantiations of a given node i in different layers become more likely to be assigned to the same community. In our experiments, we use $\omega = 0.8$.

S1.2 Null Models and Network Reshuffling

Modularity maximization produces a result for any network, even when there is no modular structure. Naturally, we also automatically obtain a value Q_B for every network, so we want to compare this value for the network of interest with what we obtain in randomized networks. From the perspective of applications, it is desirable to know whether a putative modular structure reflects real ecological processes [93], and one can use suitable randomizations to try to explore such questions. As a simple comparison, we construct a set of 1000 random multilayer networks by adjusting the probabilistic null model from [63] for a multilayer network. The monolayer version of the null model assumes that the probability of drawing an interaction is proportional to the degree of both the host and the parasite. Thus, the probability of an

¹See Bazzi *et al.* [65] and Sarzynska *et al.* [91] (and some references therein) for discussions of null models for multilayer modularity maximization.

interaction between a host and a parasite in a given layer $s \in \{1, \dots, S\}$ is

$$\phi_s = \frac{1}{2} \left(\frac{\sum_{i=1}^H A_{ijs}}{H} + \frac{\sum_{j=1}^R A_{ijs}}{R} \right), \quad (3)$$

where A_{ijs} denotes the interaction between host $i \in \{1, \dots, H\}$ and parasite $j \in \{1, \dots, R\}$ in layer s . Averaging over all layers, the probability of an interaction between i and j is

$$\Phi = \frac{\sum_{s=1}^S \phi_s}{S} \in [0, 1]. \quad (4)$$

An interaction in a reshuffled network $\tilde{\mathcal{A}}$ is

$$\tilde{A}_{ijs} = \begin{cases} 1, & \text{if } r = U([0, 1]) \leq \Phi, \\ 0, & \text{otherwise,} \end{cases}$$

where $r = U([0, 1])$ is a random number drawn from the uniform distribution on the interval $[0, 1]$. This null model assumes that the distribution of species across years is uniform.



Figure S1. Affiliation of host and parasites to modules across six years. A colored box indicates the presence of the species in a module. An empty space signifies that the species was not present in a given year.

Matlab code

This code was modified from the code in <http://netwiki.amath.unc.edu/GenLouvain/GenLouvain>. It shows how to open a set of csv files, each containing a matrix of a bipartite network which is a layer in the multilayer network and how to analyze modularity of the multilayer network. It also specifies the differences from the unipartite version of the code. It requires the genlouvain.m file which can be found in the link above.

```
1 files=dir('network_obs_binary_layer_*.csv');
2
3 A=cell(1,length(files));
4 for i = 1:length(files)
5     bip_data=importdata(files(i).name);
6     % Transform the pxq matrix into (p+q)x(p+q)
7     [p,q]=size(bip_data);
8     onemode=zeros(p+q,p+q);
9     onemode(1:p,(p+1):(p+q))=bip_data;
10    onemode((p+1):(p+q),1:p)=bip_data';
11    A{i}=onemode;
12    if ~issymmetric(A{i})
13        disp(['Error: layer ',num2str(i),' is NOT symmetric
14            '])
15    end
16 end
17
18 N=length(A{1});
19 T=length(A);
20 B=spalloc(N*T,N*T,N*N*T+2*N*T);
21 twomu=0;
22 for s=1:T
23     %%%%% BIPARTITE:
24     % In case of unipartite undirected networks the
25     % probability P of an edge existing between two nodes
26     % is proportional to the product of node degrees. This
27     % is
28     %  $k_{is} * k_{js} / 2m_s$  in eq.3 in Mucha 2010. Note the  $2 * m_s$ 
29     % because it is an
30     % undirected unipartite network.
31     % In the bipartite case P is  $k_{is} * d_{js} / m_s$ . and the
32     % division is over
```

```

29     % the number of edges m (see Barber 2007, eq. 15 for
        reasoning).
30     % When networks are weighted this explanation refers to
        the strength
31     % instead of degrees.
32
33     k=sum(A{s}); % this is the sum of degrees of the nodes
        in the two sets
34     k=k(1:p); % This is just the first set
35     d=sum(A{s}); % this is the sum of degrees of the nodes
        in the two sets
36     d=d((p+1):(p+q)); % This is just the 2nd set
37     m=sum(k); % Note the m instead of twomu as in unipartite
38     twomu=twomu+m; % Note that we add m and not 2m to the
        mu. In the unipartite version this is twomu=twomu+
        twom
39     indx=[1:N]+(s-1)*N;
40     % This calculates the matrix of probabilities according
        to eq. 15 in
41     % Barber 2007
42     P_ij=zeros(p,q);
43     for i=1:p
44         for j=1:q
45             P_ij(i,j)=k(i)*d(j);
46         end
47     end
48     % Here again we have to create a symmetric adjacency
        matrix out of the
49     % bipartite.
50     onemode=zeros(p+q,p+q);
51     onemode(1:p,(p+1):(p+q))=P_ij;
52     onemode((p+1):(p+q),1:p)=P_ij';
53     P_ij=onemode;
54     B(indx,indx)=A{s}-gamma*P_ij/m; % Note the P_ij instead
        of k*k' as in the unipartite version. also the m in
        stead of 2m
55 end
56 twomu=twomu+2*omega*N*(T-1);
57 B = B + omega*spdiags(ones(N*T,2),[-N,N],N*T,N*T);
58 [S,Q] = genlouvain(B,10000,0);
59 Q = Q/twomu
60 S = reshape(S,N,T);
61 % disp(S)

```

```
62 dlmwrite(['communities_', num2str(omega), '.csv'], S, ',')
63
64 disp(['P value is: ', num2str(sum(Q_null > Q)/iterations)])
```