Mesoscale network properties in ecological system models

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Abstract

Network models are among the most powerful tools in systems ecology. Since trophic relationships (i.e. who eats whom) are among the most frequent interspecific interactions, food webs serve well as system models. In order to better understand ecosystem dynamics, neither strictly local (focusing on individual species) nor strictly global (focusing on the whole ecosystem) approaches are adequate. This mesoscale view on network links suggests to quantify indirect interactions up to some reasonable range and a mesoscale view on network nodes suggests to identify a small set of nodes that are in the most important network positions. We present some examples taking this mesoscale view in ecosystem modelling and use these to discuss the mesoscale perspective. For systems-based conservation management, we suggest to focus on keystone species complexes that are determined considering their indirect interaction neighbourhood. This approach provides a systems-based alternative that hopefully increases to efficiency of future conservation efforts: a small set of system components are targeted in such a way that a large set of the remaining elements are benefited.

Challenges

Using systems models in ecology has quite a long history [1,2], supporting the view that ecology is essentially the science of coexistence among multiple players. Different kinds of interactions among organisms are the grist for the mill of network modelling: trophic networks describe carbon flows between producers and consumers [3], pollination networks represent inter-specific effects between plants and pollinators [4,5] and co-occurrence networks summarize statistically inferred interactions, typically between microbes [6]. In all of these networks, whatever is the definition of nodes (species, functional groups, OTUs) and links (predation, association), dependencies are represented, being either directional or mutual. If the network is wisely defined, it is a holistic model of a more or less „whole" system.

A general strategy of systems approaches in biology is to cross levels of hierarchical organization (i.e. individual, population, community, ecosystem; infraindividual levels not considered in this paper) by integrating pieces of local knowledge and looking for emergent properties [7]. Network analysis offer possibilities to study and quantify part-to-whole relationships: how can smaller components (like species) compose a system (like a lake community) and how can system-level properties (e.g. food web connectance) constrain the behaviour of its components (by various mechanisms including energetics, informational

theory and reliability theory). The co-evolution of organisms is the outcome of these hierarchical, multi-level processes.

It is known that certain species [8,9] and certain interactions [10] are more important than others. Certain species (keystone species, ecosystem engineers) play a major role in community dynamics, while in many other cases meaningful ecological processes can be assigned only to multi-species assemblages (functional groups). It is a major challenge to conceptualize [11,12,13,14] and quantify [15,16] the amount of redundancy in ecosystems. This may help to study the functional roles of species and to answer general questions like what do species do in ecosystems [17,18].

The network perspective

From a non-network perspective, the importance of species can be assessed by their individual attributes (e.g. home range, rarity, biomass). The network perspective considers also their biotic community, focusing on interactions and feedback loops among individual species (populations). From this viewpoint, species are important because they matter to their neighbours (in the network context outlined here, „importance" means centrality in the network, according to some of its mathematical definitions). This is true not only for mutualists (positive-positive effects) and preys (positive effects on predators) but also for competitors (negative-negative effects) and predators (negative effects on preys): in the sense of population control, negative influences can also transmit important effects. Experimental results, descriptive field studies and models equally demonstrated that whichever species is removed from a community, many others give some kind of response (e.g. changed population size, changed behaviour), being in different network positions.

According to a first approximation, thus, more connected species in the interaction network are more important members of ecological communies. This means that node *degree* is a frequently used proxy for system-level node importance [19,20]. But this is a local approach in network terms: it may also matter how many neighbours the neighbours have.

A mesoscale view on graph links

Recognizing the importance of indirect effects in ecosystems (at least as early as in [21]) triggered an interest in considering effects spreading to the neighbours of interaction neighbours in a network. The phenomenon when the population size of species A changes and this influences the population size of species B and this influences the population size of species C is termed interaction chain effect (the chain can be longer than two steps in this example). Beyond conceptual developments [22], experiments [23,24] and descriptive studies [25], quantitative approaches have been suggested to identify and measure indirect effects. The first approach was to quantify node *status* in binary networks [26; „binary" means that information on who eats whom is „yes or no" type], providing ecologically naive results based on pioneering mathematical methods (the question was which animal is the most important in a Canadian willow forest). An ecologically more realistic attempt was the assessment of 2-step long effects in weighted host-parasitoid networks [27; „weighted" means that the strength of the interaction is measured empirically]. Simulation efforts also support the importance of considering indirect effects [28,29,30,31], suggested also by network analysis for three steps [32,33,34] or even longer [35]. Considering interaction chain effects, it is possible to quantify the strength and symmetry of the interaction between a pair of components and to identify critically strong or asymmetrical direct or indirect effects [33,36]. Figure 1 shows an example where indirect interactions may have a larger effect on other nodes than direct ones. Empirical studies also show examples for this [37]. There are studies

where keystone species are identified by network analysis using centrality measures considering indirect interactions [31,38,39,40,41]. These network analytical tools quantify which graph nodes are in critically important positions in graphs, based on several definitions (e.g. number of neighbours, distance from other nodes).

A mesoscale view on graph nodes

There are several techniques in network analysis to quantify the positional importance of individual nodes. Based on various mesures of centrality [33,38], redundancy [16] and similarity [42], we can provide importance ranks for graph nodes (representing individual species, functional groups or even OTUs). The top node(s) of these ranks may identify keystone species. However, since earlier research suggested strong context-dependency for identifying keystone species, searching for the single key element in a complex ecological interaction network is a risky approach.

    Beyond ranking nodes individually (in the context of the network), there is an old interest in looking for important sets of species. In vegetation science, core species are defined by biomass contribution [43] or local abundance [44]. For microbial communities, similarly, the core set of species can be the ones being most abundant [45] but more integrative approaches also exist, where core organisms are defined by habitat similarity, behaviour and connectivity [46].

    In community ecology, a seminal empirical study suggested to identify keystone species complexes by their role in community assembly [47]. This paper suggested that 4 organisms, together, form a core in community assembly: if they coexist, the rest of the community is quite consistent in terms of constant species composition. If some of them are missing, community composition is more variable.

    Several papers using loop analysis (i.e. semi-quantitative studies on effect signs) offer models of different size in a nested arrangement, i.e. core models of the most important components and enlarged models for a larger system [48,49]. The importance of a small set of nodes is often linked to autocatalytic loops as well [50,51]: in these subcommunities, species A has a positive effect on species B, species B has a positive effect on Species C and species C has a positive effect back on species A (and the loop can be longer). In network analysis, subsets of graph nodes can be defined in several ways (cliques, motifs, modules) and there is recent interest in conceptual clarification and classification [52].

    In social sciences, a key player group of k species is defined in network terms, as k nodes that have maximal values for either reachability or fragmentation. These offer two different ways how to look at positonal importance [53,54]. From a reachability point of view, we may think of messages sent from certain nodes to others. Sending a message from a hub (highly central node) will reach many others. Sending a message from two hubs may not be much more efficient, since their neighbourhoods generally largely overlap. Instead, sending a message from a hub and another, less central node can be a much better option. The hub is connected to a large part of the network and the other node can help to reach some other distant region in the network. A good combination can dramatically increase reachability of other nodes from two particular nodes. From a fragmentation point of view, the argument is similar: here, we delete nodes from the network model and register to what extent the network falls apart (i.e. how many new graph components appear and how does the averge distance between graph nodes change).

    Multi-node approaches have been recently applied for plant-pollinator networks [55], food webs [56,57,58] and habitat networks in landscape ecology [59,60]. Figure 2 shows an example for a food web where the identity of the three most important individual nodes are very different from the most central set of the three nodes. It was also suggested to use several

approaches to define network cores in parallel [57], for example, to combine the KP approach with quantitative trophic models and loop analysis.

A mesoscale systems view suggests to protect neither a single keystone species nor all of the species in the community. One question is how to choose k nodes in such a way that most of the other n-k nodes are reachable (or fragmented). One of the challenges in applying these mesoscale approaches is how to standardize the aggregation of food webs (how to define graph nodes in ecological networks, see [61]), which is a highly context-dependent problem [56,57].

Conclusions and perspectives

The mesoscale view on graph links and graph nodes is being increasingly used at several levels of biological organization. Beyond food webs, it has been used also for landscape graphs [59] and this research framework helps to link hierarchical levels vertically, i.e. to study the relationships between individuals and populations, between populations and communities as well as between local communities and metacommunities in a large-scale ecosystem [62]. Indirect interactions are increasingly considered and key network elements are identified in various systems (see already [53] for social network examples).

The mesoscale view on both indirect effects and key sets of species provides a methodological framework to combine importance by centrality and importance by uniqueness in ecological networks [63]. Several organisms that do not interact directly can be suggested to form a joint core of ecosystem dynamics and only network analysis can reveal these hidden relationships. In marine food webs, these can be central shrimps and uniquely positioned large sharks [63] or sea urchins, sea stars and algae [57]. Latest results suggest that members of keystone species complexes are typically positioned at different trophic levels and they are connected to a core trophic chain in the food web [64]. This may have important consequences to better understanding minimal ecosystems and functional redundancy in ecological systems. If this general pattern will hold for several other ecosystem models, multi-node centrality analyses can contribute to making conservation efforts more efficient and holistic.

Redundancy in ecological systems is generally understood in different ways. The real kind of redundancy means identical or quasi-identical elements performing the same processes: in this sense, large population size within a species or ecologically almost equivalent species are examples. In a more functional sense, similar food web positions (i.e. similar interaction neighborhood) or trait-based similarities may detect functional redundancy [42,61] which is more in line with the concept of degeneracy [65,66]. In this latter case, elements of different origin perform similar or overlapping functions and this may result in their replaceability. The consequences for robustness and adaptability are clear: the narrowly defined redundancy increases robustness but offers only limited adaptability (mutation and divergence still needed), while degeneracy offers immediate adaptability beyond increasing robustness. Studies on the relationship between species diversity and ecosystem reliability 67,68] provide experimental evidence for the importance of degeneracy in ecosystem functioning.

An evolutionary context helps to understand the origin and maintenance of redundancy and degeneracy. Quasi-identical, redundant elements of an ecological system may be in strong competition and their coexistence may not be stable on the long term. In case of degeneracy, the strong overlap in one function may be compensated by differences in other features and coexistence can be stabilized, maintaining this kind of functional redundancy. This can be reflected in modular system design and the consequent patterns of connectivity [69] (and see already [70] for raising similar problems). The challenge of aggregating food

webs is exactly how to match redundancy, degeneracy and biological traits, and to quantify network structure in terms of mesoscale neighborhoods like modules and connectivity patterns.

Systems approaches, in general, may help to understand the relationship between network position and extinction in toy networks (a very old problem: [71]) and scale up this problem in order to identify organisms in critically important positions of real complex networks [72]. Further developing a mesoscale view on ecological system models can be crucial for systems-based conservation [73], ecological economics [74] and fisheries management [75]. Current strategies in conservation management focus mostly on individual species (typically rare ones at the brink of extinction) or ecosystems (typically where rare species live). Focusing on rare species (and their habitat), can be replaced by novel approaches, focusing on protecting small groups of important species (and their interactions). This could indirectly benefit several other neighbours so positive effects can be maximized at the scale of the ecosystem, while efforts can be minimized on carefully selected target species. The mesoscale approach can optimalize conservation management by incresing both feasibility (not too many species) and realism (not only a single species). In marine fisheries, the maximum sustainable yield of different species should be assessed in a multi-species context [75] instead of evaluating individual species one by one. In these cases, we face the problem of predicting and managing the behaviour of complex systems and we have to optimize our efforts by selecting the target of action between too local (i.e. a single species) and too global (i.e. the „whole" ecosystem) approaches. We suggest that the relevant and still manageable scale is the mesoscale, i.e. a few species carefully chosen based on their interaction system up to a few steps.

Acknowledgments

Figure legends

Figure 1. Effects spreading out from a focal network node (#11 in black). The expected effects on other nodes can be assessed by network analysis considering only the topology of the network [Jordán 2009]. Node size is proportional to expected effect. Neighbours (in violette) are typically more influenced (like #15) but some of them are not so much (like #16). Non-neighbours (in red) can be influenced only by indirect effects, typically to less than neighbours: some of them are still more strongly (like #43), while others are just weakly (like #17). Depending on the maximum length of indirect effects, some distant non-neighbours (in green) may not be influenced at all (like #38). Note that the red node #43 is larger than the violette node #16: in this case, a second neighbour is more strongly affected than a (first) neighbour. This is the network of the Chesapeake Bay food web [76].

Figure 2. The Mauritania food web [77]. The most important network positions are calculated by closeness centrality here, and they can be identified either by evaluating individual nodes (a) or by evaluating groups of nodes (b). The individually most central three nodes are not the same as the most central set of three nodes. Trophic groups are vertically organised according to their trophic level (*TL*). The organisms suggested to be keystones here are *PrimProd* (primary producers), *MesoZoopl* (meso-zooplankton) and *MicroZoopl* (micro-zooplankton) according to the single-node approach (a), while they are *PrimProd* (primary producers),

LElasminv (large invertebrate-eater Elasmobranchs) and *Orc* (orca) according to the multi-node approach (b). Note that the multi-node approach generally identifies a core set of species at several trophic levels, defining a core trophic chain in the food web.

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