Network ecology: topological constraints on ecosystem dynamics

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PACS code(s)= 87.23.-n, 87.10.+e

Abstract

Ecological systems are complex assemblages of various species with interactions between them. The interactions can be even more important than the species themselves for understanding how the whole system is functioning and organized. For the representation of the topological space of interspecific relationships, graph theory is a suitable mathematical tool: the network perspective and the various techniques of network analysis are more and more elaborated and invading ecology. Beyond a static view on networks, fundamental questions can only be answered if dynamical analyses are also made, and now it is clear that structural and dynamical studies must not “compete” but strongly complement each other. Our aim is to give a menu of classical and more recently suggested network indices and to discuss what do we know about their relations to ecosystem dynamics. Since ecologists have very diverse problems, they need diverse techniques and a good insight in matching the adequate method to a particular problem. The main question is how to link certain graph properties to understanding and predicting the behaviour of an ecosystem. We wish to contribute to bridging the gap between extreme structural and extreme dynamical views.

Key words: community organization, food web, graph theory, ecosystem stability

"Most of what is interesting about biological communities cannot be pinned, stuffed, pressed onto herbarium sheets, or preserved in alcohol.” (Thompson 1982)

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Preprint submitted to Elsevier Science 25 August 2004
1 Introduction

Definitions of ecology are highly variable from Haeckel (cited in (11)) to the modern textbook definitions (11). The common message is the emphasis on interactions between living individuals and their abiotic environment, between conspecific individuals, between populations, between different groups of species or between ecosystems. Depending on which of these interactions is of particular interest, one can be an autecologist, a population ecologist, a community ecologist, a systems ecologist or a macroecologist. Although at each level, there are a number of entities whose interactions are to be studied, typically a couple of them are considered only (for simplicity or because of science policy constraints). The analyses of more or less complete interaction networks belong to the minority: these approaches are mostly developed in systems ecology. Thus, the network perspective in ecology has been rooted in this field. What the motto wants to suggest is that, just like it is not nerve cells themselves but their interaction pattern what is the most important in understanding the functioning of the brain, similarly it is not species themselves but the topology of their interspecific interactions what is the most important for understanding the functioning of an ecosystem.

The origins of network ecology date back to the early years of graph theory (56), developed by receiving input from economical network analysis (52) or sociometry (55). Nevertheless, the most ecologists are still interested in a single or two abiotic factors affecting an organism, in one or two species, in a couple of functional groups or in a single ecosystem. Only global ecologists do not have to be blamed for this, since the number of known blue planets is exactly one.

The new hope for popularizing the systems view in ecology is the conjuncture in network science suggesting interesting, but sometimes premature, conclusions for ecological network analysts. Ecologists are being told, again, that they cannot understand an entity without its appropriate context, they cannot interpret pairwise interactions without considering the whole interaction network and they cannot assess the importance of a species without regarding it as a part of the ecosystem machine. Thus, the hierarchical view on biological organization and the network perspective at each level are being married again in contemporary ecology. Our review wants to contribute to a stable marriage.

Natural scientists always look for characteristic patterns, rules and laws in nature. Whereas laws are reserved for physicists, rules are for biologists (and patterns remain for ecologists). This is not because of laziness or mental weakness but comes from the complexity and diversity of living beings. Discussing the science of complexity in detail is beyond the scope of the present review: we
only mention briefly that what follows tries to bridge the gap between mathematical rigor and ecological field experience, possibly applicable in predictive conservation biology.

We do not dare to focus on every level of hierarchical organization, instead, we will speak mostly of populations of coexisting species, functional groups and the "entire" communities they form. We will discuss interaction networks representing various kinds of pairwise interactions (e.g. predation, parasitism, direct competition etc., see (139)) but if real data will be analyzed, we will be constrained to talk mostly about food webs representing only predation (who eats whom), since data bases mostly describe only these, probably the most important interspecific relationships. If not stated explicitly otherwise, we will discuss food webs in this narrow sense. Nevertheless, we will see that if nothing else than trophic interactions are studied, a good deal of conclusions can already be drawn.

We summarize how food webs were analyzed in the past, what now we can tell about their topology and structure, and how it can be linked to the actual and long-term dynamics of the community represented by them. Connecting structure to function, or structure to dynamics has always been a primary aim of ecologists but, as far as we see, the tools for structural analyses were very poor (compared to the arsenal of dynamical analyses, bursting since (96)). We review the novel tools of structural analysis and discuss their relevance.

2 Brief history

Since the first food webs had been published, many ecologists have been interested in collecting these diagrams (25), critically discussing their relevance (116) and looking for typical patterns in their structure (129). Two problems have always been persisting. The first one, which we do not discuss here, was the methodological background of describing trophic relationships in the field and constructing the networks. The second one was the analysis of more or less reliably created food webs. For a long time, the structure of food webs has been characterized by parameters of very limited use (cf. (149)). These network indices wanted to reflect the basic mathematical properties of food webs: these are directed flow networks with one or more sources, one or more sinks and several transmitters. Self loops are possible but typically out of the interest of ecologists (except for some interesting research areas), just like symmetric relationships (when species A and B eat each other). Interaction networks, defined in a broader sense, may represent also nontrophic interactions (e.g. mutualism, (104), or direct competition, (117)): here, the antagonistic pattern of positive and negative signs (food supply and predation, respectively, in narrowly defined food webs) is not a restriction. Both food webs and interaction...
webs may be weighted (valued) graphs: for the first, we have many examples (162; 134) showing the material fluxes of mostly carbon, while the second case is much rarer (but see (117) for weighted competition or (77) for weighted mutualism). For many purposes, undirected webs can be considered (tracing indirect effects), while sometimes direction is evidently necessary (e.g. in case of energy transfer (91)). The presence of detritivore loops and parasitoids frequently causes problems in looking for general patterns and interpreting these rules. Finally, ecologically interesting and sometimes important subwebs of food webs include sink and source webs, representing a particular species and everything providing food to it directly or indirectly and a particular species and everything receiving food from it directly or indirectly, respectively (25). These are the subgraphs of community webs.

By the end of the seventies, a collection of food web patterns statistically characteristic in nature have been produced (25; 127; 129; 132). (Some concepts in this paragraph will be defined and explained later.) First, it was argued that food chains are seldom longer than four or five steps, for various reasons including thermodynamic efficiency (88), population dynamics (125; 85) or body size constraints (40). Second, it was found that both omnivores (126), especially those feeding on non-adjacent trophic levels, and loops are rare in real food webs (129). Third, it seemed to be convincing that prey overlap graphs do not typically contain holes and predator overlap graphs do not contain rigid circuits (154) but see (30). Fourth, more or less fixed ratios of species at different trophic levels and interactions between certain trophic levels have been identified (132). Fifth, a characteristic prey:predator ratio was declared to be around 3:4 (25). Sixth, however debated, ecologists typically believed that food webs depicting a single habitat are not compartmentalized (128).

Following the serious criticism on the ”classical” era of food web research (124; 116; 118), a pragmatic methodological unification (29) suggested, for example, to produce higher resolution webs. The early results of modern food web analysis presented trophic networks in much greater detail, for example, in the Little Rock Lake (93), in the Ythan Estuary (51) and in a Caribbean island (50). These webs are generally said to be of ”high quality” (37) but this only refers to either greater efforts during field work or less strong aggregation of data. In fact, the ”quality” of a web is context-dependent: it depends on the adequate matching between the actual problem and the chosen level of data aggregation. Both strongly aggregated webs (of low resolution) and weakly aggregated ones (of high resolution) can help in answering certain questions. One thing is for sure: field data on trophic relationships need some level of aggregation.

The recent advances in ”network science”, a multi-disciplinarily motivated intention to understand the universal architectural principles of different kinds on real networks (9; 5; 153) encouraged ecologists to study the number of neighbours of species in food webs and its distribution (i.e. link distribution
(150; 107; 37; 38)). This connection of global network structure to the most local properties might be dangerous for jumping the intermediate scale of organization, i.e. effects more than local but less than global, which is possibly of the most relevant interest in ecology. In the following chapter, we review some recently introduced “mesoscale” indices that are possibly more sensible in characterizing food webs and discuss their relevance.

3 The network context

In food web ecology, studies have been said to focus on the structure (130), topology (37) or architecture (159) of trophic networks. If we want to avoid conceptual ambiguity, we have to make clear what is meant here by topology and structure (the third expression will not be used here). We will call ”topology” the information whether there is any trophic relationship between two species. If the directedness (who eats whom), the sign (a negative effect, like predation, or a positive one, like food supply) or the weight (strong or weak, even quantified) of an interaction will also be given, we will call it ”structure”. We think this is suitable for bridging the gap between mathematical rigor and ecological practice. We also note that we will use the words ”graph” and ”network” interchangeably.

The key message of topology is to keep the ”whole” in mind while studying the ”parts” and vice versa. The network context is unavoidable if the embedded entities are to be understood. Many ecological problems are essentially topological ones. For example, a current key topic in ecology and conservation biology is how to link species and ecosystems ((66), i.e. what do species do in a forest, and what does the whole forest community do with its species). If the role of species is to be understood within a community context, we have to map the relationships and use this map for quantification and prediction. Ecologists are more and more aware of the significance of indirect effects in the functioning of ecological systems (1; 59; 121; 3; 175; 177) but see (92).

For many ecological analyses, it can be enough to look at one or two species. In these cases, the detailed mechanisms influencing the behaviour of the species are to be understood in deep details. For larger systems, it is not feasible and possibly also not necessarily important. Just like chemists look at simple molecules, like $H_2$, through the lens of an atomic physicist, they need the lens of a mathematician when looking at the structure of an alkane or another large molecule (135; 61). Different levels of our interest may use quite different approaches. If we agree that topology is an important tool for analyzing the key problems of community ecology, we still have to decide how to apply it, which particular network indices should be trusted. Our preliminary answer, but also a key message, is that we do not need to choose the one and only
Fig. 1. A hypothetical food web. Lettered circles represent species (A and B are top predators, while H and I are producers) and links represent various types of interactions between them: thick and thin solid lines = trophic interaction (e.g. BJ, predation in one direction, food supply in the other), solid arrow = predation pointing at the prey (e.g. AD), horizontal dashed-dotted line = indirect exploitative competition (FG), vertical dashed-dotted line = indirect trophic cascade (BH), vertical dashed arrow = nontrophic effect (BC). Note that some links are directed (AD), signed (BC) and/or weighted (EH).

graph property for the pleasure of ecologists. Instead, we have to keep an arsenal of network indices in our mind, and as different problems come up, we always have to match the adequate indices to the particular problems.

4 Network topology and structure

Typically, we will discuss topological and structural indices in parallel, and whenever possible we will begin with topology (in this chapter, we intend to mention dynamics only slightly). Additional methods are needed and as possible topology is complemented by information on the direction, sign or weights of links. The majority of the topological indices have some version taking this added information into account. Fig. 1 will stand as a hypothetical reference network for illustrative examples and explanations.

4.1 The classical description

For even a quick orientation, several measures are typically quantified for a food web: the number of nodes ($N$ equals 10 in Fig. 1) representing species, trophic groups or any suitably defined group of individuals, the number of links ($L$ equals 13 in Fig. 1) representing direct trophic relationships in food webs (the BC link in Fig. 1 would appear only in a broadly defined interaction network, while BH and FG links show indirect effects unnecessary to be
shown), the link density ($L/N$ equals 1.3 in Fig. 1) and connectance:

$$C = \frac{2L}{N(N - 1)}, \quad (1)$$

i.e. the ratio of realized and possible links in the network (in Fig. 1 $C=0.288$). The directed connectance is calculated as:

$$C_d = \frac{L}{N^2}, \quad (2)$$

where self-loops and direction may also be taken into account ((93), in Fig. 1, $C_d=0.13$). Of course, the number of possible links is not exactly equal to the denominators of these formulae, but is often very far from in many particular cases. For example, in host-parasitoid networks we only have maximally $KM$ interactions, where $K$ is the number of hosts and $M$ is the number of parasitoids (this graph is a bipartite graph).

Some network statistics have been given for traditional reasons but not being used very frequently in recent analyses: the number of prey species ($PY=8$ in Fig. 1, species consumed by anything), the number of predators ($PR=8$ in Fig. 1, species consuming anything), the number of basal species (i.e. producers, $B=2$ in Fig. 1, not consuming anything in the food web), the number of top species (i.e. top predators, $T=2$ in Fig. 1, consumed by nothing in the food web), the number of intermediate species ($I=6$ in Fig. 1, both consumed and consuming), and the number of links between these groups (in Fig. 1, $BI=6$, $II=3$, $IT=2$ and $BT=0$). The ratios of these simple quantities ($PY : PR$, $B : I : T$, $BI : IT : BT$) have been extensively used in classic food web analysis, and some rules of thumb have been set, but now it is evident that these measures are extremely sensitive to methodology and are not very sensible in an ecological sense.

4.2 Neighbourhood

The most elementary property of a node, and the ultimate information for a network, is the number of other nodes connected to it, i.e. its degree ($D$, for species $J$ in Fig. 1 it equals 2). This is the representation of direct interactions between the entities composing the network. In directed graphs (digraphs), the number of links pointing at and pointing from the focal node are called in-degree ($D_{in}=1$ for $J$) and out-degree ($D_{out}=1$ for $J$), respectively:

$$D = D_{in} + D_{out}. \quad (3)$$
The in-degree of a node can be interesting, for example, if the effects of nutrient enrichment or pollution transfer through the plants are analyzed. It has been shown that polyphagous herbivore populations (large $D_{in}$) are more variable in size (142). The orientation of links can be characterized by

$$D' = D_{in} - D_{out},$$

a very simple but still informative and possibly sensible index ((71), for species $C$ in Fig. 1 it equals 1).

Anything else we will say about networks and network indices is less local. Of course, the degree can be averaged over all nodes in a network ($D_{av}$), its standard deviation can be calculated ($D_{std}$), or its distribution can also be analyzed ((150; 106; 107; 38; 37), but these latter network properties are not real global indices: these network indices result from averaging the local ones (cf. really global, ”emergent” indices are not defined and understood locally).

If we do not consider more distant nodes but still broaden our interest into the links connecting not the focal node to its neighbours but its neighbours to each other, we can study how their direct interactive partners are connected to each other, i.e. the clustering coefficient of a node ($CC$), defined as

$$CC_i = \frac{2L_i}{N_i(N_i - 1)},$$

where $L_i$ is the number of links between the $N_i$ neighbours of node $i$ (for species $C$ in Fig. 1 it equals 0.66, since there are two links instead of the maximal three between its three neighbours). $CC_i$ can be averaged over all nodes giving the average connectedness of nodes’ neighbours (19; 106; 108). We note that the use of clustering coefficient can be very limited in certain kinds of networks. For example, it works very well for social networks but is seriously limited in case of studying landscape graphs (because of the realization of the graph in the 2D space, e.g. corridors do not cross habitat patches - many pairs of neighbouring patches cannot be linked to each other) or food webs (because of the strict limits on ecologically plausible interactions, e.g. plants do not eat each other - the maximal clustering for herbivores is far below one).

For simplicity, in certain cases we can treat species with similar neighbourhood equal and it is practical to lump them into single nodes (e.g. species $J$ and $E$ in Fig. 1). The aggregation of graph nodes of equal neighbourhood represents a trophospecies, cf. (176), corresponding to a structural equivalence class (90), while the aggregation of nodes of similar neighbourhood (defined suitably) is based on the less strict concept of regular equivalence (90): two nodes are regularly equivalent if their neighbours are equivalent too. A maximal regular coloration means a coloration of a graph, where nodes belonging to different
regular equivalence classes are coloured differently, and the minimal number of colours is used. The definition of differently strict equivalence classes and the corresponding coloration of food webs give a key also to inter-ecosystem comparisons. Otherwise, the majority of topological and structural network indices will be understandable only within the context of a single community network. From this perspective, role coloration of food webs is possibly a major step for predictive macroecology.

A global network property is the compartmentation of the food web. It quantifies whether there exist groups of species with many interactions within the group but only a few interactions between members of different groups. It is defined as

\[ C_l = \frac{\sum_{i,j} p_{ij}}{N(N-1)}, \]  

where \( p_{ij} \) is the ratio of the number of species interacting with both species \( i \) and species \( j \) and the number of species interacting with either species \( i \) or species \( j \) (128). (It follows from the definition that greater \( C_l \) defines more compartmented web.) Some analyses had suggested that the existence of compartments is advantageous for local asymptotic stability (defined below, (96)) but later it has been demonstrated that the compartmentalized nature of food webs is typically an artefact and not a general property in natural webs describing a single habitat ((129), p. 160).

Another approach in looking for compartments is the application of the cohesive subgroup index from sociometry (82). This index, similarly to the clustering coefficient, should be used carefully for analyzing trophic networks: the use of \( N(N-1) \) directed links as a reference state is unrealistic, just like \( N(N-1)/2 \) links between a nodes neighbours in the case of the clustering coefficient.

In directed signed graphs, a recently suggested group on possibly interesting nodes is the autocatalytic set (ACS): a set of nodes where each node receives a positive link from any other member of the group. It has been suggested that the appearance and fast growing of ACSs is a characteristic property of some large and complex networks (62; 63). Since ACSs can be divided into core and periphery regions, and cores may overlap, a definition of keystone nodes has been given as nodes in core overlaps. This is in concert with the ideas below: a node can also be important because it is connected to critical nodes, i.e. it has many "second-order" neighbours.
4.3 Distance

As soon as we are interested in the relationship between a focal node and more distant ones, we are supposed to be interested in their distance \( d \) measuring the minimal number of links connecting them, i.e. the length of the shortest path between them ((106), for example, the distance between species \( J \) and \( A \) in Fig. 1 equals 3). A network can be characterized by the average distance between pairs of nodes, i.e. the distance between two random nodes (106; 20),

\[
d_{av} = \frac{2 \sum_{i,j} d_{ij}}{N(N-1)},
\]

where \( d_{ij} \) is an entry in the \( D \) distance matrix. Novel results indicate that the average distance between nodes can be very low in food webs ((171), but note that the reality of ecological conclusions drawn from this result depends strongly on the nature of interactions, especially their directedness). It has been suggested that food webs are networks with two degrees of separation (105).

A special version of distance, in case of directed graphs, is the distance of the focal node from source nodes (in food webs: producers). For food webs, several measures of trophic height or trophic level have been proposed (172). Conventionally, producers have trophic level zero, so the trophic level of a non-producers species equals one plus some measure of its distance from the producers. Even if only web topology can be considered, we can use the following distance measures: (1) the modal chain length (\( MCL = 2 \) for species \( C \) in Fig. 1), the mode of all possible different path lengths from the producers to the focal node, had been used conventionally for a long time (129); (2) the minimal path length or shortest chain (\( SC = 1 \) for species \( C \) in Fig. 1) equals the minimal number of links connecting the focal species to any of the sources; (3) the maximal path length or longest chain (\( LC = 2 \) for species \( C \) in Fig. 1) equals the longest directed path from sources to the focal species, i.e. the path containing the largest number of links; (4) the chain average (\( CA = 1.66 \) for species \( C \) in Fig. 1) is the mean of every possible different path lengths from the sources to the focal species; (5) the prey average (\( PA = 1.5 \) for species \( C \) in Fig. 1) is one plus the mean of \( CA \) values characterizing the direct prey species of the focal species; and it is possible to gain more elaborated measures as the average of either (6) \( SC \) and \( PA \) or (7) \( LC \) and \( PA \) (short-weighted, \( SW \), and long-weighted, \( LW \), respectively). If we have a weighted digraph, we might consider link strengths by calculating (8) the flow-based distance (\( FB \)), i.e. the weighted average of chain lengths from the sources to the focal species.
(cf. effective trophic level, (86; 23; 24). For the jth species:

\[ FB_j = \sum_{i=1}^{s} FB_i p_{ij}, \]

where \( FB_i \) is the similar value for its \( i = 1 \ldots S \) direct prey species and \( p_{ij} \) is the relative contribution of its \( i^{th} \) prey to its food. Thus, weights only on the direct trophic links leading to the focal species are considered. Note that trophic level equals always one plus any of these seven measures. It was shown that if chains are long, abundances vary more (137), there are more extinction events (137), it is easier to cause disturbances (65) and regeneration is slower (131). It can also be demonstrated that trophic height predicts well extinction risk in many cases (higher level species are more at risk, (34)) and habitat fragmentation also has selective effects on different trophic levels (79). These are not clear examples for the topological determination of behaviour but it can be concluded that certain biological features (habitat area, body size etc...) predict both trophic height and extinction risk, i.e. they correlate with the same ultimate factor. In marine conservation biology, an actual problem has been since the seventies the fishing down of marine food webs, i.e. the shortening of the average trophic chain length in marine food webs (122; 123). According to a classical model of community organization, trophic height determines the main mechanisms of population regulation: plants at the first trophic level and species at odd levels are primarily regulated by competition, while species at even trophic levels are mostly regulated by predation (cf. (114) and references therein). As higher predators have been the primary targets for fishing industry, food webs have been truncated seriously in many cases. It can be shown how considering the main pathways of energy can change our view on the actual trophic height of particular species (72). The dynamical effects of higher predators on lower species can give a key to the field assessment of predators’ trophic height. Another way to assess trophic height in the field is the measurement of isotope ratios in gut content analysis. The diversity of species at particular trophic levels may influence the dynamics of species in the whole community, e.g. the diversity of predators does influence the plant functional group through trophic cascades (44).

The majority of problems related to omnivory are of conceptual and methodological nature. Omnivory, at least in the food web literature, means feeding on different trophic levels. Of course, this definition was given for integer trophic height values kept in mind (i.e. discrete trophic levels). Despite serious critiques on the discreteness and the existence of trophic levels (136), it is possible to give a topological measure quantifying the omnivory of species \( j \) (\( OI_j \)) as the standard deviation of the weighted average of trophic levels of
the preys of species $j$ (86; 23):

$$OI_j = \sum_{i=1}^{S} (TL_i - TL)^2 DC_{ij},$$  \hspace{1cm} (9)$$

where species $j$ has $S$ preys, $TL_i$ is the trophic level of the $i$th prey, $TL$ is the average trophic level of the preys of species $j$ (i.e. $TL_j - 1$), and $DC_{ij}$ is the relative contribution of prey $i$ to the food of the focal $j$ species. For characterizing a whole web, it is possible to use the average of $OI$, simply the number of omnivores (nodes where $OI > 0$, (149), species $C$ and $A$ in Fig. 1), the proportion of omnivore species to $N$, or to give the proportion of omnivores feeding on non-adjacent trophic levels. Classical statistical analyses showed that the latter proportions are low, especially the latest one (126; 129).

What is of similar nature but can be even more interesting is the diversity of pathways connecting producers to focal species (91) or, more technically speaking, the structural reliability of network flows (67; 73). Reliability theory defines and studies the way to increase the probability of successful operation of complex systems and machines (10; 4). Network flow reliability ($R$) in model sink webs has been defined as the probability that the single top-predator will be unconnected to any of the sources after deleting other nodes (except the sink node) with a fixed, uniform $p$ probability:

$$R = 1 - \sum_{i=1}^{N-1} \binom{N-1}{i} p^i q^{(N-1-i)} F_i,$$  \hspace{1cm} (10)$$

where $i$ is the number of nodes deleted, $p$ is the fixed and uniform probability of deletion for all nodes (except the sink), $q$ is the probability for a node of being not deleted, and $F_i$ is the topology dependent proportion of the combinations of $i$ nodes disconnecting the sink from the sources if deleted (fatal ratio). Of course, incident edges are deleted together with deleted nodes. We note that if webs of equal complexity ($N$ and $L$) are compared (cf. (67) and see Fig. 2), the relationship between reliability and network design can be analyzed independently of the evident fact that increased complexity typically enhances reliability. These network properties are relevant if, for example, poisons are accumulated in a food chain and the final outcome is to be assessed.

If a directed graph is considered, the minimum spanning tree can be identified and analyzed (47). A minimum spanning tree is a $G'$ graph derived from a $G$ graph, where the $N'$ node set is the same as $N$ but the $E'$ edge set is a subset of $E$ such that the number of components is not reduced, there is no cycle in $G'$ and the cost of building the edges in $E'$ is minimal (for unweighted graphs, it is equivalent to the number of edges). Spanning tree is the loopless subset of the
Fig. 2. The 25 possible sink webs with five nodes and five links. Species 1 is always the single top-predator (i.e. sink webs). Link direction is not shown for simplicity: the higher always eats the lower (after (67)).

It can be shown that the topological properties of minimum spanning trees do not depend on their size, i.e. a scale-free relationship (with an exponent $1.13 < \eta < 1.16$) exists between $A_i$ and $C_i$, where $A_i$ is the number of species in the out-tree of species $i$ plus one, and $C_i$ is the sum of $A_k$ values for all predators of species $i$ (species $i$ included). According to the approach based on spanning tree analysis, weak links (redundant links not contained in the spanning tree) may contribute more to stability, while the strongest links (in the spanning tree) contribute more to efficiency.

4.4 Position

One of the key aims of conservation biology is to quantify the importance of species within ecosystems. It is extremely difficult to do with manipulative field or laboratory experiments, because of the range of relevant spatiotemporal scales. But, as a current research area of theoretical ecology, one aspect of importance, i.e. the positional importance within the community interac-
tion network, is suggested to be quantified in many ways. We overview these important positional indices and emphasize already here that ecologists do not want to find the one and the best index for ecological purposes. Instead, regarding the inherent diversity of their problems they (should) prefer a large set of network indices to choose the most adequate one from, for each problem they have.

Network analysis has traditionally been a key area of sociology. Sociometric indices for positional importance include centrality and prestige indices (betweenness centrality, closeness centrality and information centrality, see (167); we do not list "degree centrality" here, since this is nothing else than the comparison of degree values). These sociometric indices are not discussed here in detail because their application just started in ecology. In fact, the first attempt to characterize positional importance in ecological networks had been made by Frank Harary (55). Here, status, contrastatus and netstatus as sociometric indices (54) have been applied to analyzing a food web. The status of node \( x \) \((s(x))\) in a directed strong hierarchy is the number of its out-neighbours plus twice the number of their out-neighbours and so on. Turning the hierarchy upside down (reverting the direction of directed edges), the same calculation will give the contrastatus of nodes \((s')\), and

\[
\Delta s(x) = s(x) - s'(x)
\]

is called the net status of node \( x \). This kind of analysis has been once applied to quantify the "power" of animals (55). Later, this method was modified and improved from an ecological point of view, and the keystone index, as a measure of positional importance emphasizing mostly vertical food web effects (e.g. trophic cascades) has been introduced (68) and subsequently applied (69). The keystone index of species \( x \) is defined as

\[
K_x = \sum_{c=1}^{n} \frac{1}{d_c} (1 + K_{bc}) + \sum_{e=1}^{m} \frac{1}{f_e} (1 + K_{te}),
\]

where \( n \) is the number of predators eating species \( x \), \( d_c \) is the number of prey of its \( c^{th} \) predator, \( K_{bc} \) is the bottom-up keystone index of the \( c^{th} \) predator, and symmetrically: \( m \) is the number of prey eaten by species \( x \), \( f_e \) is the number of predators of its \( e^{th} \) prey, and \( K_{te} \) is the top-down keystone index of the \( e^{th} \) prey. Within this index, the first \((1/d_c (1 + K_{bc}))\) and second \((1/f_e (1 + K_{te}))\) sums quantify bottom-up \((K_{ba})\) and top-down \((K_{td})\) effects, respectively. Products containing \( K \) values \((K_{bc}/d_c + K_{te}/f_e)\) refer to indirect effects \((K_{indir})\), while products not containing \( K \) values \((1/d_c + 1/f_e)\) refer to direct ones \((K_{dir})\). Both \( K_{ba} + K_{td} \) and \( K_{indir} + K_{dir} \) equals \( K \). While the degree of a node \((D)\) characterizes only the number of its directly connected (neighbour) points, the keystone index gives information also on how these
neighbours are connected to their neighbours. Even if a predator has only a single prey ($D = 1$), its trophic field measured by the keystone index can still be strong (115). We note that there is considerable ecological reason for taking both bottom-up and top-down spreading effects into account simultaneously: however food flows only from the bottom up, per definitionem, trophic effects flow also in the opposite direction (think of secondary extinction caused by the primary extinction of the predator, cf. (60). Since this index is neither local nor global, but sensitive to both distance and the degree of intermediate nodes, it can quantify the dampening nature of ecological effects spreading through a network (on the contrary, effects spreading through the Internet do not change, i.e. your e-mail message is the same no matter whether checked in Alaska or Patagonia). It must be noted that there is a general debate whether direct or indirect interactions are stronger in ecosystems; the majority of ecologists agree that individual indirect interactions are weaker as their length increases. Whether or not the sum of many long and weak indirect interactions exceeds the sum of a few short and strong direct interactions is an interesting question (70). In fact, indirect chain effects, sensu Wootton (173; 174), can be considerably long (43) and strong (120). Since the magnitude of effects spreading through a particular chain of direct interactions decreases step by step, we can define a ”discrete field” of the effects spreading out from a given node and call it the trophic field of a species (69).

Ecologists showed early interest in the graph theoretical analysis of niche overlap, i.e. in what extent the needs of different species are in conflict. Sugihara (154) analyzed the structure of two kinds of graphs derived from food webs, the predator overlap graph and the resource graph (Fig. 3), constructed after the original food web graph data bases (25) containing feeding data. The $N$ node set of these graphs is the same as in the case of food webs, but the $L$ set of links differs. In predator overlap graphs (consumer overlap graphs, niche overlap graphs), nodes $i$ and $j$ are connected if they have at least one shared predator in the original food web, i.e. links mean shared predators. In resource graphs, two nodes are connected if they have a common prey in the original food web, i.e. links mean shared prey. Both kinds of derived graphs have a property which is statistically significant in real trophic data bases: predator overlap graphs only very rarely contain nonrigid circuits (they are triangulated or chordal graphs), i.e. it is rare that there is a shared predator for species $A$ and $B$, another for species $B$ and $C$, a third for species $C$ and $D$, and a fourth one eating species $A$ and $D$ but not $B$ or $C$ (a similar property is the intervality of a food web (25): when intervals representing the niche space can be arranged in one dimension and only those intervals overlap representing overlapping niche spaces). Resource graphs contain no holes, i.e. species consume either small and medium-sized prey, or medium-sized and large prey, but it is rare that a species eat both small and large prey but dislike the medium-sized one. As a conclusion, Sugihara suggests that the probability of a successful invasion depends on whether the new community configuration
Fig. 3. The predator overlap and prey overlap graphs of the hypothetical food web depicted in Fig. 1. Nodes and their identifying letters are the same as there but links correspond to different relations (after (154)). See details in text.

will fit to these rules. If not, the invader will be excluded from the community. Not only the patterns but also the invasion sequences are constrained by topology: certain configurations are possible but cannot be realized in certain pathways. If these rules, as well as others are satisfied, the invader has the chance to fit to the local community and survive (provided that it also fits the abiotic environment, e.g. temperature).

A positional index quantifying the strength of the trophic field around a species, but not biased for vertical interactions like the keystone index, is derived from a former analysis of the strength of apparent competition. Apparent competition means that if two host species (e.g. leaf-miners) share one or more parasitoid species (e.g. dipteran or hymenopteran species), an increase in one population results in a decrease in the other, through an increase in the shared parasitoid population(s). Godfray and colleagues assessed the strength of apparent competition, this horizontal trophic indirect effect based on the number of parasitoids parasiting particular hosts and the number of hosts parasited by particular parasitoids, i.e. based on the topology of a bipartite interaction graph (111; 49; 146; 87). Considering parasitation frequency data measured on the field they also took into account weights on links, thus, they analyzed
a weighted bipartite graph:

\[
    a_{ij} = \sum_{k=1}^{n} \frac{\alpha_{kj}}{\sum_{l=1}^{m} \alpha_{kl}} \sum_{k=1}^{n} \frac{\alpha_{ik}}{\sum_{k=1}^{n} \alpha_{ik}},
\]

where \( a_{ij} \) is the strength of the indirect effect (apparent competition) of host \( j \) on host \( i \), \( n \) and \( m \) are the number of parasitoid and host species, respectively, \( \alpha_{xy} \) is the parasitisation frequency between species \( x \) and \( y \), while \( k \) and \( l \) are appropriate parasitoids and hosts, respectively (146). This approach has been extended to longer pathways (up to ten steps length, in an additive and multiplicative way) and the strength of the trophic field of each species has been quantified \((TI\ index, (75; 76))\). In the first case (75), both interaction strength, interaction symmetry and positional importance have been calculated also for the weighted network.

An approach complementing topology by both the strength and sign of interactions has been suggested recently for quantifying the interactions between parasitoids and herbivores \((net\ interaction\ effect, NIE, (108))\). Weights are based, again, on parasitisation frequency data. This model is additive again but there is no need for multiplication: the weights of indirect effects are calculated from pairwise interaction strengths, while their sign is the product of pairwise signs, thus, this index combines direct weights with indirect signs.

Recently, inspired by the inconsistencies of existing measures of positional importance, novel indices have been suggested (14). Important positions can be identified if their deletion results in the fragmentation of the original network. Finding these positions is called the Key Player 1 problem \((KPP - 1)\). Two solutions have been suggested, the first is defined as:

\[
    F = 1 - \frac{\sum_{k} s_k (s_k - 1)}{N(N - 1)},
\]

where \( s_k \) is the size of the \( k^{th} \) component. It can be reasonable to take into account the distances between nodes being in the same fragment \((graph\ component)\). Since, by the nature of the problem, the graph is fragmented, it is wise to consider reciprocal distances \((otherwise,\ disconnected\ nodes\ are\ infinitely\ distant\ from\ each\ other,\ by\ definition;\ see\ (61))\). This distance-based fragmentation index is defined as:

\[
    F_D = 1 - \frac{2 \sum_{i \neq j} \frac{1}{d_{ij}}}{N(N - 1)},
\]

where \( d_{ij} \) is the number of links connecting nodes \( i \) and \( j \) along the shortest path \(\text{(i.e. minimal path length, shortest path)}\).
Another view on positional importance is not to quantify the role of node deletions in network fragmentation but to characterize their position in the intact network, quantifying how easily (shortly) other nodes are reachable from the focal one (the KPP-2 problem). A crude approach is to set an $m$ limit on the number of steps (maximal path length) and calculate the number of nodes within this range. A more elaborated method is sensitive to distance, it weights the reachability of node $i$ from node $j$ by their distance. The index is

$$R^D = \frac{\sum_j \frac{1}{d_{ij}}}{N},$$

where $d_{ij}$ is the distance of node $j$ from the node(s) of interest, i.e. the $S$ set of nodes. Here we note that in all the previous three cases, it is possible to characterize the positional importance of a set of nodes, and not only that of a single node. If there is an algorithm finding the set of $n$ nodes where any of the following indices is the largest, we may have the solution of the KPP-1 or KPP-2 problems and we can identify the $KP$-sets of $N$ nodes. The algorithms have been used for the analysis of different social networks including terrorist and acquaintance networks (14). These indices have been applied for the detailed study of a food web as well, where topological keystone species were identified by many approaches. It is an interesting problem whether the $KP$-set of $N$ nodes perfectly includes the $KP$-set of $N - k$ nodes ($k < N$), i.e., how nested are the $KP$-sets and how might it depend on topology. If graph properties correlating to nestedness will be described, it will be possible to give very interesting keys to multispecies management in conservation biology (Jordán, in preparation).

Another positional index, strongly based on distances considered both from the sources (producers) and from the sinks (top predators), has been introduced as the "centre of gravity" in food webs ($CG$, (46)). It measures the distribution of species along a bottom-top axis in the food web. The calculation needs only topological information:

$$CG = \frac{\sum_{i=1}^{N} \frac{\mu_i}{\mu_{max}}}{{Nmax}_i},$$

where $0 < CG < 1$ and $\mu_i$ is the maximum chain length linking species $i$ to the producers. The higher is $CG$ the higher is the density of species at high trophic levels. $CG$ is independent of the presence of omnivore links. The center of gravity measure has been used for characterizing food web complexity and it was shown that a higher ratio of species near the bottom of the web (low $CG$) reduces the frequency of chaotic population dynamics (46).

All in all, we have to emphasize that these positional indices give different
importance ranks for graph nodes: an interesting and important challenge for ecologists is to match the adequate techniques to particular problems.

4.5 Network flows

A characteristic area of interest in network ecology, which is very close to the origins and the common roots with economy, is the study of matter and energy fluxes in ecosystems. Input-output analysis and information theory had been the starting point for this kind of investigations (52). Material exchanges (mostly carbon (6) but also nitrogen (8) and phosphorous (166)) have been quantified by isotope techniques since the mid-seventies (in terms of mg of material per area unit per time unit, e.g. mgC/m²/season). However carbon transfer is only one of many aspects of the interaction between a prey and a predator, because of the richness of the data bases, it is very comfortable to consider the magnitude of these fluxes as interaction strength, but we have to note that probably it never will be easy to express different kinds of interspecific effects by the same dimension. Ecosystem level indices derived from material flux data include, for some examples, the Finn Cycling Index (FCI: the ratio of throughflows to cycled flows (45)), ascendency (A, (162)), flow diversity (165), overhead (163) or medium articulation (MA, (168), for more, see (7)). To present and interpret these flow-based indices in details would lead much beyond the scope of this review. We only note that these indices are suggested to characterize the maturity and health of ecosystems, but give no information about the roles individual species play in communities. An exception is the mixed trophic impact analysis (164), where the net sign of direct and indirect interspecific interactions between species i and j can be gained.

Other standard ways of how to weight network links is estimating interaction strength in the field by manipulative experiments (119) or descriptive field work (33), time series analysis (152; 160), assessing the parasitation frequency of host species (146), or simply estimating semiquantitative effects (138). Interaction strength values can serve as constructing interaction webs (graphs of the most important interactions and species only involved in them (116)), filling interaction matrices (replacing randomly generated coefficients), or studying loop weights: the geometric mean of interaction strength values assigned to interaction loops of various length (113). It was found that low weights in long loops stabilize food webs, sensu May (97). A seemingly general field result is that communities are dominated by weak interactions containing also a few strong ones (119). De Ruiter and colleagues have used feeding rate (interaction strength) data measured in the field for stability analyses and found that the natural patterning of interaction strengths is advantageous for achieving stability, compared to random models: repatterning interaction strength typ-
Table 1
Graph properties used in classical food web analyses. See definitions and discussion in text.

<table>
<thead>
<tr>
<th>graph property</th>
<th>abbreviation</th>
<th>ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>number of nodes</td>
<td>N</td>
<td>(25; 132)</td>
</tr>
<tr>
<td>basal:intermediate:top species ratios</td>
<td>B : I : T</td>
<td>(25)</td>
</tr>
<tr>
<td>prey to predator ratio</td>
<td>PY : PR</td>
<td>(25)</td>
</tr>
<tr>
<td>number of links</td>
<td>L</td>
<td>(25; 132)</td>
</tr>
<tr>
<td>link ratios</td>
<td>BI : II : IT : BT</td>
<td>(26)</td>
</tr>
<tr>
<td>connectance, directed connectance</td>
<td>C, C_d</td>
<td>(132; 93)</td>
</tr>
<tr>
<td>compartmentation</td>
<td>C_f</td>
<td>(128)</td>
</tr>
<tr>
<td>modal chain length</td>
<td>MCL</td>
<td>(126; 129)</td>
</tr>
<tr>
<td>longest chain</td>
<td>LC</td>
<td>(25)</td>
</tr>
<tr>
<td>chain average</td>
<td>CA</td>
<td>(25)</td>
</tr>
<tr>
<td>flow based chain length</td>
<td>FB</td>
<td>(86)</td>
</tr>
<tr>
<td>number of omnivores</td>
<td>N_omni</td>
<td>(126; 149)</td>
</tr>
<tr>
<td>proportion of omnivores,</td>
<td>N_omni/N</td>
<td>(126; 127; 129; 37)</td>
</tr>
<tr>
<td>omnivory of a species</td>
<td>OI</td>
<td>(86)</td>
</tr>
<tr>
<td>rigidity, triangulatedness</td>
<td>-</td>
<td>(154)</td>
</tr>
<tr>
<td>boxicity, holes</td>
<td>-</td>
<td>(25; 154)</td>
</tr>
<tr>
<td>intervality</td>
<td>-</td>
<td>(25)</td>
</tr>
</tbody>
</table>

...ratically leads to reduced stability (32). The most widely used graph properties in the classic food web analyses and suggested recently are presented in Table 1 and Table 2.

5 Topology and ecosystem behaviour at multiple temporal scales: population dynamics, community assembly, ecosystem evolution

This chapter aims to overview how ecosystem do processes at different time-scales depend on the topology and structure of the interaction network. We cover a wide range of time-scales from the phenomena of population dynamics through community assembly to the evolutionary ecological processes. We note that the following discussion will be very heterogeneous, since problems at different time-scales need quite different approaches and methods.
Table 2
Graph properties recently suggested in food web analyses. See definitions and discussion in text.

<table>
<thead>
<tr>
<th>graph property</th>
<th>abbreviation</th>
<th>ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>degree (in-, outdegree)</td>
<td>$D, D_{in}, D_{out}$</td>
<td>(150; 37; 71; 73; 142)</td>
</tr>
<tr>
<td>link orientation</td>
<td>$D'$</td>
<td>(71)</td>
</tr>
<tr>
<td>link distribution</td>
<td></td>
<td>(38; 37; 150)</td>
</tr>
<tr>
<td>clustering coefficient</td>
<td>$CC$</td>
<td>(106; 19)</td>
</tr>
<tr>
<td>structural and regular equivalence</td>
<td>SE, RE</td>
<td>(90)</td>
</tr>
<tr>
<td>cohesive subgroups</td>
<td>CS</td>
<td>(82)</td>
</tr>
<tr>
<td>distance, average distance</td>
<td>$d, d_{av}$</td>
<td>(106)</td>
</tr>
<tr>
<td>shortest chain length</td>
<td>$SC$</td>
<td>(? 79; 179)</td>
</tr>
<tr>
<td>prey average</td>
<td>$PA$</td>
<td>(172; 46)</td>
</tr>
<tr>
<td>short- and long-weighted</td>
<td>$SW, LW$</td>
<td>(172)</td>
</tr>
<tr>
<td>flow reliability</td>
<td>$R$</td>
<td>(67; 73)</td>
</tr>
<tr>
<td>minimal spanning outtree size, sum for predators</td>
<td>$A_i, C_i$</td>
<td>(47)</td>
</tr>
<tr>
<td>centrality (betweenness, closeness, information)</td>
<td>$BC, Cc, IC$</td>
<td>(167)</td>
</tr>
<tr>
<td>status, contrastatus, net status</td>
<td>$s, s', \Delta s$</td>
<td>(54; 55)</td>
</tr>
<tr>
<td>keystone index and its components</td>
<td>$K, K_{bu}, K_{id}, K_{dir}, K_{ind}$</td>
<td>(68; 71)</td>
</tr>
<tr>
<td>apparent competition overlap</td>
<td>$a$</td>
<td>(49)</td>
</tr>
<tr>
<td>topological importance</td>
<td>$TI$</td>
<td>(75)</td>
</tr>
<tr>
<td>net interaction effect</td>
<td>$NIE$</td>
<td>(108)</td>
</tr>
<tr>
<td>fragmentation-based key player, also distance weighted</td>
<td>$F, F^d$</td>
<td>(14)</td>
</tr>
<tr>
<td>reachability-based key player (distance weighted)</td>
<td>$R^d$</td>
<td>(14)</td>
</tr>
<tr>
<td>centre of gravity</td>
<td>$CG$</td>
<td>(46)</td>
</tr>
<tr>
<td>autocatalytic sets</td>
<td>$ACS$</td>
<td>(62; 63)</td>
</tr>
</tbody>
</table>

The characterization of topology and structure typically assumes intact networks with fixed topology. However, topology may abruptly change from one state to another, like in the case what is called prey switching in ecological literature (2). This means that, for some reason, a predator decides to eat...
something else. A nice example is the case of certain freshwater copepods (Acartia bifilosa and Eurytemora affinis (48)). These copepod species feed on phytoplankton. If the turbidity of the water is increased, the photosynthetic rate will be decreased and the primary production of phytoplankton will also decrease. Some copepods (like E. affinis) are capable in this case to switch from phytoplankton to zooplankton as the main prey. This is advantageous for two reasons. First, the amount of phytoplankton will not decrease so quickly, second, the amount of zooplankton consuming phytoplankton will decrease, thus, through an indirect mechanism (called trophic cascade) the amount of phytoplankton will not decrease so rapidly, again. Interestingly, other copepod species (like A. bifilosa) are incapable of this switching behaviour, and it can happen that finally the phytoplankton will be close to be locally extinct and both the copepod and the zooplankton will follow to do so as well. Prey switching is like the binarisation of interaction dynamics. In the following, we discuss the mathematical description of the dynamics of populations and model communities of only a few species.

A more specific question addressed here is: How the stability of the food webs depend on their topology (109)? To discuss this problem in detail we have to deal with the link between ecosystem stability and the hypotheses for community assembly. Then we can compare the topology of generated and experimental webs with their stability.

5.1 Stability and population/community dynamics

Food webs are complex dynamical systems, so their stability, independently of how it is defined, is determined by the characteristics of these systems. Let the node $i$ in a web represent a species with density $x_i$. Densities vary according to the trophic interactions among species (as well as non-trophic and abiotic effects). The dynamics of the system are generally described by ordinary differential or difference equation systems, nevertheless some authors use partial differential equations, cellular automaton or metapopulation dynamics to model the spatial processes. The generally used model system is

$$\dot{x}_i = x_i f_i(x_1, x_2, ... x_n), \quad x_i(0) > 0, \quad i = 1, 2, ... n,$$  \hspace{1cm} (18)$$

where $f_i(x_1, x_2, ... x_n)$ describes the direct effects of other species on the unit density of species $i$. (Naturally, if species $i$ is not in a direct trophical connection with species $k$ then $f_i(.)$ does not depend on $x_k$.) This dynamical description suggests to define stability as local or global asymptotic stability of the fixed points of eq. 18. However, from an ecological point of view, it is more adequate to consider the system to be stable if it remains persistent. Others suggested to use temporal variability of population densities as an in-
dex of stability. More variable persistent ecosystems are considered to be less stable. The practically most important measure of stability is probably the species deletion stability. Here a web is more stable if fewer other species will go extinct after a random or preferential species deletion (127). Reliability (discussed above) is similar to the species deletion stability, but here the system is considered to remain stable after a species deletion if the top predator (sink) species is connected to at least one resource species (67).

These most frequently used stability criteria with their definitions, advantages, disadvantages and corresponding references are listed in Table 3.

5.2 Models of food web organization

Since it is not easy to understand the functioning of the entire ecological community, it is essential to construct theoretical community assembly models and to compare these models with available data. There are roughly two types of web generating models: webs are constructed by simple stochastic rules in the first group (constructed models), while in the second group, the dynamical interactions among species also have a crucial role in the creation of the web (dynamical models).

The simplest constructed model is the random model, where every two species of the web are in predator-prey connection with a constant probability \( C \), where \( C \) is the expected value of connectance in the web. The direction of links is selected randomly too, so every species can be a prey or a predator with the same probability (97). The advantage of this model on the one hand is its simplicity, and the numerous exact mathematical results corresponding to its topology (13), and, on the other hand, it can be a good starting point for the dynamical models too. However, the traditionally accepted but recently hotly debated presence of trophic levels in real food webs is neglected in the random model. The multитrophic assembly model defines trophic levels (basal, intermediate, top) with their species and interactions assigned randomly between any two trophic levels (89; 108). The trophic level structure is taken into account in the cascade model too (27), where every species \( i = 1, 2, \ldots n \) is assigned by a random \( \nu_i \) number distributed evenly within the unit interval. Species are ordered according to \( \nu_i \). If \( \nu_j < \nu_i \) then species \( i \) has a probability of zero to eat species \( j \), while species \( j \) has a probability of \( C/n \) (\( 0 < C < n \)) of eating species \( i \). This model explains some important properties of natural webs, such as the number of species within a trophic level (28). The problem with the cascade model is its hierarchical rigidity. This is the reason why feeding loops (\( a \) eats \( b \), which eats \( c \), which eats \( a \) again) and cannibalism, which are present in real webs are missing in the cascade model. The niche model is really a stochastic generalization of the cascade model. Here, species \( i \) with
<table>
<thead>
<tr>
<th>Stability</th>
<th>Definition</th>
<th>Advantages</th>
<th>Disadvantages</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Local asymptotic stability (l.a.s)</td>
<td>The l.a.s of the fixed points of dynamical system assigned to the web</td>
<td>It can be computed frequently even for larger systems, there are exact mathematical results</td>
<td>Biological relevance seems to be weak since neither dynamical stability nor small perturbation are frequent</td>
<td>(97)</td>
</tr>
<tr>
<td>Resilience</td>
<td>The speed of relaxation towards the fixed point after a local perturbation</td>
<td>It can compare different l.a.s. fixed points, and systems</td>
<td>The same as l.a.s.</td>
<td>(129)</td>
</tr>
<tr>
<td>Global asymptotic stability (g.a.s)</td>
<td>The g.a.s of the fixed points of the dynamical system assigned to the web</td>
<td>It measures fixed point’s stability against large perturbations</td>
<td>Difficult to treat mathematically (to find a Ljapunov function) and numerically</td>
<td>(129; 22)</td>
</tr>
<tr>
<td>Persistence</td>
<td>Starting from positive densities there is no trajectory which leads to one or more species becoming extinct</td>
<td>Biologically more relevant than l.a.s. or g.a.s.</td>
<td>Mathematically less tractable than l.a.s.</td>
<td>(129)</td>
</tr>
<tr>
<td>Variability</td>
<td>The average variance of species densities after a long time (species level) or the variance of average densities (community level)</td>
<td>It can be measured in field experiments</td>
<td>It is hard to use in mathematical model systems</td>
<td>(130; 133)</td>
</tr>
<tr>
<td>Species deletion stability</td>
<td>How the stability of the web changes if a species deleted from the web randomly (or preferentially)</td>
<td>It has a high biological importance and can be tested experimentally</td>
<td>Sometimes it is estimated from the topology of the web, dynamics is neglected or not known</td>
<td>(127; 15)</td>
</tr>
<tr>
<td>Reliability</td>
<td>The probability that a top predator remains in connection at least with one primary resource after a random species deletion</td>
<td>It is easy to compute even in large webs, it use that energy flows in a directed way</td>
<td>Dynamical aspects of the web are neglected, problematic to use in non-sink webs</td>
<td>(67; 73)</td>
</tr>
</tbody>
</table>
"niche value" $\nu_i$ consumes all species falling in an interval $\delta_i$. The center of $\delta_i$ is selected randomly from the $[\delta_i/2, \nu_i]$, and $\delta_i$ is chosen from the interval $[0, 1]$ using a beta function with expected value $2C$ (170). Niche model allows species to feed on species with higher niche values, thus loops and cannibalistic predation are both possible. After constructing these models, the general task is to compare topological characteristics of the models with the topology of real webs. According some recent works, niche models seem to be the best construction (170; 38).

It is generally assumed that we observe only the dynamically stable food webs among the numerous possible ones. (As we can see below there are numerous alternative definitions for stability in this field.) Consequently, a specific dynamical system (with its parameters) have to be defined and only the stable ones have to be considered as successfully generated webs. It is a classical assumption that stability means local asymptotic stability (l.a.s.) of the system (18) in the fixed point $x^*$, so (18) can be approximated by its linear Taylor expansion around $x^*$

$$
\dot{x}_i = x_i \left( r_i + \sum_{j=1}^{n} a_{ij} x_j \right), \quad x_i(0) > 0, \ i = 1, 2, \ldots n.
$$

This is the well-known Lotka-Volterra (LV) model with $r_i$, the intrinsic rate of increase ($r_i > 0$) or decrease ($r_i < 0$) of species in the absence of other species, $a_{ij}$ is the interspecific interaction coefficient. In food webs if $a_{ij} > 0$ then $a_{ji} < 0$. The LV-models are relatively simple and their parameters can be estimated from the field data, however neither the effect of active predator’s searching and switching nor the saturation effect of high amount of resources are taken into account in this model. More elaborated dynamical models assume that $a_{ij}$ depends on the density of all species in the following way

$$
a_{ij}(x) = \frac{a_{ij} \omega_{ij} x_j^\beta}{\gamma_j + \sum_{k \in L_i} \omega_{ik} x_k^\beta + 1},
$$

where $1 > \omega_{ij} > 0$ if species $i$ is the predator of species $j$ and $-1 < \omega_{ij} < 0$ in the reversed case indicates the preference of species $i$ consuming on species $j$. Thus $\sum_{k \in L_i} \omega_{ik} x_k^{\beta+1} = 1$, where $L_i$ denotes the indices of all alternative preys of predator $i$. $\gamma_j$ is the half saturation density of prey $j$ and $\beta$ is either 0 (Holling-II type functional response) or $\beta = 1$ defining Holling-III type of model. Since these models remain valid in cases when the system is far from the fixed points they applications are connected with a less strict definition of stability, such as persistence or variability. While the above defined Holling-type models are relatively good descriptions of trophic interactions, mainly in
aquatic ecosystems, they ignore the limited dispersal of individuals, the environmental heterogeneity, the presence of refugees, the evolutionary processes and the presence of non-trophic (mutualism, interference competition) interactions for example. In contrast with physics, there is no "good" dynamical model in food web ecology, but there are alternative models trying to catch some important aspects of these complex systems.

Dynamical models mostly assume either a random food web as an initial state (95) or consider small webs with specific topology, and study the stability of dynamical systems on the selected topological skeleton (129; 130; 71; 73). Some works investigate dynamical stability of webs generated by the cascade (21; 22; 80; 81) or niche model (16). Others build complex food webs by a web-evolution or web-succession process, where new species can connect according to specific rules to the previously existing stable web. The modified dynamical relations can change the structure and the species pool of the new web, which is a new starting point of a recurrent evolutionary or successional step (35; 155; 89; 18; 107). In the web-evolution models, the invading species are mutated from a resident species, consequently the invader’s ecological behaviour is similar to their "mother species", while species are selected from a species pool randomly in the web-succession models.

A classical, but living problem in ecology is how does web complexity correlate with its stability (for simplicity, let complexity mean the number of nodes and links in the graph - of course, other parameters could also be considered, like the homogeneity of network structure). Based on field observations and behaviour of simple mathematical models the traditional opinion was, in the sixties, that complexity begets stability (41; 91). Some years later, Robert May’s mathematical analyses changed the view just into the reverse: complexity decreases stability (95; 97). May considered a random network of \( n \) species with connectance \( C \). He assumed that the community is in a fixed point \( x^* \), so their l.a.s. can be computed by \( \xi(t) = A\xi(t) \). Here \( \xi(t) \) is the perturbation of \( x_i^* \), and \( A \) is the so called community matrix. Using notations of eq. 18, the elements of \( A \) are

\[
a_{ij} = \frac{\partial [x_i^* f(x_1^*, x_2^*, \ldots x_n^*)]}{\partial x_j}.
\]

For the mathematical tractability, May assumed that \( a_{ii} = -1 \) for every species and for \( i \neq j \), \( a_{ij} \) is chosen randomly with mean zero and variance \( s^2 \) with probability \( C \) otherwise \( a_{ij} = 0 \). (Thus we define a web with the mean connectance of \( C \).) It can be shown analytically that if \( n \gg 1 \) then the eigenvalues are in a circle defined over the complex plane with the center at \( a_{ii} = -1 \) and radius \( s\sqrt{nC} \). Consequently, the fixed point is almost certainly stable if \( s\sqrt{nC} < 1 \) and becomes unstable if \( s\sqrt{nC} > 1 \). If web complexity is measured by \( nC \), then increased complexity and increased average interaction
strength (s) increase the real value of the maximal eigenvalue, consequently decrease stability. This result suggests that connectance would be smaller in larger webs assuming that average interaction strengths remain constant. This relation is roughly true for plant-parasitoid communities (143; 26), nevertheless in other food-webs rather the constant connectance is the valid rule (94). Since May’s results are in contradiction with the traditional view, it initialized a vivid debate and gave a new push to the mathematical study of complex ecological webs. Despite the numerous strict and biologically unrealistic assumptions used by May (84), his analyses were recapitulated in biologically more adequate models only decades later (57; 58; 64). One of the most crucial assumption in May’s model is that $a_{ii}$ is constant. Using the Gershgorin theorems (169) Haydon has shown that if the $a_{ii} \leq 0$ self-regulating coefficients are different in the matrix $A$ then the stable webs become more stable if the interaction strength or/and connectance increases. Stable webs will be less stable if there are more species in the web as in May’s model, but this trend is less pronounced than in the original model (57). Depending on the parameters, these two opposite trends may lead to either increasing or decreasing of the stability with complexity. Haydon studied the following related problem recently (58): if a random $A$ matrix is given, what kind of $a_{ij}$ structure can be chosen for having the most stable system. The assumption behind his question is that real ecosystems are the products of evolutionary refinement selecting only the stable systems are present in the Nature. He concluded that in webs where $a_{ii}$ differs to each others, (compare it with May’s assumption) higher probability of connectance($C$) and greater average interaction strength ($s$) are beneficial for the selection of more stable systems (that is, its eigenvalue with the maximal real part is the lowest). The connectance between weakly ($a_{ll} \approx 0$) and strongly ($a_{kk} \ll 0$) self regulating elements is of essential importance. Assuming that there is no perfect balance between the negative and positive interaction coefficients ($\langle a_{ij} \rangle \neq 0$) the probability of stability is in a U-shaped relation with complexity, so depending on the statistical properties of the interaction matrix stability can increase or decrease with complexity (64; 78).

Naturally, assuming random topology as done before is at least as strict as the balance in interaction coefficients. Chen and Cohen (21; 22) studied the l.a.s., g.a.s. and persistence of food webs generated by the cascade model. They used an LV model for the dynamics where interaction coefficients were selected randomly either in a balanced or in a non-balanced manner. After detailed numerical simulations, they concluded that increased complexity (by increasing the number of species or connectance) leads to decreased probability of stability, independently of which definition for stability is used. A further improvement could be attained if not only the topology but the dynamical equations are fitted to the biological reality better. Kondoh (80) applied the random and cascade models and the LV dynamical system to investigate the complexity stability relations. However, he assumed that fractions of predators
Fig. 4. A food web with three trophic levels with species belonging to the same functional group. Two species belong to the same functional group (denoted by the same color) if they consume the same preys and are eaten by the same predators can change their foraging efforts to maximize the net energy intake. It means that these predators can fine-tune their prey preferences to the optimal one. He pointed out that persistence stability decreases with complexity if there is no adaptation in foraging efficiency, whereas stability increases with connectance if the food web is large enough. Brose et al. (16) criticized these results arguing that every species was a ”primary producer” in Kondoh’s model and they suggest a Holling-II type model for the community dynamics. They found that stability decreases with complexity in the niche model and can increase in the cascade model even if connectance is high and almost all predators can change their resource preferences. However, the second part of this statement depends on the parameters they used and how the ratio of primary producers change with increased webs (80). To summarize, the theoretical results connected with the stability/complexity debate seem to be simply inconsistent with each other at the first glance. However, building more and more reality into the models, the ”complexity increases stability” rule becomes more and more pronounced.

The vertical structure and the functional diversity within each trophic level are
general properties of food webs (Fig. 4.) Thus, it is natural to ask how perturbations in a trophic level or how functional diversity correlates with stability. Pimm (127) designed small webs with three trophic levels (plants, herbivores, carnivores) containing up to four species on each. He was interested in the species deletion stability, studying the l.a.s. of the LV system after deleting one species from an originally stable web. He found that species deletion stability increases if a plant or a herbivore species were removed while the tendency is reversed after deleting a carnivore species (127). In a similar model, Borrvall et al. (15) focused on the functional diversity and species deletion stability. They used the LV model too, but interaction strengths (a_{ij}, i \neq j) were either evenly distributed or skewed in their simulations. Skewed distribution, that is predators consume only one prey intensively and some other marginally are observed in experiments (119; 174; 147) and in theoretical models (80) as well. They found that (1) increasing the number of species within a functional group increases the species deletion stability, and (2) rectangular webs (equal number of species in different trophic levels) are less stable than triangular webs (decreasing number of species with increasing trophic level). This result is a complement of that increased species diversity within the function groups enhances the functional predictability observed in aquatic microcosm experiments (103; 112) and in terrestrial communities (157; 158). Interestingly, in contrast with other theoretical results (78; 80), if interaction strengths were skewed (or unbalanced) then the webs were less stable than at the evenly distributed cases. Further, Borrvall et al. (15) found that omnivorous interactions stabilize the system.

Besides complexity, the level of omnivory is another topological index which is traditionally studied in the context of web stability. The proportion of omnivores varies in a wide range in webs from zero up to 80% (126; 170). On the other hand, Pimm and Lawton’s first theoretical study suggested that the number of omnivores would be small in the most realistic food webs (126). They considered a linear web with four trophic levels where the number of omnivores and the trophic levels where omnivores act can be changed (Fig. 5)

The dynamics were determined by the LV model. The interaction coefficients were chosen randomly, but they used different types of asymmetries in interaction coefficients to model vertebrate, vertebrate-insect, and parasitoid food webs (126). They studied the percentage of l.a.s. webs and the resilience of the persistent ones as well. Their most important conclusions are that as the level of omnivory increases the percentage of l.a.s. system decreases, but for the stable webs resilience increases. Since there are practically no l.a.s. webs for more than one omnivores in the vertebrate and vertebrate-insect models, they concluded that omnivory makes the system unstable. Since the result of Borrvall et al. is just the opposite, it is probable that the conclusions connected with the omnivory-stability relations are not robust against the stability criteria, the dynamical equations, and the topology of webs used in the model.
McCann and Hastings (100) used the simplest topological construction where omnivory can be studied (Fig. 6), but the dynamical system they applied was more elaborated. They used the Holling-II type functional response for the consumer and the top predator, and the logistic equation for the resource. The strength of omnivory can be changed according to the prey preference ($0 \leq \omega \leq 1$) of the top predator. At different biologically plausible parameters, the system without omnivory ($\omega = 0$) can be transiently chaotic, chaotic, can move along a limit cycle or tend to a fixed point. Increasing $\omega$ increases the minimal value of top predator up to a critical level of $\omega$ in every case, increases the minimum of primary resource except in the case of fixed point attractor and practically does not change the minimum of the consumer density. The chaotic dynamics become a limit cycle and a fixed point as $\omega$ increases. So, omnivory with a weak or moderate strength decreases the chance of extinction by random fluctuations by increasing the minimal densities and increases the dynamical stability as well. It is shown in similar but more general systems that not only the omnivorous but all types of weak interactions stabilize the webs dynamically (101). Since field experiments demonstrate that interaction strength is skewed strongly towards the weak (119; 32; 174), this work supports
the importance of weak interactions in stabilizing food webs (101; 102).

The possible stabilizing role of weak interactions encouraged Emmerson and Yearsley (42) to repeat Pimm and Lawton’s classical study but they concentrate on interaction strengths. They investigated the l.a.s., resilience and permanence of LV systems of simple food webs containing omnivores (see Fig. 5). In their model, interactions were skewed towards weak ones. They found (similarly to Pimm and Lawton’s results) that omnivory destabilizes the webs, although omnivory tends to be weak in the stable omnivorous webs. By removing the omnivorous species, stability decreases in these webs, indicating that weak omnivory stabilizes the web.

The chance of chaos in food webs and other ecological systems has been an open question for decades (98; 12; 148). While simple models producing chaos have increased annually, data analysis suggests that rather the periodic patterns are common and chaos is rare in natural populations (12; 39). Recently, Fussmann and Heber (46) studied the probability of chaos in permanent food webs.
Fig. 7. The general architecture of webs used by (46). With the deletion of interactions 28 topologically different connected webs can be generated.

They considered 28 different simple webs with different levels of complexity, omnivory, center of gravity ($CG$) and average trophic length ($CA$) indices (Fig. 7). The dynamical equations were similar to those used by McCann et al. (100; 101). Their general conclusion was that the frequency of chaotic dynamics among the persistent webs is decreased as omnivory or complexity increased. However, the frequency of chaotic behaviour increased with the $CA$ and $CG$. On one side their work confirms McCann’s results, and on the other side, it suggests that topological properties of natural food webs can decrease the probability of chaotic dynamics. We note here that low $CG$ indicates a web with more species in the lower trophic levels, that is these webs are dynamically more stable in concert with Borrall et al.’s conclusions about the increased deletion stability of rectangular webs, despite that the two works
Fig. 8. The 125 nodes of the 25 graphs in Fig. 2. For a given set of nodes with the same local configuration (degree, \(D\), and link orientation, \(D'\)), we give the number of nodes out of 125 belonging to the group \((n)\) and the average number of extinctions out of 2000 simulations \((E)\). A not surprising rule is that without predators \((D_{out} = 0)\) the more prey you have the less risky is your survival. A surprising result is that with the same number of prey species \((D_{in} = 1, 2\) or \(3)\) it does not matter whether you have zero or one predator species (after (71)).

used absolutely different stability criteria.

Since numerous stability criteria have been used in this field, we could select them easier if they were in a clear relation to each other. To address this question directly, Jordán et al. (73) studied how network reliability is related to the persistence of webs. They investigated all the 25 food webs possibly designed from five nodes and five links, with a single top-predator (Fig. 2). According to the reliability stability criterion, the webs were classified into four groups (67). Jordán et al. used the LV and the Holling II dynamical models with balanced \((\langle a_{ij} \rangle \approx 0)\) or non-balanced \((\langle a_{ij} \rangle < 0)\) interaction coefficients. Selecting interaction coefficients from the intervals defined in advance, they studied the probability that a web remains persistent after a small perturbation in the interaction strengths. Their numerical simulations pointed out that reliability and persistence are in positive correlation if the Holling-II functional response was used. The correlation is strong if the asymmetrical model was applied. The LV model is in weak negative or no correlation with flow reliability. Since the Holling-II model is a better (but practically less applicable) description of food web dynamics and interactions are frequently non-balanced, this work suggests that flow-reliability, as a simple topological index of the web can be a good predictor of dynamical stability as well.
The presented works concentrate mainly on how some global topological characteristics of the webs correlate with the stability of the web. Now we turn to the question of how do local or mesoscale topological indices inform on the stability of species within a web. Jordan et al. (71) studied the 25 sink webs with five species that were introduced before. Since $C$ always equals 0.5 and each web contains only a single top predator (see Fig. 2), these models are ideal for studying the effects of local (also mesoscale) topology on food web dynamics independently of the effects of changing complexity (usually defined as the number of nodes and links, see (67; 71)). Those authors measured the degree of graph nodes ($D$), the orientation of neighbours ($D' = D_{in} - D_{out}$) and the standard deviation of $D$ within the web ($stdD$). The ”topological importance” of species $i$ was measured by the keystone index ($K$). They used the LV dynamics with interaction parameters chosen evenly from the (0, 1) and (-1, 0) intervals, respectively. For each web, 2000 parameter sets were selected randomly, and the frequency of non-permanent webs were studied numerically. The firstly extinct species was detected in every non-persistent case. The main result is that extinction probability is the greatest for species with $D' = 0$, while generalist consumers ($D' > 1$) and multiple exploited primary producers ($D' = -2$) go extinct with a lower chance. While $K$ alone does not correlate with extinction risk, $D$ and $K$ together correlate with the stability of a species: if $D = 1$, the high $K$ index is dangerous, while at higher $D$, increasing $K$ either does not increase ($D = 3$) or decreases the probability of extinction ($D = 2, 4$). This study emphasized that dynamically driven species extinctions are far from the random pattern, and can be characterized by the local and mesoscale topological indices. The average extinction values (out of 2000 simulations) for the sets of nodes with equal local configuration (similar $D$ and $D'$) are shown in Fig. 8.

5.3 Time series analysis and structure

In addition to the direct estimates of trophic interactions, the time series of population densities can help to reveal the trophic structure of the community. Since the measurement of population densities is relatively easy and cheap (but time consuming), it is important to mention some keystone works using time series analysis in collecting information about trophic structure.

It is a common consequence of the non-linear intra- and inter-specific interactions that populations frequently vary in a cyclical manner. It follows from the qualitative analysis of predator-prey models that predators cycles contain fast exponentially increasing (following the prey growing) and decreasing (because of out-depleting prey resource) phases. On the contrary, preys’ growth is prevented generally by some intraspecific self-limitation mechanism, so their cycles are blunt with saturating growing and exponential decaying periods
Based on these theoretical results, Turchin et al. (160) have analyzed the time series of Norwegian lemmings and voles. They found that the shape of lemmings cycles suggests that lemmings behave as predators, while more blunt cycles of voles indicate that this species is rather a prey. Consequently, despite that these rodents are both members of a complex food web, we can conclude that lemmings are controlled from the bottom up, and voles from the top down. Another possibility is to estimate the dimensionality of the dynamical system from the data series. The Canadian lynx and the snowshoe hare are characteristic species in boreal forests, being in predator-prey interaction. There are long time series data available for both species, indicating strong correlating periodic density cycles. Though the biodiversity of this boreal forest is low, it contains three trophic levels with 30 trophic and real species including the snowshoe hare and lynx. However, the strong correlation between the time series of these species suggest that there are only limited key interactions determine their dynamics. To estimate dimensionality of the dynamics responsible for the data series, Stenseth et al. (152) estimated the embedding dimensions for the hare and the lynx. They found that the dimension of hare series is close to three, while lynx series is roughly two. Knowing the food web structure, they suggest that (beside the intraspecific competition) the hare population density is determined by the vegetation supply and the predator density (including the lynx), while the lynx density is mainly determined only by hare density. So, despite the complexity of the boreal food web, the dynamics of hare and lynx are driven by a simple, low dimensional subsystem.

The embedding dimension cannot be estimated if the time series is short, which is typical in most ecological cases. However, there is an alternative method to get information about the web structure from this time series. On the basis of dynamical models of consumer-resource species, Murdoch et al. (110) studied the characteristic cycle lengths of these systems. They concluded that if resource recruitment is approximately constant, the consumer species’ cycles rarely exceed $4T_C$. However, if the consumer and the resource are coupled strongly by a specialized consumer, the period length is generally greater than $4T_C + 2T_R$, where $T_C$ and $T_R$ denote the consumer and resource maturation time respectively. They analyzed more than hundred populations’ time series, and pointed out that generalist species behave as ”single-species” with periods lower than $4T_C$ and specialists vary according to a consumer-resource cycle ($\geq 4T_C + 2T_R$). This work emphasizes that generalist consumers (or predators) can be considered as intact species in the web controlled only by the average of resources or consumers (but see (144)).

Difference and differential equations describe population dynamical changes at a characteristic ecological scale, but for long-term changes quite different methods are needed again. Following invasion processes, succession or evolution, these equations may not help or give the full answer, and methods
of network analysis may help in understanding community organization. Beyond the time-scales of population dynamics, invasion and recolonization, the events of community organization (or community assembly or succession) take place. These phenomena are partly based on the mechanisms at shorter time-scales. It is more and more difficult to find nice relationships between food web structure and community dynamics, and as time scales are longer the rules are weaker. As a result, ecologists have less reliable results, more theories and more debates. As we broaden our time-scales from hours (48) to seasons (6), years and decades (141) or evolutionary times (156), we can be less accurate in connecting network topology to population or community dynamics. This means that quite different approaches are needed at various scales: statistical analysis for population census time series, differential equations describing population dynamics, or assembly algorithms explaining experimental findings on community organization. However, the importance of the network perspective is evident. The interaction network always sets internal constraints on the possibilities of future interaction dynamics. For example, it is well known that pollinatory interactions almost always originate from herbivory (156), higher-order effects frequently turn to mutualistic relationships and the evolutionary conservativity of interaction types are the following in decreasing order: parasitism, mutualism, competition and predation (156). Interaction networks may also be shaped by abiotic factors, for example, the seasonal migration of birds change fundamentally the tropical rain forest food webs (141).

6 Conclusions

Our paper reviewed some key problems of food web ecology, the methods of the topological analysis of trophic networks and the ways their dynamics and long-term behaviour are linked to their topology and structure. Shortly: how is the fate of populations and whole communities linked to the network of interspecific interactions? Ecologists have been aware of the importance of the network context in understanding populations’ behaviour since at least 1927 (40), therefore it is always useful to stop and overview the new methods, concepts and conclusions of the research on linking structure to dynamics.

Since the problem is very complex, we needed to set several assumptions. We have primarily focused on food webs but many of the presented techniques can also be applied to interaction networks defined in a broader sense. Graph nodes have been mostly regarded as representing species, however, in many cases it is wiser to make groups of species (e.g. functional groups) correspond to the nodes. Finally, as another simplification, we stressed that population and community dynamics depend exclusively on the internal properties of ecological systems. This is not true, of course, since abiotic effects (climate, fires) also influence living organisms. Simply, we presented what can we say
if only internal, biotic interactions are considered, especially the constraints resulting from the topology of interaction networks. Topology is something like the ultimate factor of effects, however if multiple mechanisms influence systems dynamics, it is not easy to recognize the topological background.

The complexity of the problem, i.e. how do ecosystems behave, needs to represent them by simple network models. Network structure can then be quantified and interesting correlations between topological characteristics and network dynamics are what one looks for. This is the typical way of studying more or less complex networks in many fields of science, for example, in sociology (167) or landscape ecology (161). The structure of a food web and the positionality of particular species in the network also influence their dynamical responses to landscape ecological processes. Landscape structure and landscape level processes (e.g. subsidization, migration, recolonization) have major impact on population dynamics but field evidence suggests that the selectivity of these effects is very high. Species in different food web positions give different answers to habitat fragmentation, for example. Species at higher trophic levels (179; 31) or with narrower trophic specialization ($D_{in}$, (142)) are more probable to go locally extinct. Food web topology generally also changes as many interactions are disrupted by fragmentation (83; 151). Considering a number of recent field results, we can conclude that there is an urgent need for putting food webs, i.e. trophic networks, into a landscape, i.e. habitat network context. The first steps of ”metacommunity ecology” are already being outlined (36): metapopulation ecology (140; 53) and standard community ecology are married both in models and experiments (36). For conservation biological purposes it is of primary importance to have quantitative methods for the identification of key species and key habitat patches: the old debate whether to protect rare species or unique habitats will be replaced by topological methods helping the identification of important network elements both in food webs and landscape graphs (74).

The recent interest in networks, supported by technics having been intensively developed in the meantime, gives new keys to better understanding the importance of the network perspective (9; 153). The network perspective seem to be interesting and probably well applicable in ecology, and especially in conservation biology: designing reserve networks (17), or for example, considering indirect effects in fisheries research (99; 178) are among the recent top issues. What conservation biology still needs is a more rigorous and more quantitative network perspective. We emphasize again that the aim of biologists is not to find the ”best” (e.g. the easiest to prove, the fastest to calculate or the most efficient to use) topological characteristics describing food webs. Instead, they are looking for a variety of network indices characterizing many aspects of trophic networks and providing a palette to find the most adequate technique in case of a particular problem. Ecological problems are inherently diverse, thus, the actual network index giving a key to the answer varies. For most of
the theoretical ecologists, this very selection is the most interesting part of the process. And here, the logic of physicists can help to bridge the gap between biological problems and mathematical methods.

Acknowledgments

The authors were supported by a grant of the Hungarian Scientific Research Fund (OTKA T 37726). FJ was also supported by a Branco Weiss Fellowship of Society-in-Science, Zürich, and enjoyed the hospitality of Collegium Budapest. We are grateful for the invitation to write this review to PoLR.

References


[33] de Ruiter PC, Griffiths B, Moore JC. Biodiversity and stability in soil


[53] Hanski I. Habitat connectivity, habitat continuity, and metapopulations


