# COMPARABILITY: THE KEY TO THE APPLICABILITY OF FOOD WEB RESEARCH

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**Abstract.** However food webs have always been considered as a central issue of ecology, their value and usefulness are frequently questioned. In this paper, I overview some causes of this skepticism and discuss in which cases two or more food webs can be compared. I suggest that the comparability of different food webs is a key to possible applications. I show how are two important topics of recent community ecology (keystone species and food web aggregation) related to the comparability problem. Finally, I overview some recent applications of food web research, where comparability can help understanding.

**Keywords:** *food web, indirect interaction, aggregation, keystone species, comparability*

## Introduction

In order to understand how an ecological system operates, it is something very fundamental and important what animals feed on. As information on what animals of a certain community feed on has been collected, a matrix or a food web graph can give these trophic relationships. Then, food web graphs are used either only for illustration or as substrates for analyses. Since the acknowledged value of food webs and the appreciation of food web research vary widely between strong enthusiasm and deep skepticism, it is always interesting to review the status of food web studies, in the light of actual problems and results. In this paper, I intend to do this, with emphasis on comparability, and its relationship to the future applicability of food web research.

## Food webs, in general

Food web graphs (and the corresponding matrices) represent the trophic relationships between species in a community. In the graph, nodes (points) refer to species (or trophic components) and edges (links) refer to a feeding interaction between them. Trophic interactions are generally asymmetrical, i.e. it is rare that both A eats B and B eats A (but see [7]). Thus, food webs are directed graphs, however, convention permits to sketch undirected graphs, too – in these cases, higher species eat the lower ones (I will frequently use the term „species” instead of „trophic group”, „trophic component”, „trophospecies”, etc; terms to be discussed later). Exceptions are noted (e.g. [94]).

Three basic types of food webs were defined by Cohen in his seminal book [12]. Community webs are more or less complete descriptions of trophic relationships of whole communities. A sink web is a subnetwork of a community web showing only a chosen species and all of the pathways (containing nodes and links), which may transport materials from producers to the chosen species (e.g. [65]). A source web depicts which species feed directly or indirectly on a selected species: it contains all

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nodes and links constituting pathways of energy originating from the source species (e.g. [89]).

Another important property of a food web is whether it is a binary web giving information simply about the existence of a link between two selected species (a link exists between them or does not; in the matrix, „1” stands for yes and „0” stands for no), or it is a weighted web giving any information about differences between links: feeding can be characterised qualitatively (e.g. species A „eats a lot” of species „B” but species „C” eats only a little of species „D”) or quantitatively (species „A” consumes 15 mg of species „B” per year per square meter). Quantitatively weighted webs are much closer to reality. Some authors think that energy flow magnitudes are even more important than standing stocks themselves [83, 95].

It is evident that a food web graph cannot take any shape (imagine a community with a single plant, a single herbivore and 869 carnivore species!). Following the publication of the first food web database [12] early theoretical studies tried to find general patterns in food webs, based on comparative approaches. For example, food webs seemed to have only a few omnivore species [79], and extremely few „non-adjacent omnivores” and short food chains [73, 78, 79]. The most important conclusions of early food web research were given by Pimm and colleagues [75, 77, 81]

At the first glance, it may seem to be very easy (both methodically and conceptually) how to construct a food web. One has to choose a community, list the species living there, determine who eats whom, and draw the graph. Before we go on, we need to discuss the problems of performing this recipe.

## Fundamental problems

Food webs represent absolutely important properties of species and the basic architecture of ecosystems. They inform on pathways of energy, routes of nutrient cycling, the topology of trophic interactions, and the feeding habits of individual species. These are crucial for understanding how communities are organised and how do ecosystems work. Moreover, a food web also tells us implicitly where can we hope to find the kinds of indirect interactions which are mediated by only trophic direct links (exploitative competition, apparent competition and trophic cascade). Other kinds of indirect effects that need also non-trophic interactions (i.e. indirect defense, indirect mutualism) cannot be read out from food webs, of course (for excellent overviews of the basic types of indirect effects, see [58] and [1]). But in order to gain all these information we have to construct food webs on solid methodical basis.

The representation of various kinds of organisms is highly heterogeneous in traditional food webs. Trivially, mammals and birds are, first, much easier to identify at the species level, second, typically of higher interest than lower organisms. For example, the food web database of Cohen and colleagues [13] presents 113 webs, only 8 containing fungi, 9 containing Protozoa, and 20 containing bacteria. Nevertheless, microorganisms dominate energy and material fluxes in both marine and terrestrial ecosystems [86] Some basic food web properties seemed not to apply to webs where parasites were included [26, 47].

It is not an isolated phenomenon in recent natural sciences that individual scientists can solve only tiny parts of big puzzles. Accordingly, it is typical in food web research that somebody, working hard in the field, collects dietary data of species, another scientist, possibly sitting in the library, tries to draw a food web graph, and the third part of the machine, mostly sitting in front of a computer, wants to analyse the network. The basic problem is that if we have an aggregated food web (or, in general, a developed field database), it is not easy to regain the original information (see *Figs. 1* and *2* for illustration). This organisation of research is, at one hand, unavoidable, but on the other, it results in many mistakes, misunderstandings, and artefacts. For example, Waloff [106] analysed in the field and published which species consume broom in an English meadow and Dempster [18] described the insect predators of Heteroptera living on broom. Based mainly on these works, among others, Memmott and colleagues constructed the source web of broom (i.e. species feeding directly on or receiving energy indirectly from broom, [57]). Recently, Solé and Montoya [91] analysed this source food web and found an interesting distribution of trophic link number per species. Their conclusions were very interesting from the viewpoint of community organisation and robustness. However, it has been shown that the interest of the original authors, as ecologists, in the sixties, and the questions recently posed by physicists were absolutely different, so, the new results are artefacts [38]. Thus, it is of key importance to emphasize that food webs can be helpful only if we have „intelligent" data produced for answering our actual problem. The problem-dependence of wise data collection, clever network-construction and sensible network analysis is something often forgotten. Many debates have been published on, for example, how to aggregate species into larger trophic groups. This question is absolutely unintelligent until we have a particular problem. If we have a problem, we are able to define reasonable trophic groups, aggregate species, and determine the trophic linkages.

In general, both the nodes and the links of the food web graphs were shown to be hard to define: nodes called for wise aggregation (see below), while links called for the analysis of interaction strength, symmetry and spatiotemporal plasticity. Serious

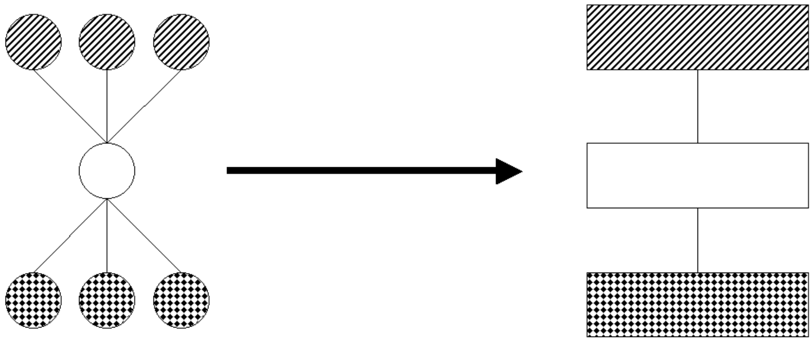

***Figure 1****. A hypothetical community consisting of seven species (graph nodes in the food web: three plants, an herbivore and three carnivores) can be aggregated into a system-model of three components (boxes of the trophic network: producers, primary consumers and secondary consumers). In this simple case, the trophic position of aggregated species fulfills the strictest criteria for aggregation (they share exactly the same prey and predators, i.e. these are aggregated into trophospecies, sensu* [105]*). Whether this simplification causes information loss or helps analysis and understanding of the community depends on the actual problem. Indirect interactions between species can be studied on the left food web, while the basic energetics of the system can be investigated better on the right trophic flow network.*

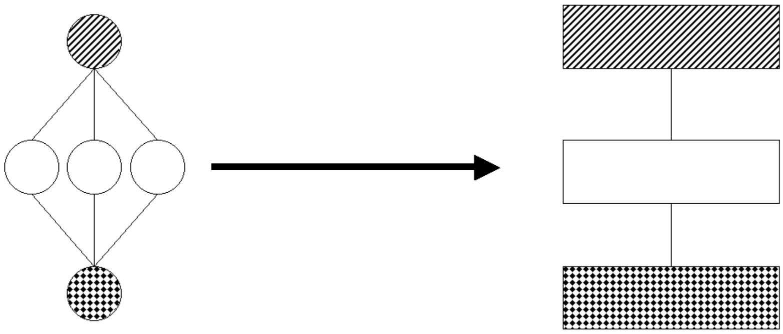

*Figure 2. The aggregated trophic network in Fig. 1 (on the right) may have been constructed from a completely different topological arrangement of species (compared to that on the left in Fig. 1). Low-resolution system models give no information about these details.*

methodological and conceptual criticism [67, 68, 80, 84] led to skepticism at one hand [43], and a novel research programme on the other [14]. Interestingly, one of the first basic problems (how to assess interaction strength on the field, [67]) was tried to be solved first only more than a decade later (and by the same author, [69]).

## Linking species to communities: key players

For the majority of ecologists, mostly ones of taxonomist style, constructing a food web is the crown on a project. Collecting individuals in the field, identifying them and their prey items, and determining trophic linkages are the dirty work followed by the elegant step of drawing a web. It is really a reasonably large amount of work but it is less useful if the graph is presented only for *illustration*. For the minority of theoretical ecologists, the work of *analysing* the web just begins. Food webs, if constructed adequately to our problems, may tell a lot information about the community, help a lot in answering our particular question, and reveal emergent or system-level properties of the ecosystem. Moreover, they can generate a number of new hypotheses and questions. Thus, the food web itself is, first, the result of many people's work, and second, the substrate of a good deal of analytical investigation.

For example, if the food web is drawn, our focal species of interest can be put in a network context, meaning that we have impressions to the identification of its exploitative competitors, cascading interactors, or apparent competitors. We can have some information about its trophic height, about its position in the web, or whether one of its interacting partners is a key network element (i.e. positional keystone species, [37]).

A very important problem for both fundamental and applied research (e.g. conservation biology) is how to link species to communities. This means two things, according to an *inter*relationship. First, how disturbing a species will cascade through the whole interaction network, e.g. [65, 66], which species will be affected and to what extent. Second, how will certain species be affected by a given system-level perturbation e.g. [98, 32]. However there are very intensive recent investigations on this area [31], we hardly can say anything nice. Especially, we lack quantitative approaches. To predict, by numbers, which species are of central importance to the community, is the essential problem of keystone studies [9, 59, 87].

Some species in ecological communities have exceedingly large effects on others. This can be possible because of their large effect on the abiotic environment (ecosystem engineers, [30]), or because their cascading interspecific interactions. Either a few or many, as well as either weak or strong direct interactions may lead finally to a community-wide effect, depending on the details of ecosystem function and the dynamics of interactions (e.g. types of functional responses). Interactions themselves can be of either trophic (like predation) or nontrophic (like facilitation) nature. An important species is termed a keystone species [66] if its large effect is disproportionately large to its biomass (after Tilman [87]). Keystones have been identified in all trophic positions (top-predators, plants, intermediate species, parasites, etc. [9, 82]). According to a simple but informative and inspirative definition, keystones are one-species functional groups [9] while as the number of species increases in a certain well-defined functional group, they are less close to be a keystone. Thus, ecological redundancy is roughly the contrary of „keystoneness". Of course, this approach is mostly of conceptual value, since functional groups are also dependent on the actual problem and do not „exist" *a priori* (many ecologists' failure is to refer to functional groups as they were „real" ecological objects; *a priori* defined functional groups can be termed „fictional groups" – Malmqvist, pers. comm.).

An issue easier to study for theoreticians than for experimentalists is what will be the effect of deleting a species from a community. Earlier works with dynamical emphasis [72, 74] were recently followed by purely structural analyses [21, 37, 46, 91]. Exciting theoretical constructions, unfortunately, are rarely followed by nice field studies.

A major problem with keystone research is how to identify exactly (quantitatively) keystone species. Quantitative approaches could provide predictive power and the possibility of *a priori* identification instead of recognising the large effect of a species only after it has gone extinct. Following an early attempt (CI, community importance, [59]), recent investigations on outlining a quantitative framework are based on the positions of species in food webs; critical network positions may refer to species whose deletion (extinction) would cause a dramatic effect on the whole community. These studies, thus, refer to keystone species mainly on theoretical grounds [21, 27, 28, 34, 37, 38, 54, 91]. Approaches searching for the topological connection of local to global scales may help in understanding the „linking" problem [34, 38, 102]. The importance of a species, based on these trophic assumptions, can be highly contingent with environmental factors and is expressed only in the context of a single community. However, for the purpose of inter-community analyses, the construction of comparative food webs would be a minimal criterion. The changes in importance of a certain species can now be traced only in a single ecosystem, where comparable food webs characterise different states of the system (four seasons: [33, 35], stress versus no stress: [32]).

## Why only species? – problems of aggregation

One of the rare food webs of uniformly species-level resolution, maybe the only one, is the source web based on broom described in an English meadow [57]. The final aim, according to the view of many food web researchers, is to include exclusively species in food webs. I try to show shortly why is this aim impossible, conceptually senseless and absolutely illogical. Finally, I will show how could wise aggregation help in comparability.

Mammals and birds are surely easy to classify. The species complexes of frogs and many polyploid plants, among many other cases, may cause problems. But even if we analyse a community where these „problematic” taxa do not live, we surely will find bacteria and they will stop us to realise the „final aim”. It is not easy to define bacterial species and even the bacterial species concept is questionable.

Even if somebody has a high-resolution web, maybe containing only species, it will probably turn out that many species have exactly the same set of sources and consumers, thus, they can be unified in a single trophic group. Moreover, very importantly, in the case of other species the trophic difference between conspecific individuals may be much larger than the difference between individuals belonging to different species. Thus, sometimes we could stop at higher resolution, but sometimes we need to go below the species level in order to detect reasonable dietary differences (*Fig. 3*). Tadpole and adult frog should be represented by different nodes in the food web graph, but desert spiders may frequently belong to a single or few nodes.

Desert spiders, if tried to sensibly separated to several nodes, will be represented according to their size instead of taxonomic position. In other words, it does not matter which species they belong to, feeding habits depend only on their size class: they eat „everything” smaller that moves around. If functionality is intended to taken into account, the relevance of taxonomy is much smaller if not disappears. Soil nematodes are wisely represented by a bacterivore, a fungivore, a predatory and a parasitic trophic group of species [19, 20]. Another example for the unavoidability of functionality reports on the redundancy of algae in wet ecosystems [93]. Functionality is a key issue in ecology: if a food web is created to represent trophic relationships in a community, it cannot be constrained by „empty” taxonomical classification. In fact, many „bad” food webs are created by taxonomists thinking too rigidly in categories reflecting no function at all. Taxonomists are people without whom food webs cannot be constructed but after they have done their work, ecologists of more functional thinking have to finalise the construction of food webs.

A problem apart of the above ones is that trophic interactions are highly plastic in space and time. If we study a community at the species level, it does matter whether we collect our (feeding) data at night or at daytime, in winter or in summer, and at a particular place or ten meters away. For a trivial example, observing feeding relationships at daytime, we will have no owl in the food web. The spatiotemporal variability of trophic interactions [107, 111, 112] calls for lower levels of resolution: larger trophic components change less, for example, the group of benthic suspension feeders remains functioning even if species come and go [15]. Looking at food webs at the species level may lead to unnecessary complexity.

Of course, lower resolution may also cause problems, for example, indirect interactions between species cannot be detected if they are aggregated into the same trophic group. Thus, as the only robust conclusion, we have to say that the optimal level of resolution (way of aggregation) depends on the context of the actual problem. There is no general recipe, but it is useless to restrict to species. More exactly, it is wise to know a community at the species level, but only for being able to aggregate the species wisely into reasonable larger groups.

From the above, it follows that there is neither qualitative nor quantitative aggregation algorithm accepted widely. However, a practical procedure is to eliminate

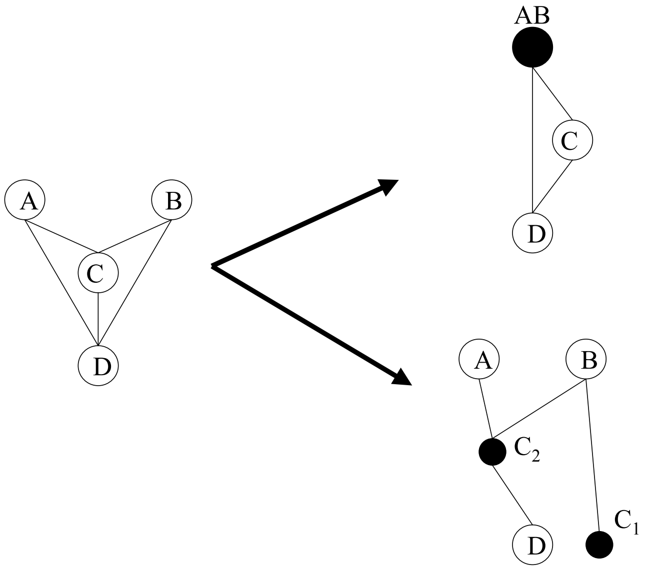

***Figure 3.*** *Whenever the species list of a community is transformed to a list of ecologically reasonable compartments of the ecosystem, functionality can (and need to) be taken into account. The upper graph on the right shows a graph where species „A" and species „B" of an original food web (on the left) have been aggregated into a single trophic component (black circle), since they have exactly the same trophic links („AB" is a trophospecies,* [105]*). But it is not a rule that trophic groups reflecting functionality have always to be above the species level: the lower graph on the right shows a situation where the division of species „C" of the original food web into two smaller trophic components was logical: „$C_1$" may be a larval form, not eating „D" and eaten only by „B", while „$C_2$" may represent the adults of „C", eating „D" and eaten by both higher species („A" and „B"). If the feeding habits, i.e. the trophic status, of a species' individuals change fundamentally through their life cycle, this is well reasonable. Differences in feeding between two individuals of the same species belonging to different developmental stages (for example, a tadpole and a frog) can be much larger than differences between two individuals of two species (for example, in the case of desert spiders,* [84]*).*

trophic groups and/or trophic links below certain well-defined biomass and material flow limits, respectively (see [111]). Proposed exact aggregation algorithms [25, 99] criticised for distortions resulted from aggregation [64]. It has been shown that the aggregation of real field data is easier than that of simulated data [92]. Even if we have an exact algorithm, serious problems still remain. An illustrative example is given for that:

Let us assume that our aim is to create larger groups from the species of the broom source web [57], based on nothing else than trophic similarity. The originally described 154 species (more exactly, 153 species and the group of „immature spiders") can be first aggregated into 82 trophospecies [105] containing species with exactly the same set of prey and predators (*Fig. 4*). If we need stronger aggregation (i.e. lower resolution), we may relax a bit the trophospecies criteria: the aggregation step „α" will mean the replacement of an *n*-step chain by an *n*-1 step chain (chain shortening), the step „β" will mean the fusion of two species if they have exactly the same predators but there is a subset relationship between their prey-sets (a relaxed condition), and the step „γ" will mean the fusion of two species if they have exactly the same prey but there is a subset

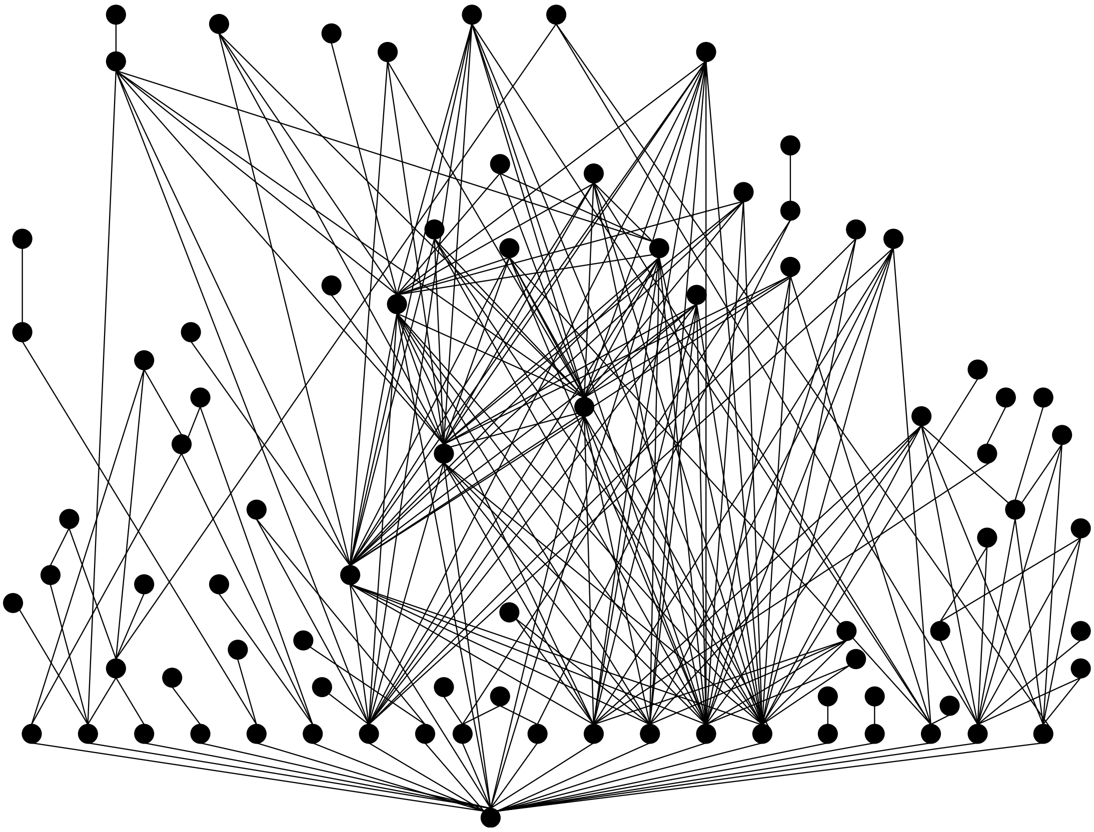

***Figure 4****. The 82 trophospecies living on broom (Cytisus scoparius): they were aggregated from 154 species, based on perfect trophic similarity* [57]. *We do not give the list of species (see it in* [57]*). Higher species always feed on or parasite lower species. The lowest species is broom (this is a source web).*

relationship between their predator-sets (another condition is relaxed now). Combining steps „α", „β" and „γ", we can aggregate the original network according to six sequences. The aggregated webs (*Fig. 5*) are of different size, even if the same aggregation steps were made, only their sequence differed. The connectance of the aggregated six webs also differs widely: for the original web, $C$ = 0,06, and the connectance values after aggregation procedures range from 0,11 (α-γ-β) to 0,22 (γ-α-β). This illustrative example only shows that exactly defined rules may still lead to fundamentally different results when applied – and there are no exact aggregation algorithms to date.

Quantitative aggregation methods would provide exactness and objectivity. Aggregation based on field expert would help to save reality. The best solution would be to have a realistic but also quantitative aggregation procedure, but it may not exist considering problem- and context-dependency. But we have seen that some kind of aggregation is necessary, since species-level resolution has its serious limits. So, a skeptical voice would say that there is no way to construct a good food web. If there are no good webs, the minimal criteria of usefulness can be to compare similarly wrong food webs, thus, comparability may be the only key to useful food web research.

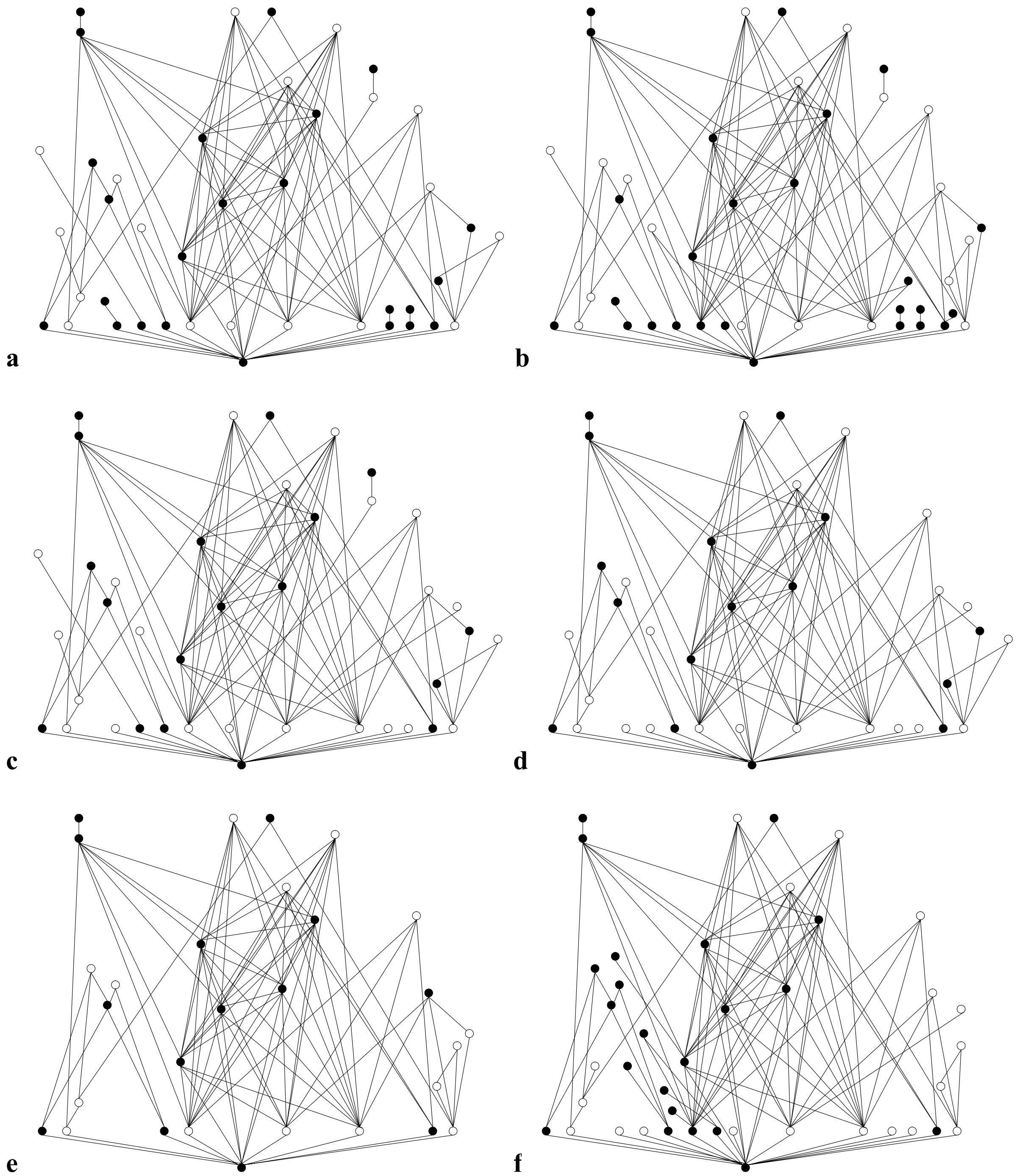

***Figure 5****. The aggregated networks of the original one shown at Fig. 4, according to various sequences of the defined aggregation steps: α-β-γ (***a***), α-γ-β (***b***), β-α-γ (***c***), β-γ-α (***d***), γ-α-β (***e***) and γ-β-α (***f***). Black nodes are not affected by aggregation, while white nodes are aggregated groups of two or more species of the original network. Note that the same three steps lead to different final states, even if only their sequence differs. See more discussion in text.*

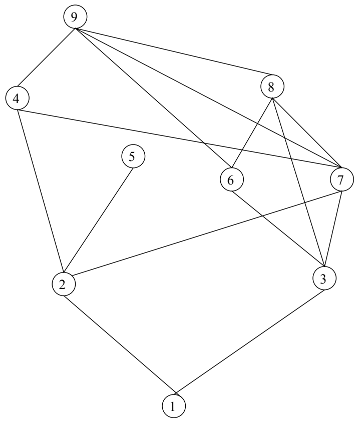

***Figure 6.*** *The food web of the Schlei Fjord ecosystem (N-Germany). In this low resolution web, species are strongly aggregated into large functional groups: 1, Phytoplankton; 2, Zooplankton; 3, Zoobenthos; 4, Planktivores; 5, Temporary planktivores; 6, Whitefish; 7, Small fish; 8, Medium predators; 9, Apex predators (modified after* [11, 34, 62]*). Graph nodes mark functional groups, while links represent trophic interactions: higher groups always feed on lower ones (direction is not marked, for simplicity). The whole community is presented „by and large".*

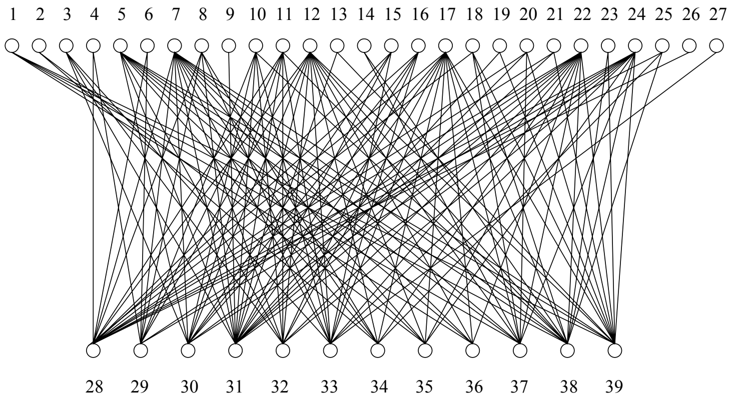

***Figure 7.*** *The food web of a leaf-miner – parasitoid community living on four tree species of a meadow (S-England). In this high resolution web, species are shown with no aggregation: 1, Cirrospilus diallus; 2, C. lyncus; 3, Elachertus inunctus; 4, Pnigalio longulus; 5, P. pectinicornis; 6, P. soemius; 7, Sympiesis gordius; 8, S. grahami; 9, S. sericeicornis; 10, Achrysocharoides splendens; 11, A. niveipes; 12, A. latreillii; 13, A. zwoelferi; 14, Chrysocharis laomedon; 15, C. nephereus; 16, C. phryne; 17, Pediobius alcoeus; 18, P. saulius; 19, Minotetrastichus ecus; 20, Holocothorax nepticulae; 21, H. testaceipes; 22, Colastes braconius; 23, Apanteles sp.; 24, Apanteles circumscriptus; 25, Hormiinae sp.; 26, Scambus sp.; 27, Campopleginae sp.; 28, Phyllonorycter salicicolella; 29, P. dubitella; 30, P. harrisella; 31, P. heegeriella; 32, P. lautella; 33, P. quercifoliella; 34, P. ulmifoliella; 35, P. cavella; 36, P. froelichiella; 37, P. kleemanella; 38, P. rajella; 39, P. stettinensis (modified after* [41, 90]*). Nodes and links represent species and parasitoid interactions, respectively, where the higher 27 species are parasitoids and the lower 12 species are leaf-miner hosts. Only selected species of the whole meadow community are shown but in fine details.*

## Comparable food webs

Both the classical [10, 12, 13] and the modern [22, 23, 50, 57, 103] databases of food webs inspired ecologists to compare trophic networks described at quite different places and representing quite different communities. Considering the extreme methodological heterogeneity of field studies and network construction, it is strongly questionable whether the results of any comparison can be useful. For example, Melián and Bascompte [54] compare the food webs of the Little Rock Lake [50] and that of the El Verde tropical rain forest in Puerto Rico [88]. The former database contains nearly exclusively species and genera (i.e. a web of high resolution, 182 graph points), while the latter one contains only 20 trophic components of much lower resolution, such like „birds" (three times), „bats" (twice) and „termites". I suggest to be skeptical with analyses of this kind, because these webs are completely incomparable.

I believe that two or more food webs can be compared only if they were described for the same purpose, and by the same methodology [33]. If there was any bias or failure in the fieldwork or there was any inconsistency when the web was constructed, then these problems are expected to be minimal as the *differences* between comparable webs are analysed. But if one compares two webs described for different purposes and by different methods, then methodical problems will just grow and give unavoidable artefacts.

Presently, two rich databases of comparable food webs are known; one for systems ecologists and one for population / community ecologists:

Several marine and estuarine habitats are characterized by the energy language popularised by Odum [63]. These give the exact values of carbon flows (in mg C × $\text{year}^{-1}$ × $\text{m}^{-1}$) between the identified trophic components of these ecosystems. Respiration losses and recycling pathways are also characterized. Some databases present the trophic flow networks of different elements given to the same ecosystem (carbon: [3]; nitrogen: [6]; phosphorous: [100]). These databases are very robust grounds for analysing quantitatively weighted interactions. These flow networks of energy are of low resolution, i.e. they are highly aggregated (*Fig. 6*).

Recently, Charles Godfray and colleagues are collecting rich databases of host–parasitoid communities from both the tropics and temperate habitats [45, 55, 56, 61, 90, 100]. These webs show less exact weights on links and present only a part of the studied community, however, it is generally known that these subcommunities are relatively well isolated from other species (*Fig. 7*). The great values of these webs are, among others, that they belong to the very few terrestrial food webs, and they constitute a database of similarly described, comparable food webs.

Finally, a colourful database of more or less comparable food webs is the result of a meta-analysis of phytotelmata food webs (describing the fauna of the water-filled pitchers of *Nepenthes* pitcher plants: [42]). These webs roughly satisfy the criteria of comparability, however, they give only a little information on these little communities inhabiting pitcher plants.

Comparing only comparable food webs sounds very logical and I suggest that this is the only right way for future food web research in order to have any chance for applicability.

## Applications

However ecologists have recognised very early that purely structural descriptions of food webs are not realistic enough and, thus, should be complemented by dynamical analyses, they had shown only a very limited interest even in possible structural properties. Species were ordered to trophic levels, and they were classified as an omnivore (feeding on different trophic levels, [79]) or not. Food webs were characterised nearly exclusively by their connectance (actual per maximal link number, [12], and see also [108]). These indices were poor structural descriptors of trophic flow networks. It is no wonder that dynamical simulations made models much better. But, as recently we have much more structural indices applied in ecology (for some examples: characteristic path length, [110]; structural equivalence, [29, 46]; clustering coefficient, [109]; keystone index, [37]; network flow reliability, [36]; web diameter, [2], etc.), the original question could be asked again: what does pure structure predict? Of course, dynamical contributions [51, 52, 53, 76] are by no means to forget, but novel structural approaches are beginning to be married with dynamics, again [39, 40]. Attempts have been made also for considering the pattern of flow magnitudes in weighted flow networks [32, 35, 95, 98] and, thus, gaining some information on dynamics.

Food webs are built frequently only for illustrative purposes. These webs do not give quantitative information and have no predictive power. They frequently just help understanding and reviewing existing information. In the following, I list some qualitative and quantitative examples for how to apply food web research in approaching particular problems.

Food webs may be useful in assessing the impact of a poison (e.g. DDT) being transported bottom-up through trophic chains. Here, the simple index of trophic height gives information on bioaccumulation probability and the „time” needed to reach a certain group. Trophic height analysis can help also in assessing and quantifying the problem of fishing down marine food webs [71]. This is in no contradiction with the idea that discrete trophic levels do not exist [85]: it is now generally accepted that there is no reason to order each species or trophic group to an integer trophic level. However, it is clear that it has an ecological meaning that herbivores are closer to plants in a trophic topology, than higher carnivores. A measure of trophic height, if not restricted to integers, provides very important information on organisms.

As food web structure tends to change in a given area, landscape ecological trends may be indicated. Shortening food chains may reflect habitat fragmentation, since top-predators are among the mostly sensitive species to this effect (see Crooks and Soulé [16]). Their large area and particular feeding habits permit them to survive in small, fragmented patches. Habitat fragmentation is rapidly indicated by the loss of higher predators (and, later, by additional changes, such as mesopredator release and secondary loss of herbivores).

Marine (mostly pelagic) food webs help to understand why pelagic ecosystems are so sensitive to the fisheries of some species (e.g. anchovy, hake). Pelagic food webs are frequently of wasp-waist nature [17], meaning that species diversity is very high at the bottom and at the top of the food web, however, the middle region is dominated by a single or a few species (e.g. anchovy). These are the commercially most important species, thus, the effects of fisheries spread easily and rapidly within the trophic network.

Ecologically sensitive network indices of trophic flow networks may help in monitoring ecosystems at the system level. For example, the community-wide effects of thermal stress have been indicated by changes in network ascendency [98] and in the congruency of important flows and important trophic components [32].

High-resolution food webs may help in tracing indirect interaction pathways within ecosystems (of course, only kinds of indirect effects caused by trophic direct effects). The set of affected species can be more or less assessed if a particular species is disturbed [103]. The web tells where to expect responses and helps in predicting the net impact of a pulse perturbation experiment [102]. Methods begin to be developed for quantifying the range of reasonably strong indirect effects of a species, i.e. the strength of its „trophic field" in a topological space [34, 41]. Conservation biology may use these kinds of analyses [104], while as for theoretical interests it can help in understanding the link between species and ecosystems. In general, food web studies may help in clearing the results of experiments (e.g., by calling attention to indirect effects, [9]).

## Concluding remarks

If, accordingly to many recently suggested views, we accept that the assembly and functioning of ecological communities is easier to understand from a network perspective [24, 48, 49, 70, 96, 97, 99], questions of central importance are how to create and how to use these networks. Recently introduced terms such as „network algebra" and „network anatomy" are good starting points but approaching reality still depends on, for example, how to incorporate nonlinearity and nonadditivity into these models. This is an area where structural and dynamical models have to meet.

Either local or global network indices can be applied and developed, the basic problem of how to construct food webs from field dietary data remains. If basic methodological problems pervasively exist, „networking" cannot help in better understand ecosystems. There are no universally good food webs, only webs described reasonably in the light of a particular problem. A possible solution is to gain information from the comparison of comparable webs. Thus, databases of food webs described by exactly the same methodology can only help if food web research wants to be applied in future. These groups of comparable webs can be either of low or of high resolution, but similarly described. Both the growing marine and estuarine food web database (e.g. [4,5]) and the collection of mostly terrestrial quantitative host-parasitoid food webs (e.g. [61]) are good examples in this direction. But comparing webs belonging to different groups is meaningless (see [54]). To date, we can skeptically conclude that the predictive power of food web research is probably large but still masked by methodological inconsistencies.

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