

Food Webs

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Food webs are the networks formed by the trophic (feeding) interactions between species in ecological communities. Their relevance for population ecology follows directly from the importance of trophic interactions for maintenance and regulation of populations. Food webs are crucial for community ecology whenever trophic interactions control competition, and hence community composition and species richness. Theoretical representations of food webs range from simple directed graphs to complex dynamic models integrating much of theoretical ecological.

I Status of the theory

The study of food webs developed from a science that simply records data, through a phase of cataloging and identifying patterns in the data, and then moved towards interpreting data and patterns, first in terms of phenomenological models and later in terms of general ecological mechanisms. A stage in which the theoretical foundations would be settled and their implications studied in depth has not been reached, yet.

By now, a large number of food-web models have been developed that combine elements from a certain set of recurring model components with specific original ideas. As these models are becoming more complex, work to systematically evaluate and compare their predictive power is limited by computational issues, differences in model focus, and deficits in the available data. There is currently no “standard model” for food-web structure and/or dynamics. Understanding the roles played by different model elements in generating the patterns found in data remains a major theoretical challenge.

Fisheries management is perhaps the only area where progress has been made in applying complex food-web models to real-world problems. While long-term forecasts of the dynamics of interacting, harvested fish populations are limited by high model sensitivity and the problem of food-web stability (see below), food-web models of fish communities help understanding medium-term changes in abundances, mortalities and population growth rates.

II Basic elements of food-web models

II.A Topological and quantitative food-webs

Food webs are often represented as in Fig. 1, by directed graphs in which species form the nodes and feeding interactions are represented by arrows (trophic links) pointing from resources to consumers, i.e., in the direction of energy flow. By convention, consumers are drawn above their resources whenever possible, so that energy flows upwards and “top predators” are on the top.

Some empirical food webs restrict the set of species included to those that are directly or indirectly eaten by certain consumers (*sink webs*) or those directly or indirectly feeding on certain resources (*source webs*). Theory nearly exclusively considers *community food webs*, implying the idealizations of sharply delineated ecological communities and well-defined sets of member species.

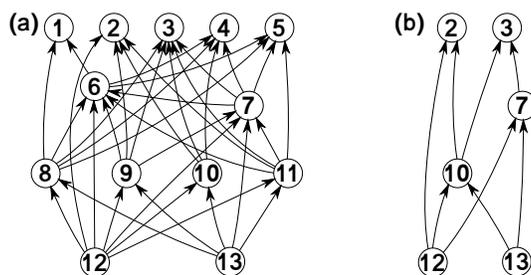


Figure 1: The food web of (a) Morton Creek (after G. Wayne Minshall, *Ecology*, 48:139-149, Fig. 3) and (b) the community that persists in the model described in Box 1.

A food web described exclusively by a species list and an adjacency matrices $A_{ij} = 0, 1$, indicating whether j eats i , or a corresponding graph is called a *binary food web*. This distinguishes *topological food webs* from *quantitative food webs* that are described by a link-strength matrix C_{ij} and, potentially, species abundances.

II.B Link-strength functions and trophic niche space

The trophic link strength C_{ij} between a resource i and a consumer j is often modeled as a function of characteristics of these two species. That is, one assumes that each species i is characterized by a set of vulnerability traits \mathbf{v}_i and a set of foraging traits \mathbf{f}_j such that, with an appropriate choice of the link-strength function $c(\cdot, \cdot)$, trophic link strength is given by $C_{ij} = c(\mathbf{v}_i, \mathbf{f}_j)$. Vulnerability and foraging traits may not be independent. Body size or preferred habitat, for example, affect species in both their roles as resources and as consumers.

The function $c(\cdot, \cdot)$ is often modeled such that for any biologically possible (or technically allowed) combination of vulnerability traits \mathbf{v} there is one specific combination of foraging traits \mathbf{f} that maximizes the interaction strength $c(\mathbf{v}, \mathbf{f})$. Disregarding those \mathbf{f} that do not match any \mathbf{v} , one can then identify the set of biologically possible \mathbf{v} with the set of maximizing \mathbf{f} . This unified set of trophic traits is called the *trophic niche space*. Under some mild conditions on the convexity of $c(\cdot, \cdot)$ (i.e., that $c(\mathbf{v}, \mathbf{f})$ decreases the more \mathbf{f} differs from the value matching \mathbf{v}), satisfied in most models, the interaction strength between two species i and j is then the stronger the closer \mathbf{f}_j is to \mathbf{v}_i in trophic niche space. By fixing some threshold value c_t , one can assign a *foraging niche* to each consumer j as the set of all \mathbf{v} for which $c(\mathbf{v}, \mathbf{f}_j) > c_t$. The foraging niche of a consumer j surrounds \mathbf{f}_j in trophic niche space. Many food-web models are defined by combining a link-strength function with rules for assigning trophic traits to species.

An example for a link-strengths function is

$$c(\mathbf{v}, \mathbf{f}) = c_0 \exp \left[v^{(0)} + f^{(0)} - \frac{1}{2} \sum_{i=1}^D \sigma_i \left(v^{(i)} - f^{(i)} \right)^2 \right]. \quad (1)$$

In this case, the trophic traits \mathbf{v} and \mathbf{f} are $D + 1$ dimensional real-valued vectors with components $v^{(0)}, \dots, v^{(D)}$ and $f^{(0)}, \dots, f^{(D)}$, respectively, σ_i equals either $+1$ or -1 , and c_0 is a scale constant. Many link-strength functions found in the literature can be brought into this or similar forms. Although mixed sign structures are conceivable as well, theorists generally assume $\sigma_i = +1$ for all i . For a given \mathbf{v} and fixed $f^{(0)}$, trophic link strength is then maximized by matching $f^{(1)}, \dots, f^{(D)}$ with $v^{(1)}, \dots, v^{(D)}$.

Table 1: The sets of species lumped into each network node in Fig. 1a (after G. Wayne Minshall, Ecology, 48:139-149).

1	<u><i>Phagocata gracilis</i></u>	9	<u>Ephemeroptera:</u>
2	<u>Decapoda:</u>		<u><i>Baetis amplus</i></u>
	<i>Orconectes rusticus rusticus</i>		<i>Baetis herodes</i>
	<i>Cambarus tenebrosus</i>		<i>Baetis phoebus</i>
3	<u>Plecoptera:</u>		<i>Epeorus pleuralis</i>
	<i>Isoperla clio</i>		<i>Centroptilum rufostrigatum</i>
	<i>Isogenus decisis</i>		<i>Pseudocloeon carolina</i>
4	<u>Megaloptera:</u>	10	<u>Trichoptera:</u>
	<i>Nigronia fasciata</i>		<i>Neophylax autumnus</i>
	<i>Sialis joppa</i>		<i>Glossoma intermedium</i>
5	<u>Pisces:</u>	11	<u>Diptera:</u>
	<i>Semotilus atromaculatus</i>		<u>Tendipedidae</u>
	<i>Rhinichthys atratulus</i>		<i>Simulium</i> sp.
6	<u><i>Gammarus minus</i></u>		Tipulidae
7	<u>Trichoptera:</u>		<i>Pericoma</i> sp.
	<i>Diplectrona modesta</i>		<i>Dixa</i> sp.
	<i>Rhyacophila parantra</i>		Other
8	<u>Asellus:</u>	12	<u>Detritus</u>
	<i>A. brevicaudus</i>	13	<u>Diatoms:</u>
	<i>A. intermedius</i>		-unresolved-

Thus, trophic niche space is here a D -dimensional vector space. The *trophic baseline traits* $v^{(0)}$ and $f^{(0)}$ determine the overall vulnerability of a resource and the overall aggressivity of consumers, respectively.

The idea that trophic link strength depends only on the consumer and the resource is a simplifying idealization (think of prey hiding in bushes). A modification of trophic link strength by a third species has been called a *rheagogy* (based on the Greek *rheô*, flow and *agôgeô*, influence). Rheagogies can complicate the interpretation of food webs and, when sufficiently strong, qualitatively affect community structure.

II.C Dynamic food-web models

Population-dynamical food-web models describe how the abundances of all species in a community change over time as a result of trophic interactions. They build on the premise that trophic interactions dominate population dynamics, so that non-trophic effects can be modeled in highly simplified form. Historically, population sizes have been quantified by the number of individuals, recent models generally operate with biomass or bio-energy instead. Minimal ingredients for population-dynamical food-web models are appropriately parametrized sub-models for (1) functional and numerical responses of consumers to varying resource abundances, (2) non-trophic losses (death and/or metabolic losses), and (3) the population dynamics of basal species. Box 1 provides an example.

Food-web assembly models describe how the structure of food webs changes as a result of a sequence

Box 1 A simple population-dynamical food-web model

This model describes trophic interactions between 13 (trophic) species. The population dynamics of consumer species ($i = 1-11$) is modeled by a generalized Lotka-Volterra model of the form

$$\frac{dB_i}{dt} = -RB_i + \epsilon \overbrace{\sum_j C_{ji} B_j}^{\text{numerical response}} B_i - \sum_j \overbrace{C_{ij} B_i}^{\text{functional response}} B_j \quad (2)$$

and that of the basal species ($i = 12, 13$) as

$$\frac{dB_i}{dt} = \overbrace{r(1 - B_i/K) B_i}^{\text{basal dynamics}} - \sum_j \overbrace{C_{ij} B_i}^{\text{functional response}} B_j. \quad (3)$$

With A_{ij} denoting the adjacency matrix corresponding to Morton Creek (Fig. 1a), trophic link strengths are set to "pseudo-random" values $C_{ij} = A_{ij} \cos(13i + j)^2$, the efficiency for conversion of resource biomass to consumer biomass to $\epsilon = 0.5$, the effective consumer respiration rate to $R = 0.2$, the growth (or replenishment) rate of basal species to $r = 1$ and their carrying capacities to $K = 1$. Simulations are initiated by setting all $B_i = 1$ and continued over 1000 unit times. Species with $B_i < 10^{-10}$ are removed as extinct. The remaining community, shown in Fig. 1b, approaches a stable, feasible fixed point.

of invasions and extinctions. Invading species are either chosen from a predetermined species pool (representing a metacommunity) or generated at random. Assembly models in which trophic traits of invading species are determined by randomly modifying traits of resident species are called *evolutionary food web models*. This is often described as "speciations" of resident species in large "mutation" steps. The scheme is perhaps more realistic than this interpretation. The actual speciations can have occurred allopatrically or at distant locations or times. In the focal community, such processes would simply be reflected by invasions of species that are more or less similar to existing ones.

Examples of evolutionary models in the literature cover cases with small and large mutation steps, and cases where the decision which species to invade or to extinguish is made depending on population dynamics (populations falling below a given threshold are removed as extinct), depending on other properties of the food web, or purely at random (neutral evolution).

III Patterns and Mechanisms

III.A Models and data

Generic models of complex systems such as food webs are unlikely to reproduce all aspects of empirical data. One therefore has to distinguish between patterns in empirical data, on one hand, and models capable of reproducing and explaining specific sets of patterns, on the other hand. This distinction is blurred when data are characterized in terms of models fitted to them. Yet, models fitted to data are useful even on purely theoretical grounds, for example for identifying the mechanisms by which specific combinations of model elements reproduce particular empirical patterns, or to understand in how far different mechanisms interact under realistic conditions. The discussion here will emphasize mechanisms

that relate model elements to patterns, since understanding these should allow us to recombine model elements to balance model complexity against desired descriptive or predictive capabilities.

The sheer amount of data that accurate quantitative descriptions of complete natural food webs would require dashes any hopes that such descriptions will become available in the foreseeable future. Each food-web data set is a compromise between accuracy and completeness, and different empiricists will set different priorities. To make food webs manageable, trophic links are often inferred rather than measured, *trophic species* are introduced for special compartments such as 'detritus' or to summarize groups of similar species, especially at lower trophic levels, and interactions with neighbouring communities are not represented (see, e.g., Tab. 1, Fig. 1a). Theory interpreting such data has to take these limitations into account.

III.B Size selectivity

Big fish eat small fish. Patterns of body-size selectivity are evident in food-web data, especially for aquatic communities. Models capture this phenomenon by assigning a trophic trait "size" to each species and constraining the relative sizes of resources and consumers in feeding interactions. For models and data that focus on predatory interactions rather than parasites, pathogens, or grazing, the pattern large-eats-small dominates.

Because individuals of many species grow substantially before they mature, the size range of resources fed on by a species as a whole can be large. Pairs of species eating each others offspring lead to *loops* in food webs, species eating their own offspring lead to *cannibalism*. As a simplified representation of these complications, food-web models sometimes allow consumers to choose resources among all smaller species, admitting a few exceptions where small eats large. When no exceptions are allowed, food-web adjacency matrices can be brought into lower-triangular form by assigning indices to species according to size. One of the earliest topological food-web models, the *cascade model* conceived by Cohen, Briand, and Newman in 1989, generates adjacency matrices simply by randomly setting a fraction of matrix entries below the diagonal to 1 and leaving all others 0. The cascade model was shown to generate topologies more similar to empirical webs than other, comparably simple models.

III.C Phylogenetic constraints

Evolutionarily related species are similar, and similar species tend to have similar resources and consumers. For example, a bird eating a seed is likely to eat other kinds of seeds; and a bird eating an insect is more likely to eat other kinds of insects than to eat seeds because insects are more similar to each other than to seeds. Empiricists are taking these phylogenetic constraints on food-web topology for granted when defining trophic species taxonomically (e.g., Tab. 1). Phylogenetic analyses of food webs confirm this pattern. They also show that consumer sets of species are inherited more strongly than resource sets. For example, granivorous and insectivorous birds may differ in their diets and yet share bird-eating raptors as common consumers.

These phylogenetic constraints can be described by evolutionary food-web models in which both vulnerability and foraging traits are inherited, the former stronger than the latter. Such models generate characteristic patterns in food-web topologies, that is, patterns evident even without knowledge of the underlying phylogeny. Before considering other mechanisms to explain patterns in food webs, one should therefore always ask first whether these patterns are simply consequences of phylogenetic and size constraints, two well-established empirically facts. Most patterns discussed below are of this kind.

III.D Link-strength distributions

Food webs contain many more weak links than strong links, that is, distributions of link strengths are highly skewed towards weak links. This pattern is found independent of whether link strength is measured in terms of absolute biomass or energy flows, or normalized to predator and/or prey abundances. While early studies found link strengths to be exponentially distributed, more recent work points towards power-law or log-normal distributions (a quantity is log-normally distributed if its logarithm is normally distributed).

Log-normal and power-law distributions may be empirically indistinguishable. Assuming log-normal link-strength distributions, very strong links are unlikely to be observed because corresponding consumer-resource pairs are rare, and very weak links are unlikely to be observed because they are hard to detect. Thus, only a finite range in link-strength magnitude is empirically accessible, and it is well known that the upper tail of a log-normal distribution can, over a range small compared to the width of the distribution, be approximated by a power-law.

Log-normal distributions of trophic link strength arise naturally in models where the link-strength function is a product of many factors

$$c(\mathbf{v}, \mathbf{f}) = \prod_k c_k(\mathbf{v}, \mathbf{f}), \quad (4)$$

and the factors $c_k(\mathbf{v}, \mathbf{f})$ are all positive and depend differently on consumer and/or resource traits. An example for such a link-strength function is Eq. (1) with large D . To the extent that the trophic traits of member species are distributed randomly within a community, $\log c(\mathbf{v}, \mathbf{f})$ is then the sum of many random numbers and can be approximated by a normal distribution. Hence $c(\mathbf{v}, \mathbf{f})$ is log-normally distributed.

Two empirical patterns, (a) that link strengths are similarly distributed independent of their precise definition, and (b) that resource abundances are bad predictors of diets, are both reproduced by models in which the variance of logarithmic link strengths is large compared to that of logarithmic abundances.

Very weak trophic links are empirically indistinguishable from absent trophic links. Quantitative food-web models will therefore in general be more parsimonious if all possible link are modeled as present, but logarithmic link strengths are allowed to vary broadly, such that, as observed, the fraction of links sufficiently strong to be detected (*connectance*) is small. In this view, adjacency matrices A_{ij} derive from link-strength matrices C_{ij} , e.g., by thresholding link strengths. Empirical food-web topologies might therefore best be understood by combining a theory for link strengths C_{ij} with an observation model.

III.E Degree distributions

For directed graphs, one defines the *in degree* of a node as the number of incoming links, the *out degree* as the number of outgoing links. In food-web theory, in-degree (number of resources) is also called *generality* of a species and out-degree (number of consumers) its *vulnerability* (not to confuse with vulnerability traits).

Both, in- and out-degrees are distributed much more broadly in food webs than would be expected for links assigned with equal probability to each species pair (which yields binomial distributions). Out-degrees often have an approximately even distribution between zero and some upper limit. This pattern is reproduced by models implementing the large-eats-small rule mentioned above, but otherwise assigning links from consumers to a given resource independently and with equal probability.

Most empirical distributions of in-degrees (and sometimes out-degrees) are approximately exponential (geometric). At least, values near zero tend to be the most frequent and the distributions have long upper tails. This skewed structure can be reproduced by evolutionary models with high heredity of vulnerability traits. The skewed distribution of clade sizes characteristic of phylogenetic trees then leads to the observed skewed distribution of in-degrees, provided consumers tend to forage on a single resource clade. Near-exponential degree distributions are sometimes also found in models without phylogenetic constraints, but the underlying mechanism in this case has not been identified, yet.

For better comparison across food webs, in- and out-degrees can be normalized by the mean out-degree (= mean in-degree = link density). Distributions of normalized degrees are quite similar among food webs and have been hypothesized to follow universal functional forms.

Degree distributions and link-strength distribution are related through the *multivariate distribution* of the strengths of all links from and towards one species. For instance, the hypothesized universality of normalized in-degree distributions implies dependencies among link strengths: A link from one resource to a consumer makes the occurrence of a link of similar strength from another resource to the same consumer more likely (Rossberg, Yanagi, Amemiya & Itoh, J. Theor. Biol., 2006, 243:261–272).

III.F Network motifs

Food webs contain certain types of small connected sub-graphs with 3 or 4 species more often (others less often) than expected by chance. Using smart randomization algorithms, it can be shown that the prevalence of these *network motifs* is not explained by the degree distributions particular to food webs. Yet, it remains unclear in how far network motifs are simply consequences of phylogenetic and size constraints, or whether some motifs call for independent explanations.

III.G Intervality

For small food webs it is often possible to re-index species such that, in each column of the adjacency matrix, the 1s form a contiguous block (consecutive ones property). For larger food webs this is usually not possible, but the number of 1s one would need to add in the matrix to archive this is much smaller than expected by chance. This phenomenon is called *food-web intervality*, with reference to a related concept in graph theory.

Evolutionary food-web models with high heredity of vulnerability traits naturally reproduce this phenomenon (see Fig. 2). Its historical interpretation, however, was different. Influenced by an ongoing discourse on ecological niches, Joel E. Cohen, when discovering intervality in 1977, interpreted it as the signature of an approximately one-dimensional trophic niche space. In fact, food webs defined by thresholding link-strength function Eq. (1) with $D = 1$ and fixed $v^{(0)}$ will always be perfectly interval. A subsequent search for the trophic trait corresponding to this single dimension, however, remained unsuccessful. Body size, a likely candidate, does not constrain topology sufficiently to explain the pattern. By now we know that phylogenetic constraints offer a more parsimonious explanation. Yet, models constructed around one-dimensional niche spaces are still popular as simple tools to generate interval food webs.

III.H Block structure

By visual inspection, one easily recognizes large rectangular *blocks* of high connectance in empirical adjacency matrices. More precisely, there are pairs of large species sets (P_r, P_c) such that trophic

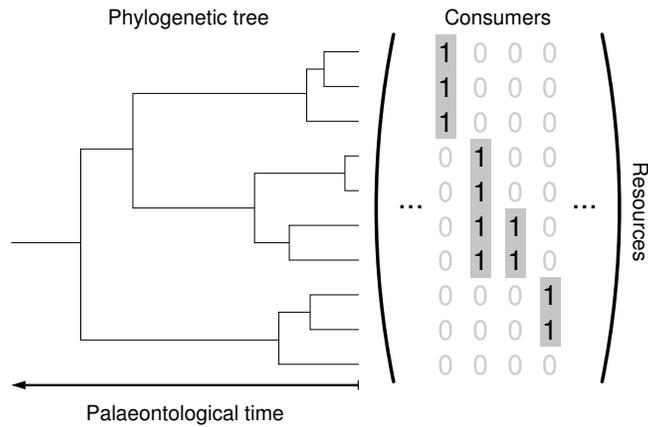


Figure 2: The phylogenetic explanation of intervality. Put a food web's member species in an order in which they could appear on the tips of a phylogenetic tree. If consumers feed on groups of species that are similar because they are related, then the 1s in each column of the adjacency matrix (shown in part) will automatically form contiguous blocks (grey boxes). That is, the food web is interval. In practice, food-web intervality in large communities is rarely perfect, neither in data nor in models implementing this mechanism *via* phylogenetically correlated vulnerability traits.

links between resources from P_r and consumers from P_c are much more frequent than trophic links on average. If P_r and P_c are identical, one speaks of a *compartment* structure. Compartments are rare in food-web topologies, but can result from joining food webs of separated habitats—and be modeled as such.

Blocks with non-overlapping or partially overlapping P_r and P_c arise in models with phylogenetic constraints. If, for example, all members of P_r are closely related and heredity of vulnerability traits is high, then all members of P_r have similar vulnerability traits. Members of P_c are those species with foraging traits located near the vulnerability traits of the members of P_r in niche space. The members of P_c are not necessarily related.

III.I Co-variation patterns

Early food-web theory worked with large collections of food-web data sets that were each too small to exhibit much structure on their own. Theory therefore focused on the question how simple quantitative properties of topological food webs, such as the number of species, the fraction of top species (species without consumers), the mean length of resource-consumer chains, etc. co-vary among data sets. Stochastic food-web models reproducing these co-variation patterns were sought.

Later, this idea was adapted to smaller collections of larger, high-quality food webs. The problem then amounts to defining a vector of food-web properties \mathbf{x} and finding models such that, for each empirical data set i , its properties \mathbf{x}_i are likely to co-occur in the output of a stochastic model for an appropriate set of model parameters \mathbf{p}_i . Model-selection methods such as the Akaike Information Criterion have been used to guard against model over-parametrization. Applicability of this analysis is limited by its computational cost. In the most advanced application so far, involving 14 food-web properties and models with up to 6 free parameters, a million independent model samples had to be

generated to fit each of 17 empirical data sets. The model most faithfully reproducing co-variation patterns was the *matching model*, which generates food-web topologies by combining a large-eats-small rule with phylogenetically correlated trophic traits.

IV The problem of food-web stability

IV.A What is the problem?

Many practical questions that food-web theory strives to address relate directly or indirectly to population dynamics. A plausible approach to answering such questions is to construct a quantitative food web for the community in question, to set up equations modeling the population dynamics of the community, and to simulate this system. However, in the majority of cases, one will find this approach to fail: As simulation time proceeds, many species in the community go extinct, despite their observed co-existence in reality.

An example is shown in Fig. 1. The empirical food web of Morton Creek is equipped with population dynamics as described in Box 1. When simulating the system, 7 of the 13 trophic species in this food web go extinct. Variations of the parametrization suggested in Box 1 lead to similarly devastating results.

The mathematical concept most adequate for the study of this phenomenon is community permanence. A community is permanent if no population ever drops below an arbitrary but fixed positive threshold, except for initial transients, and all populations remain bounded from above, independent of initial conditions. However, for the sake of simplicity, theorists often consider instead community feasibility (existence of a fixed point where all populations are positive) or the linear stability of feasible fixed points. The three concepts are related: Linearly stable communities are typically permanent, and all permanent communities have a feasible fixed point.

What follows is a critical discussion of possible explanations for these difficulties in building realistic, stable population-dynamical food-web models and of suggestions that have been made to overcome these. Efforts have been made to cover the most important ideas, yet the list is not complete.

IV.B Self-limitation of populations

Trophic interactions are not the only factors limiting population growth. For basal species (species not feeding on others), this is obvious. But even consumer population dynamics will be affected by non-trophic factors, such as the spread of diseases or competition for suitable breeding space. In models, such effects are generally captured by self-limiting, density-dependent contributions to the population growth rate (intraspecific competition). In the Jacobian matrix computed at a community fixed point (controlling linear stability, see Stability Analysis), these self-limiting terms lead to negative contributions to the diagonal, which stabilize the system. The magnitude of these diagonal contributions required to achieve linear stability has been used as a measure of system stability (*diagonal strength*).

One finds that substantial intraspecific competition is required to stabilize large food-web models by this mechanism alone. The question whether in nature self-limitation of sufficient magnitude regularly occurs appears to be open. In agriculture, population densities much higher than naturally observed can be reached simply by providing sufficient food and protection from natural enemies. Besides, one needs to ask for any mechanism of non-trophic self-limitation whether the same mechanism could also mediate competitive interactions with other, similar species, in which case this mechanism would equally contribute to destabilizing a community as it helps stabilizing it.

IV.C Adaptive foraging

In laboratory studies, consumers that are let to feed on two kinds of resources often feed disproportionately more on the more abundant resource (*adaptive foraging, prey switching*). The reasons can be active behavioural adaptation by the consumer, or passive mechanisms such as shifts in the consumer's feeding grounds. Evolutionary adaptation can have similar effects, too. Independent of the mechanism, the phenomenon leads to a release of rare species from predation pressure. Species that would otherwise go extinct can survive at low abundances. Adaptive foraging therefore stabilizes communities.

However, foraging adaptation appears difficult to measure in the field, leaving the question open how much of this effect should realistically be allowed in models. Besides, current representations of adaptive foraging in food-web models often do not allow for switching to become weaker for pairs of very similar resources, an unlikely feature, which effectively disables competitive exclusion through indirect competition.

IV.D Sparse food webs

In food-web models with self-limitation, stability breaks down when the link density becomes too large, unless other, stabilizing model elements are included. With respect to linear stability, this effect was mathematically explained in 1972 by Robert May. Later simulation studies demonstrated a similar constraint for community persistence. It appears as yet unclear if this phenomenon prevails in food-web models without self-limitation. Empirically, the question if there is a natural limit on link density is unsettled. A large number of studies indicate that link density increases with food-webs size, but these studies have been criticised for insufficiently taking account of known biases in empirical data.

IV.E Slow consumers

The larger the typical body mass M of a species, the slower its physiological and ecological dynamics are. Ecologically relevant rate constants of dimension 1/Time, such as consumption rates, respiration rates or maximal Malthusian growth rates, are known to scale approximately as $M^{-1/4}$ (allometric scaling).

Consumers are often larger than their resources. As a result, ecological processes are slower for consumers than for their resources. When defined appropriately, trophic link strength therefore decreases towards higher trophic levels. This pattern has been shown to stabilize community dynamics and to enhance the likelihood of feasible communities. Randomization of link strengths in model food webs exhibiting this pattern, leaving only the overall distribution of link strengths intact, drastically destabilizes these food webs. Further, it has been shown that for consumer-resource body-mass ratios above 10-100, typical for the observed range of values, this stabilization is particularly efficient.

IV.F Stable trophic modules

When analyzing certain three-species sub-graphs found in food webs in isolation, i.e., ignoring their interactions with the rest of the web, they are found to be stable (or feasible) more often than expected by chance. It is unlikely that this pattern is simply a consequence of the "slow consumers" pattern described above. Thus, stable trophic modules appear to be an independent phenomenon contributing to food-web stability. This is confirmed by studies directly relating the relative frequency of modules to the stability of random food webs.

IV.G Weak links

Relatively weak trophic links can damp destabilizing oscillations in food webs, that is, when removing these links oscillations become stronger. While this effect is important, it is often overinterpreted to the extent that any weak trophic link would be stabilizing. Simulations by McCann, Hastings and Huxel (Nature, 1998, 395:794-798), for instance, show that a minimum link strength is required. The broader question if specific link-strength distributions contribute to stabilization or destabilization of food webs or emerge from stability constraints requires more research.

IV.H Assembly and evolution

Population-dynamical food webs emerging in assembly models with or without an evolutionary component tend to be substantially larger and more complex than model food webs of the same type obtained by first fixing links and abundances according to some (partially) random algorithm and then simulating dynamics until a persistent community remains. Apparently, assembly selects a set of particularly stable food webs among the set of all possible webs. The particular structural features selected for remain unidentified. Food webs tend to *saturate* in assembly processes, that is, a state is reached in which the perturbations of the community resulting from the invasion of one species lead, on average, to the extinction of one species. There are indications that such saturated states have particular dynamical properties combining fast and slow relaxation processes.

It is plausible to conjecture that natural communities are in such saturated states, too. This would explain the persistent difficulties to reproduce food-web stability in models, without offering an immediate solution. Because in saturated communities populations co-exist in a delicate ecological balance, models of such communities, unless reproducing population dynamics to very high fidelity, would not be persistent or, after adding stabilizing model elements, be more stable than in reality. Recent observations do indeed indicate that natural communities saturate due to limits to coexistence. However, conclusive evidence linking these observations to community saturation in food-web assembly models appears to be missing.

Glossary

Adjacency matrix: (Food-web matrix) Representation of a food web's topology by a matrix $\mathbf{A} = \{A_{ij}\}$. Rows and columns of this matrix correspond to the food web's member species in their roles as resources and consumer, respectively. A matrix element A_{ij} is set to 1 when species j feeds on species i and to 0 otherwise. That is, by convention, the first index (row) refers to the resource, the second index (column) to the consumer.

Basal species: A species that does not feed on other species. Basal species play an exceptional role in food webs because they link the communities to extrinsic energy inputs and therefore require different descriptions of their population dynamics.

Consumer: A species in its role of feeding on other species.

Connectance: Proportion of combinatorically possible links realized. Precise definitions vary. Nowadays, the directed connectance $C = (\text{number of links})/(\text{number of species})^2$ is generally used.

Foraging trait: Trait determining a species' role as consumer.

Interaction strength: This notion encompasses trophic link strengths but is used also for quantitative characterizations of indirect interactions between species, mediated by other species and non-trophic effects (e.g. density-dependent growth of basal species).

Link density: The ratio $Z = (\text{number of links})/(\text{number of species})$ in a food web.

Resource (food webs): A species in its role of being fed on.

Trophic link: A resource-consumer feeding relationship.

Trophic link strength: Quantitative measure for the strength of direct consumer-resource interactions. Common are measures based on biomass flows between resources and consumers, potentially normalized to resource and/or consumer abundances. Because of their easy empirical accessibility through stomach/gut-content analysis, the proportional contributions of resources to the diets of consumers (*diet fractions*) are also frequently used. Other measures of link strength are defined in terms of parameters in models for functional or numerical responses to multiple resources. However, these measures can be difficult to related to empirical data.

Trophic species: A term emphasizing the fact that in empirical food webs the nodes ("species") can represent groups of similar species, life stages, or dead matter such as detritus. To reduce biases by these simplifications, data and model outputs are sometimes standardized by systematically lumping trophically similar network nodes into trophic species when comparing food-web topologies.

Trophic traits: Foraging and vulnerability traits.

Vulnerability trait: Trait determining a species' role as resource.

See also

Allometry and Growth

Assembly Processes

Food Chains and Food Web Modules

Foraging Behavior

Networks, Ecological

Predator-Prey Models

Stability Analysis

Two-Species Competition

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