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Authors

Borer, Elizabeth T
Anderson, Kurt
Blanchette, Carol A
et al.

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Topological approaches to food web analyses: a few modifications may improve our insights

Elizabeth T. Borer, Kurt Anderson, Carol A. Blanchette, Bernardo Broitman, Scott D. Cooper and Benjamin S. Halpern, Dept of Ecology, Evolution, and Marine Biology, Univ. of California, Santa Barbara, CA 93106, USA (borer@lifesci.ucsb.edu). – Eric W. Seabloom and Jonathan B. Shurin, National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA.

The topological analysis of food webs is a recently reinvigorated and rapidly growing area of inquiry in community ecology (Williams and Martinez 2000, Solé and Montoya 2001, Camacho et al. 2002, Montoya and Solé 2002). Topological studies assess system properties using the number and distribution of connections among nodes in an interconnected network. Analysis of a food web as a network of links (feeding relationships) and nodes (species) is not a new approach (MacArthur 1955, Gardner and Ashby 1970, Pimm 1979); however recent advances by physicists in the study of complex networks have revived this area of theoretical community ecology. Here we discuss a few characteristics of food webs that may cause them to respond differently to node loss than other types of networks. We also suggest ways in which empiricists can provide data to test predictions derived from complex network theory.

Complex network analysis has shown that the sensitivity of a network to node loss depends on the frequency distribution of connections among nodes (Albert et al. 2000). Current theoretical developments suggest that networks can be classified into two broad categories based on the frequency distribution of links: exponential or scale-free. Each node in an exponential network has a similar number of links to other nodes. The frequency distribution of the number of links per node in this type of network has an exponential decay (Albert et al. 2000). Because nodes in an exponential network have similar numbers of links, the loss of any given node from this type of network causes a monotonic increase in the number of links required to connect any two nodes in the network. In contrast, a scale-free network has a few nodes with a large number of links and many nodes with only a few links. Although connectivity in scale-free

networks does not decrease with the random loss of nodes as in an exponential network, scale-free networks are extremely sensitive to the loss of highly connected “hub” nodes (Albert et al. 2000). In recent work, researchers have used frequency distribution models to describe the properties of a broad array of complex networks such as social networks (Watts and Strogatz 1998), the World Wide Web (Albert et al. 1999), transportation networks (Banavar et al. 1999), and enzymatic pathways (Jeong et al. 2000).

The obvious extension of this theory to food web dynamics has renewed interest in the topology of trophic webs. Williams and Martinez (2000) show that a simple topological model can reproduce properties of complex food webs. But when we examine empirical webs, does the frequency distribution of trophic connections show a general pattern? If so, is the structure of food webs generally exponential or scale-free? A recent assessment of several food webs suggests that they share the scale-free properties of many other complex networks, implying that their structure should be resistant to random attacks but quite sensitive to loss of “hub” species (Solé and Montoya 2001).

The general applicability of recent findings in complex network theory to food web studies depends on whether topological descriptions capture key aspects of communities and ecosystems such as the flow of energy or factors regulating populations. An increase in biological realism may be merged with suitable data in future food web analyses to better understand processes structuring communities. Further work in this area will allow us to determine the appropriate role of complex network theory in the modeling and conservation of ecological communities.

In addition, future advances in community ecology that develop from network theory depend on successful communication between theoreticians and empiricists. In particular, although theoreticians must determine whether the observed structure of food webs supports existing theory, empiricists must recognize and provide information appropriate for parameterizing and testing theoretical models. Complex network theory may provide an avenue for collaboration between theoreticians and empiricists that could lead to rapid advances in our understanding of ecological communities.

Directionality

Trophic webs, unlike other networks that have been studied, have different types of nodes: those that require a network to persist (heterotrophs) and those that can persist without a trophic network (autotrophs). The connection of heterotrophs to autotrophs is critical to the maintenance of a multi-level trophic web (Polis 1999), and incorporating this directionality is crucial for using food web network structure to predict heterotroph extinctions. The effect of direct trophic interactions on autotrophs is more complex. A consumer may suppress or eliminate an autotroph in a community, in which case the autotroph would persist in (and benefit from) the absence of that consumer. Alternatively, the autotroph may persist in its community because of indirect suppression of other autotrophs by a shared consumer, in which case the autotroph might go extinct because of the loss of its consumer. The “bottom-up” and “top-down” literature in ecology is rooted in this inherent directionality of community webs.

In a simple bottom-up scenario, we might expect more species extinctions if primarily autotrophs were extirpated from a community than if an equal number of predator species were removed. In this case, species extinction and energy transfer depend on the directional flow of nutrients from resources to consumers. This pattern of extinctions was predicted by MacArthur (1955) and has been observed in model food web studies (Pimm 1979, Borrvall et al. 2000). It is not a surprising prediction given the dependence of consumers on their resources, but this dependence has plagued empirical studies attempting to look at the effects of randomly removing trophic levels (Huston 1997).

Consumers often mediate the coexistence of autotrophs, however, so incorporation of heterotroph–autotroph (top-down) interactions is also important for topological assessments of species persistence (also see Non-trophic links, below). For example, the removal of a heterotroph that mediates coexistence among autotroph competitors may cause autotroph extinctions via competitive exclusion. Predator-mediated coexis-

tence and apparent competition, for example, are common in ecological communities (Paine 1966, Holt 1977, Caswell 1978, Schmitt 1987, Shurin 2001). These examples show that autotrophs may or may not persist following the extinction of a consumer, but non-directional network theory would incorrectly predict that the removal of a consumer would cause all of the autotrophs eaten solely by that consumer to go extinct.

Directionality is an area in which food web theorists could make the largest strides, because empirical data on consumer–resource relationships are readily available. Initial investigations into the effects of food web directionality on complex network stability have begun (Camacho et al. 2002), but further work is necessary to gain insights into the factors structuring communities.

Linkage strength and species abundance

The variable magnitudes of trophic links and nodes must be examined by both food web empiricists and complex network theoreticians. For example, a species may consume multiple resources, yet derive most of its nutrition from only one. Links in food webs are highly variable in terms of energy flow or consumer impacts on resource species, therefore the number of links alone may not describe well the interdependence of species. Yook et al. (2001) have shown that the incorporation of variable linkage strength may obscure underlying network patterns.

Incorporating linkage strength in topological food web analyses may improve our understanding of several important issues in community ecology. Network analysis that considers interaction strength may allow us to identify keystone species whose impacts on their communities are disproportionately large relative to their abundances (Power et al. 1996). For example, a keystone species may have one strong trophic link to another species with many trophic links (Pimm 1980 i.e., it may attack a “hub” species in the network). If a community has a scale-free distribution, loss of a highly connected species should have a disproportionately large impact on the network (Albert et al. 2000, Jeong et al. 2001). Alternatively, the impact of the loss of a keystone species on other species may not be predicted well by the number of its trophic connections to other species. We also may find trophic cascades, for example, only in systems with strong vertical trophic links between consumer and resource species, but not in more reticulate or diffusely linked systems (Polis and Strong 1996, Polis 1999).

In addition, species’ abundances are generally distributed in a log-normal fashion within a community (Preston 1962), so species (nodes) do not represent a uniform number or density of individuals. A species’ extinction risk, and the impact of its loss on the rest of

the community, is related to both its abundance and position within the network. Rare species are most at risk of extinction (Preston 1962, Schoener and Spiller 1992), so we can explore the extinction risk of a species as a function of its abundance as well as a function of its position in, and connections to, the network. The mechanism maintaining a species' low abundance will determine the fate of that species when others are removed from the community network (Kunin and Gaston 1997). For example, a strongly self-limited species is inherently rare and will remain at high extinction risk regardless of the fate of other species. In contrast, a species maintained at low abundance through predation will likely increase in abundance with the removal of its predators (Terborgh et al. 2001). In addition, population size is often inversely related to trophic positions as predators are generally less abundant than their prey (Carbone and Gittleman 2002). Predators may be more vulnerable to extinction than species in lower-trophic positions, and loss of species from a network may therefore follow a non-random order. Variable node magnitudes may affect our ability to use complex network theory to identify underlying network patterns, as do variable linkage strengths (Yook et al. 2001).

For significant advances in food web theory, however, quantification of both absolute and relative trophic linkage strength in real communities will be a major challenge facing empiricists. Recently, Berlow et al. (1999) reviewed several methods empiricists have used to measure linkage strength (or "interaction strength"), and emphasize that only a few empirical studies have quantified interaction strength in a way that can provide model parameter estimates appropriate to food web theory. In particular, they point out discrepancies between the representation of linkage strength in food web models and the ways in which linkage strengths are measured by empiricists (see also Laska and Wootton 1998, Osenberg et al. 1999). Osenberg et al. (1997, 1999) and Berlow et al. (1999) provide an overview of the shortcomings and advantages of the current methods for measuring interaction strength, and their work may encourage future advances that merge food web theory with appropriate and rigorous empirical measures of the strengths of trophic links.

Non-trophic links

Trophic links are only one type of connection between species in food webs. Although food webs are the most complete ecological network descriptions available, the ecological literature clearly demonstrates the importance of other types of interactions in structuring communities (Hay and Taylor 1985, Soluk 1993). Habitat modification, territoriality, behavioral avoidance, and

interference competition are only a few of the non-trophic links that affect the structure of communities.

Incorporating the strength of non-trophic links into topological food web analyses may allow a more robust assessment of each species' impact on its community. For example, consumers promote the coexistence of resource species in many communities via non-trophic mechanisms such as habitat structuring or the rapid recycling of nutrients (Jones et al. 1997). Empirical ecologists have found that non-trophic interactions play a large role in community dynamics yet, at present, empiricists only have case studies of the impacts of these interactions on communities. We do not know how non-trophic links are distributed in most communities (e.g. are they exponential or scale-free?) or the role they play in stabilizing or destabilizing the community network. Although the definition of keystone species is controversial (Hurlbert 1997), the removal of some species has an unexpectedly large impact on the whole community (Power et al. 1996). Food web theoreticians can assess the trophic and non-trophic network structure of communities that contain these "important" species (*sensu* Hurlbert 1997), to determine whether communities with (or without) these species share a common network structure.

The way that non-trophic interactions are incorporated into food webs depends on the type of non-trophic interaction (Wootton 1994). For example one species can have direct, non-trophic effects on another through facilitation or interference competition. Because the abundance of the secondary species is affected by the first, these interactions can be represented by links between the two species and may have positive (e.g. facilitation) or negative (e.g. interference competition) signs. On the other hand, a species may affect direct interactions between two other species, even if it is not trophically linked to either (i.e. it may act solely as an interaction modifier). The direction and strength of the interaction between the two trophically interacting species depends on the presence of the interaction modifier species. Thus, loss of a species may completely reconfigure the direction or strength of trophic *and* non-trophic interactions in a food web. Interaction modifications primarily illustrate problems with making predictions about dynamic systems from static food web models, and emphasize that predictions based on the structure of the original food web (i.e. with the interaction modifier) may have little applicability to the new situation (i.e. lacking the modifier species).

Quantifying the strength of non-trophic interactions poses a serious challenge to empiricists and is an underdeveloped aspect of food web ecology. Although Power et al. (1996) and Paine (1992) attempted to quantify the overall "importance" of a species in its community, both proposed measures have been criticized (Hurlbert 1997). Empiricists will need to develop appropriate methods for measuring non-trophic interactions that

allow parameterization of food web models before food web ecology can make significant advances in this area. The complexity of modeling non-trophic links among species provides an excellent opportunity for collaboration between empiricists and theoreticians.

Definition of a node

Superficially, nodes in ecological networks seem simple to define: each node represents a species. But the appropriate definition of a node continues to plague food web research (Yodzis and Winemiller 1999). Many published food webs include nodes that combine vast numbers of species (e.g. plankton, detritus, algae, or fungi) (Savelly 1939, Menge et al. 1986, from Cohen 1989). Combining species into unresolved groups has occurred for a variety of reasons. Splitting the group into individual species may be intractable or unnecessary for the particular study. Investigators may combine species because they share the same resources and the same predators so their trophic roles are functionally equivalent ("trophic taxa," sensu Martinez 1991). Alternately, the focus of a particular study may have been on an exhaustive description of all species in a particular group, but with a less comprehensive list of the focal group's predators and prey. Few empirical food webs have been described with the explicit goal of parameterizing or testing food web theory, thus most theoreticians in food web ecology have relied on web descriptions that are not well suited to their analyses (Martinez 1991).

The best definition of a node will vary with the question at hand, but the implications of this definition should be considered carefully by both empiricists and theoreticians. For example, if we define each node as a "trophic taxon" rather than resolving each individual species, we ignore potentially important non-trophic differences among the individuals in these trophic groupings (e.g. species abundance, facilitative interactions, non-trophic links). Theoreticians can guide empiricists by determining the level of detail necessary to parameterize specific food web questions. Defining nodes and providing adequately detailed, quantitative data are areas of food web research in which efficient feedback between empiricists and theoreticians may provide a means for coordinated advances in the field.

Conclusion

Much remains to be learned about factors structuring communities from observed patterns and phenomena in ecological communities. Exploring the importance of linkage directionality, linkage strength, and linkage type in analyses of community networks will be a

valuable step in understanding the applicability of recent advances in complexity theory to community ecology. A topological approach, modified to incorporate some basic biological realism, may provide a framework for understanding community properties resulting from patterns of species interactions. Combined with appropriate empirical data and careful definitions of nodes, complexity theory may provide a vehicle for rapid progress in food web ecology.

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