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which the processes of interest unfold. For processes such as information diffusion, which unfold over hours or days, stable relationships such as kinship or friendship ties [with turnover times on the order of years (28)] may be approximated as essentially static. Such networks cannot be fixed in a life-cycle context, however, in which one's time scale of interest may span several decades. Likewise, the dynamics of rapidly evolving networks [such as radio communications during emergencies (Fig. 1C) (29)] are of potential importance even for fast-moving processes, such as information exchange. Failure to consider dynamics can lead to extremely misleading results.

A useful example of where static representations can go awry is provided by the case of HIV diffusion. Studies of sexual behavior generally find that the number of sexual partners possessed by a given individual over a fixed period of time is skewed (the mean is farther out in the long tail of the distribution than is the median) (30). Early studies of the behavior of simple diffusion processes on networks with extremely skewed [specifically, power-law (31)] degree distributions strongly suggested that epidemic potentials for HIV and similar sexually transmitted diseases were primarily governed by the behavior of a small number of individuals with large numbers of sexual contacts (32, 33). This conclusion was of considerable practical import because it implied that only hub-targeted strategies were likely to prove efficacious in reducing epidemic thresholds (31, 32). Although the applicability of the power-law degree model to these networks has since been questioned (30, 34), equally important is the assumption that the time-aggregated network of sexual contacts was an effective model for HIV diffusion. The timing and duration of relationships are critical factors in the susceptibility of the dynamic network to disease transmission (35), factors that are hidden by the time-aggregated representation. This can be seen in Fig. 1D; for a given network, everyone may become infected or no one may be infected, depending on the edge duration and time of onset.

Studies of diffusion on dynamic networks suggest that partnership concurrency is also an important predictor of epidemic potential; uniformly low-degree networks potentially support epidemics when relationships are long and coterminous, and networks with high-degree nodes often fail to support epidemics when relationships are short and sequential (35–37). Interventions aimed at minimizing concurrent links are not necessarily the same as hub-targeted strategies, and thus the public health recommendations that follow from a dynamic network analysis may differ from those that would seem reasonable based on the assumption of a static, time-aggregated network.

Although HIV diffusion is a compelling example, it should be emphasized that similar issues can arise in systems as apparently different as radio communication (Fig. 1C) and peer-to-peer networks. Recent work in the latter area, for instance, has emphasized the impact of the entry and exit of

network members (or “chum”) on system performance (38); in this case, edge dynamics (potential and actual data transfers) can be understood only by taking into account the dynamic nature of the set of nodes.

Conclusion

To represent an empirical phenomenon as a network is a theoretical act. It commits one to assumptions about what is interacting, the nature of that interaction, and the time scale on which that interaction takes place. Such assumptions are not “free,” and indeed they can be wrong. Whether studying protein interactions, sexual networks, or computer systems, the appropriate choice of representation is key to getting the correct result.

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PERSPECTIVE

Disentangling the Web of Life

Jordi Bascompte

Biodiversity research typically focuses on species richness and has often neglected interactions, either by assuming that such interactions are homogeneously distributed or by addressing only the interactions between a pair of species or a few species at a time. In contrast, a network approach provides a powerful representation of the ecological interactions among species and highlights their global interdependence. Understanding how the responses of pairwise interactions scale to entire assemblages remains one of the great challenges that must be met as society faces global ecosystem change.

Network approaches to ecological research emphasize the pattern of interactions among species (the way links are arranged within the network) rather than the identity of the species composing a community (the nodes of the network of interactions). The idea of a complex network of interactions among species is as old as Darwin's contemplation of the tangled

bank, showing the importance of networks in ecology (1). Despite this early realization, however, networks have only recently been incorporated into mainstream ecological theories. The “web of life”

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model depicts the global interdependence among species (Fig. 1A) and, from a basic point of view, complements theories on biodiversity that have either neglected species interactions or assumed that they are homogeneously distributed across species.

The network approach benefits from tools and concepts imported from other fields such as physics and sociology. This flow of ideas has allowed us to compare ecological networks with protein interaction networks or connectivity within Internet communities. A comparative framework is useful because it suggests that there are very general mechanisms underlying network formation. Furthermore, the identification of common architectures, robust in the face of perturbations regardless of specific details, may also emerge from such studies.

The Architecture of Biodiversity

Food webs are central to ecology, as a way to describe and quantify the complexity of ecosystems (2–7) by connecting the trophic interactions among species in a community. Large networks are built from combinations of smaller motifs; a motif is a pattern of overrepresented interrelations among nodes relative to equivalent randomizations of the network (8) (Fig. 2). Empirical food webs, for example, show a consistent overrepresentation of tri-trophic food chains (in which a predator eats a consumer which in turn eats a resource; Fig. 2A), whereas omnivory (the predator eats both the consumer and the resource; Fig. 2B) is overrepresented in a majority of food webs but underrepresented in some (9). How these motifs combine into larger networks (Fig. 2C) may influence the stability of the overall network, as suggested by Robert May on theoretical grounds (5). The search for empirical evidence of this theory is a currently active area of research (10). Analyses of food web motifs have also been extended to include quantitative information such as the strength of the interactions (11) and body mass ratios (12) between predators and their prey.

More recently, ecologists have studied interactions beyond predator-prey webs to include mutually beneficial interactions, such as those between plants and their animal pollinators or seed dispersers. These interactions play a major role in the generation and maintenance of biodiversity on Earth (13) and organize communities around a network of mutual dependences (Fig. 1A). Such mutualistic networks are (i) heterogeneous, in which the bulk of species interact with a few species, and a few species have a much higher number of interactions than would be expected from chance alone; (ii) nested, in which specialists interact with a subset of the group of species that generalists interact with; and (iii) built on weak and asymmetric links among species (for example, in some cases when a plant interacts strongly with an animal, the animal tends to depend less on the plant) (14). Therefore, mutualistic networks are neither randomly organized nor organized in isolated compartments, but built cohesively around a core of generalist species.

Groups of species coevolve in time and space (13), and the study of this phenomenon has been facilitated by a network approach. If these groups of species and their interactions are overrepresented in the network, they can be considered to be motifs, in which case they are the basic building blocks from which we can scale up to full networks. These motifs often vary and develop in predictable ways among ecosystems, resulting in a well-defined geographic mosaic of coevolution (13). Two frequently assumed misconceptions arose from non-network analysis of coevolution: first, that coevolution leads toward highly specific, direct one-on-one interactions; and second, that coevolution within species-rich communities generates diffuse assemblages that are intractable to generalization. The documentation of geographically varying network motifs and the determination of well-defined structures of large networks are dispelling these assumptions.

Architecture Influences Robustness

Without an understanding of the structure of ecological networks, we cannot assess the robustness

of networks to species extinctions, habitat loss, or other anthropogenic influences. Models of such networks have led to the prediction that the random extinction of species will result in coextinction cascades among remaining species because of a loss of resources. In such simulations, food webs are found to be robust to the random extinction of species, but rely on a few well-connected species that act as glue keeping the whole network together. If these key species disappear, it is expected that the entire network will collapse very rapidly (7, 15, 16).

Such simulations have looked specifically at the number of species, but not at their identity. The next step was to superimpose the phylogenies of the plants and animals on the network of interactions. Phylogenetic relatedness (for example, species belonging to the same genera) partly explains the patterns of interactions between species (17). As a consequence, coextinction avalanches tend to involve taxonomically related species, which may lead to a nonrandom pruning of the evolutionary tree and a faster erosion of taxonomic diversity (17). Related to this, coex-

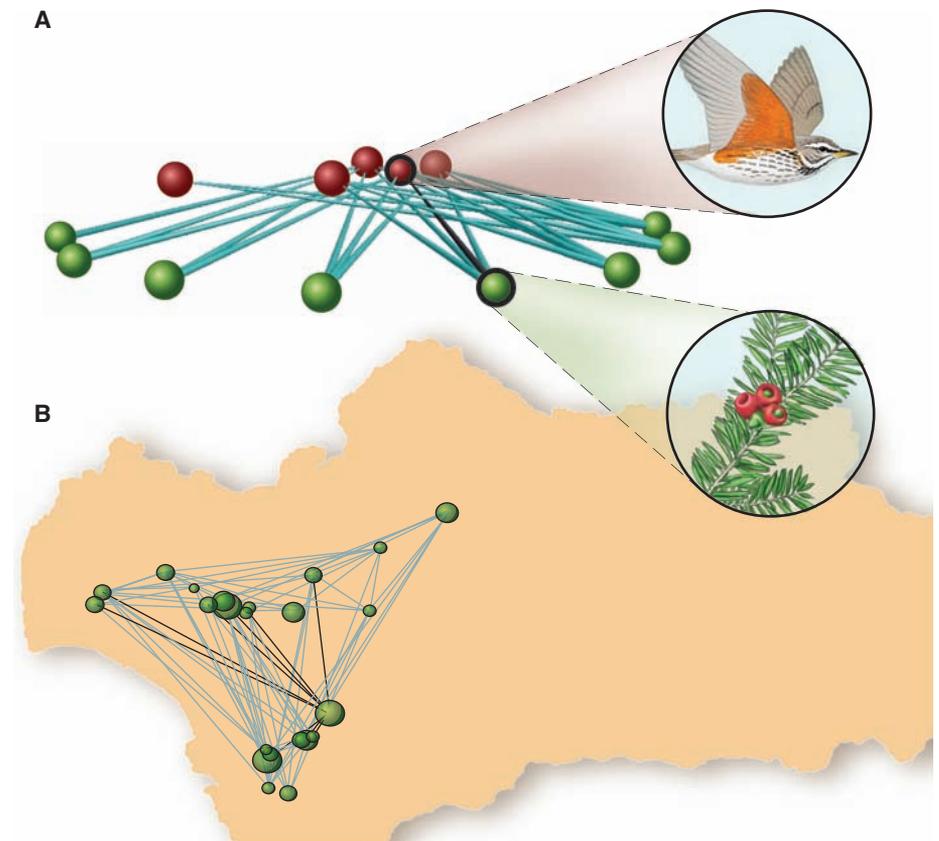


Fig. 1. The web of life is a powerful representation encapsulating ecological connectivity among elements. Examples of ecological networks illustrate how to scale from pairwise interactions to the entire assembly: (A) a plant-animal mutualistic network depicting the interactions of mutual benefit between plants and their seed dispersers and (B) a network of spatial genetic variation across habitat patches in a heterogeneous landscape inhabited by a Mediterranean plant. Studies such as (A) focus on coevolution at a community scale and set the foundation for predicting how global change will propagate through such networks. Studies such as (B) provide a framework to address the simultaneous influence of all patches on gene flow and quantify the importance of a single patch for the persistence of the entire metapopulation.

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Pushing Networks to the Limit

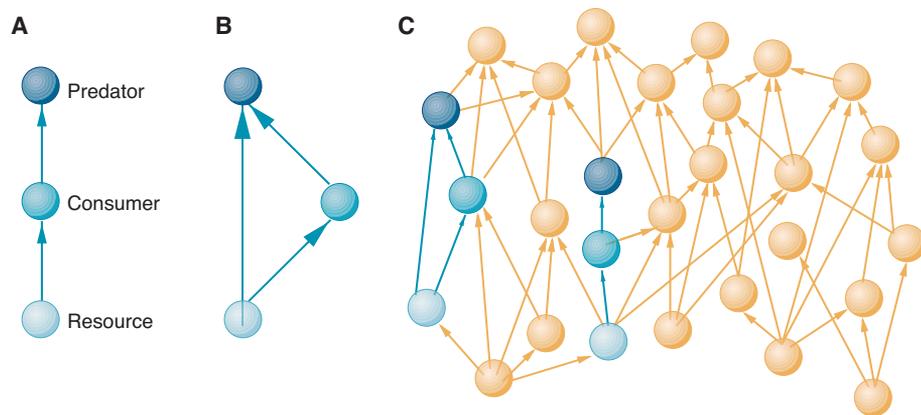


Fig. 2. The basic building blocks of ecological networks. **(A and B)** Two trophic modules: a tri-trophic food chain **(A)** and an omnivory chain **(B)**, which have been the subject of dynamical analyses. Some of these modules can be overrepresented in entire networks, in which case they are considered network motifs **(C)**. Future studies hopefully will assess to what extent the stability of an entire network is explained by the stability of its basic blocks.

Extinction cascades in food webs tend to involve species that are trophically unique; that is, that tend to be eaten by a set of predators and/or eat a set of prey with little overlap with other species in the community (18). Therefore, trophic diversity—the range of trophic roles played by species—decreases faster than would be expected on the basis of looking only at the number of coextinct species (18). Future studies should now complement these simulations of coextinction cascades by mapping the loss of ecosystem services that a species performs (19), such as pollination or biological control.

One topological way of simulating the consequences of species extinction assumes that species are fixed nodes without dynamics. The alternative is to use population dynamic models for each species. Traditionally, the dynamic approach has been performed with the most basic descriptions of trophic interactions, such as a tri-trophic food chain (Fig. 2A). These basic descriptors of trophic interactions, known by theoreticians as trophic modules, provide a bridge between the complexity of entire communities and the simplicity of pairwise interactions (20). Indeed, trophic modules can be represented mathematically on the basis of the abundance of each species and how each is affected by the abundance of other species, which may be predators or prey. However, there is still a wide gap between the stability of these simple models of trophic interactions and that of the entire food web.

To reduce such gaps, network motifs provide a means by which to assess the most important trophic modules on the basis of their relative frequency within a food web. Modules that are overrepresented (motifs) tend to be most relevant to understanding food web dynamics (9–11). However, we cannot assume that the stability of the entire network can be deduced from the stability of its component parts, because the sum of the parts does not add up to a complete network.

Thus, we need studies to add to our comprehension of the stability of entire food webs.

Recently, ecologists have analyzed the dynamics of large food web models. Two ingredients characterize these models. First, they incorporate realistic interaction networks among dozens of species occupying several trophic levels (6, 7). Second, they use realistic estimates of species body sizes and metabolic rates (21), in contrast with traditional Lotka-Volterra models, in which parameters are assigned randomly. With these models, researchers have explored the stabilizing role of network properties, such as the observed body size ratios between predators and their prey (12), and predicted the effects of species removal on the abundance of the remaining species (22). The accuracy of these predictions increases with the size of the food web, so that the more complex the food web, the simpler the prediction of the consequences of species extinctions (22).

Architecture Influences Network Size

Network structure can affect not only the robustness of a given network (at what rate biodiversity will be lost) but its original size (how many species can be supported to begin with). Extensions of theory testing the roles of competition and mutualistic interactions in determining the maximum number of species that can stably coexist (23) showed the potential increase in species richness resulting from the architecture of mutualistic networks. For any given number of interactions, the nested structure of mutualistic networks maximizes the number of coexisting species (23). For example, two plant species that compete to attract shared pollinators gain when they coexist because more pollinators are attracted to the area by the total number of available flowers. In such cases, there is a balance between the opposing forces of competition and facilitation, which depends on the structure of the mutualistic network (23).

To properly study the relationship of network architecture to function, three challenges need to be faced. First, models need to be developed incorporating both how population dynamics affect network topology and how topology affects dynamics (6). Second, analyses of networks need to incorporate multiple interaction types, because it is probable that stability is related to how multiple interaction types function in combination (23). This may be particularly relevant if mutualistic and antagonistic effects are nonadditive, because until now networks have primarily been studied independently (24). Third, species invasions, climate change, and other current challenges to ecological and environmental systems will require a network focus because multiple species are likely to be perturbed in face of the many ongoing changes at both the local and global scales (25). For example, mutualistic pollination networks have demonstrated that such networks appear to facilitate the integration of invasive plant species and that the structure of the network also seems to buffer the consequences of such invasions (26).

Beyond Species Interactions

The application of networks in ecology is not restricted to species interactions but can also be applied to population dispersal across heterogeneous landscapes. For example, a node can be a patch of available habitat, and a link connecting two such patches can indicate the movement of individuals or genes. As habitat modification transforms continuous habitat into islands of disjointed patches (Fig. 1B), the regional persistence of a species inhabiting such a fragmented landscape will be determined by the balance between local extinction and migration among local patches (27). Indeed, networks may be a simplified representation of heterogeneous landscapes even in cases where parametrizing demographic data is not possible. The topology of these networks provides information about the relative importance of individual patches to the overall landscape connectivity. For example, network theory has been applied to the endangered Mexican spotted owl by mapping the discrete patches of original habitat as the nodes and using information on maximum dispersal distances to assess whether two such patches are potentially linked. This representation leads to the prediction that this species will survive even if substantial habitat transformation occurs, as long as a subset of the network of habitat patches is preserved (28).

Additionally, such methods can be used to visualize and analyze networks of genetic variation in space (Fig. 1B). Traditional approaches use the summary of pairwise effects of one population on another, but the network approach makes it possible to fully address the simultaneous influence of multiple local populations in shaping genetic variability (29). Finally, when network theory is applied to population biology,

it can address the inherent heterogeneity in who meets whom. This application can be extended to social networks as a way to estimate the spread of disease (30) and the evolution of cooperation (31) in heterogeneous societies.

Conclusions

Networks are useful descriptors of ecological systems that can show the composition of and interactions between multiple elements. The application of networks to ecosystems provides a conceptual framework to assess the consequences of perturbations at the community level. This may serve as a first step toward a more predictive ecology in the face of global environmental change. Networks are also able to introduce heterogeneity into our previously homogeneous theories of populations, diseases, and societies. Finally, networks have allowed us to find generalities among seemingly different systems that, despite their disparate nature, may have similar processes of formation and/or similar forces acting on their architecture in order to be functional. Although we have only begun to understand how changes in the environment affect species interactions and ecosystem dynamics through analyses of simple pairwise interactions, network thinking can provide a means by which to assess key questions such as how overfishing can cause trophic cascades, or how the disruption of mutualisms may reduce the entire pollination service

within a community (25). As the flow of ideas among seemingly unrelated fields increases (a characteristic attribute of research on complex systems), we envision the creation of more powerful models that are able to more accurately predict the responses to perturbations of food webs, a major challenge for today's ecologist.

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PERSPECTIVE

A General Framework for Analyzing Sustainability of Social-Ecological Systems

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A major problem worldwide is the potential loss of fisheries, forests, and water resources. Understanding of the processes that lead to improvements in or deterioration of natural resources is limited, because scientific disciplines use different concepts and languages to describe and explain complex social-ecological systems (SESs). Without a common framework to organize findings, isolated knowledge does not cumulate. Until recently, accepted theory has assumed that resource users will never self-organize to maintain their resources and that governments must impose solutions. Research in multiple disciplines, however, has found that some government policies accelerate resource destruction, whereas some resource users have invested their time and energy to achieve sustainability. A general framework is used to identify 10 subsystem variables that affect the likelihood of self-organization in efforts to achieve a sustainable SES.

The world is currently threatened by considerable damage to or losses of many natural resources, including fisheries, lakes, and forests, as well as experiencing major reductions in biodiversity and the threat of massive climatic change. All humanly used resources are embedded in complex, social-ecological sys-

tems (SESs). SESs are composed of multiple subsystems and internal variables within these subsystems at multiple levels analogous to organisms composed of organs, organs of tissues, tissues of cells, cells of proteins, etc. (1). In a complex SES, subsystems such as a resource system (e.g., a coastal fishery), resource units (lobsters),

users (fishers), and governance systems (organizations and rules that govern fishing on that coast) are relatively separable but interact to produce outcomes at the SES level, which in turn feed back to affect these subsystems and their components, as well other larger or smaller SESs.

Scientific knowledge is needed to enhance efforts to sustain SESs, but the ecological and social sciences have developed independently and do not combine easily (2). Furthermore, scholars have tended to develop simple theoretical models to analyze aspects of resource problems and to prescribe universal solutions. For example, theoretical predictions of the destruction of natural resources due to the lack of recognized property systems have led to one-size-fits-all recommendations to impose particular policy solutions that frequently fail (3, 4).

The prediction of resource collapse is supported in very large, highly valuable, open-access systems when the resource harvesters are diverse, do not communicate, and fail to develop rules and norms for managing the resource (5). The dire predictions, however, are not supported under conditions that enable harvesters and local leaders to self-organize effective rules to manage a resource

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