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OXFORD BIBLIOGRAPHIES IN “ECOLOGICAL NETWORKS”

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Introduction

In any given ecological community individuals of hundreds of different species interact in multiple ways, forming networks of interacting species. A network is defined by a set of elements connected by links between some of the elements. An ecological network is a network in which the elements are often species and the links represent ecological interactions. Until the end of the 1990s, most of the studies on ecological networks focused on food webs, the trophic interactions between species within an ecological community. Nowadays, the notion that a variety of ecological interactions form networks of species—from predation to mutualism, from parasitism to competition—has become more pervasive. The structure of these ecological networks may provide information on the ecological and evolutionary processes generating and shaping biodiversity. Moreover, the structure of ecological networks may also tell us about the fragility of ecological communities to different kinds of perturbations, from species extinctions to the invasion of alien species, from climate change to the poaching of keystone species. The perception that species form networks of interacting species is not new, and the study of ecological networks cannot be separated from some of the long-lasting, unsolved questions in ecology and evolution. Examples of these questions are: Are static representations of feeding interactions useful to infer ecological dynamics? What is the relationship between complexity and stability of ecological communities? Are assemblages of interacting species coevolving in specific ways? Analysis of the network structure has suggested that we can infer about ecological organization using information on feeding interactions (see Pattern Description and Biological Correlates), challenged the long-lasting view that complex communities are intrinsically more stable (see Ecological Dynamics), and provided insights on how to understand the evolution and coevolution of large interacting assemblages of species (see Evolutionary Dynamics). The field of ecological networks blossomed in the turn of the 21st century, fueled by the appearance of large databases, the development of new approaches and tools, and the finding that disparate complex systems such as human societies, biochemical pathways, ecological interactions, and the Internet share similar network organization. This bibliography focuses on the study of networks formed by ecological interactions among individuals of different species. The suggested readings explore different aspects of this topic, including references on networks studied in other scientific fields, classical works on ecological networks, descriptions of main types of ecological networks, studies exploring the underlying processes shaping ecological networks, and the evolutionary, ecological, and conservationist consequences of the network organization of species interactions. The term *ecological networks* has been used to describe not only the organization of multispecies assemblages, but also the spatial networks formed by natural habitats and/or reserves connected by migration. This review focuses on the networks formed by species interactions.

Foundational Works

The study of ecological networks is deeply rooted in some of the long-lasting questions in ecological science. To represent feeding interactions among species as webs or networks is not new, as seen in Pascual and Dunne 2006 (cited under Types of Ecological Networks), and the perception that ecological interactions connect species directly or indirectly led to the definition of the term *food chain*, introduced in Elton 2001. The view that ecological communities are formed by interacting assemblages of species led to studies on the role of different species in organizing biological diversity. Empirical manipulations of a particular species, as in Paine 1966, illustrated the importance of patterns of interaction in shaping biodiversity and the remarkable role that species such as top predators can have in shaping this organization. At the same time, the study of how energy and mass flow across the elements of the ecosystems in Odum 1960 and the search for generalizations on the structure and dynamics of ecological systems in Margalef 1963 pointed out the importance of these patterns of interaction for ecological dynamics and community stability. Cohen 1978 shows how the use of mathematical tools led to a quantitative characterization of the organization of ecological communities. Moreover, the analysis of community matrices depicting the effects of each species on populations of interacting species led to the complexity–stability debate; the view that stability is an inherent property of diverse ecological communities is challenged in May 2001. An additional major advance was the realization that simple assembly models derived from random graph theory were able to reproduce the organization of food webs, which are the networks describing trophic interactions among species, as reviewed in Pimm 2002. The seminal paper Jordano 1987 generalized ideas first used for characterizing food webs to mutualisms, anticipating the exploration of the network structure of different kinds of species interactions (see Types of Ecological Networks). All these studies illustrate the previous work that, together with the explosion of complex network theory (see Fundamentals of Networks) and the development of computational approaches allowing us to handle large datasets, allowed the emergence of the field of ecological networks at the turn of 21st century.

Cohen, Joel E. 1978. *Food webs and niche space*. Princeton, NJ: Princeton Univ. Press.

The main elements of current ecological network analysis are present in this foundational book, including the aim to contribute to a central question in ecology (how many dimensions are needed to characterize food webs?), the compilation of a large database of empirical networks, the use of graph theory concepts such as intervality to characterize empirical networks, and the conclusion that similar patterns occur in several disparate ecological communities.

Elton, Charles S. 2001. *Animal ecology*. Chicago: Univ. of Chicago Press.

This book introduces the idea of food chains together with the idea that food chains can be combined in food cycles, now called food webs. This reprint includes new introductions for the chapters, describing the influence of Elton's work. It is a classic book in ecology and still a source of inspiration for the subject. Originally published in 1927.

Jordano, Pedro. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *American Naturalist* 129:657–677.

This paper explores the structure of assemblages of plants and their mutualistic partners (seed dispersers and pollinators). It uses the concepts of connectance and asymmetries to characterize the organization of mutualistic assemblages, anticipating the debate on the role of abundance and coevolution in shaping mutualistic networks.

Margalef, Ramón. 1963. On certain unifying principles in ecology. *American Naturalist* 97.897: 357–374.

This classic paper illustrates the long-lasting search for general principles in ecology. Margalef explores the relationships among the complexity of ecosystems, energy flow, perturbations, and the maintenance of complex organization in space and, especially, in time. Available online for purchase or by subscription.

May, Robert M. 2001. *Stability and complexity in model ecosystems*. Princeton, NJ: Princeton Univ. Press.

This book challenged the long-lasting view that stability is a natural consequence of complexity, firing up the complexity–stability debate. Originally published in 1973, this work popularized the qualitative stability analysis in the ecological literature, one of the most often used ways of exploring the stability of ecological networks.

Odum, Howard T. 1960. Ecological potential and analogue circuits for the ecosystem. *American Scientist* 48.1: 1–8.

This article is a key paper on the idea that ecosystem dynamics can be modeled using approaches derived from physics. The study is based on the analogies between mass and energy flow across the interactions connecting trophic levels with Ohm's Law. Available online for purchase or by subscription.

Paine, Robert T. 1966. Food web complexity and species diversity. *American Naturalist* 100.910: 65–75.

This article describes one of the central results of empirical experiments in ecology. It illustrates how the removal of a top predator—a starfish—led to a reduction in the diversity within food webs due the releasing of top-down control imposed by starfish on their prey. Available online for purchase or by subscription.

Pimm, Stuart L. 2002. *Food webs*. Chicago: Univ. of Chicago Press.

This book is a well-organized and clear review of the main findings of empirical and theoretical studies on food webs prior to the 1980s. It is a wonderful introduction and summary for researchers interested in how the network approach would allow the characterization of interacting assemblages. Originally published in 1982 (London: Chapman and Hall).

Books

Many books are available on ecological networks, and several of them are cited in other sections of this bibliography. Here, a few books are cited that review some specific aspects on ecological networks. For example, Kitching 2000 describes what we learned on food webs from studies on species interactions within plant-held water bodies. Reagan and Waide 1996 builds the food web of a tropical rainforest through the impressive assessment of the natural history of different animal groups in El Verde, Puerto Rico. Belgrano, et al. 2005 reviews the structure and dynamics of aquatic food webs. Moore and de Ruiter 2012 integrates the findings on network organization with the flow of energy within ecological communities. The flow of nutrients at multiple spatial scales is the central theme of Polis, et al. 2004. Terborgh and Estes 2010 reviews the current evidence for the role of top consumers in shaping the organization of communities through trophic cascades in different ecosystems. McCann 2012, another recent book, introduces basic concepts on distinct views of food web research in an integrative way.

Belgrano, Andrea, Ursula M. Scharler, Jennifer Dunne, and Robert E. Ulanowicz, eds. 2005. *Aquatic food webs: An ecosystem approach*. Oxford: Oxford Univ. Press.

This book describes a variety of topics of aquatic food webs, from structural analysis of these networks to stability. Particular chapters investigate the structure and dynamics of food webs of lakes, estuaries, and marine ecosystems, whereas other chapters focus on the role of spatial and temporal scales in the organization of food webs.

Kitching, Roger L. 2000. *Food webs and container habitats: The natural history and ecology of phytotelmata*. Cambridge, UK: Cambridge Univ. Press.

Many plants form natural water containers, such as tree holes, which are colonized by diverse species of animals. The topic of this book is the food webs formed in these container habitats, which are an appropriate system for exploring experimentally the structure and dynamics of food webs. The book reviews the rich literature on the topic and introduces new ideas about the food webs in container habitats.

McCann, Kevin S. 2012. *Food webs*. Monographs in Population Biology 50. Princeton, NJ: Princeton Univ. Press.

This book focuses on the available theory for the structure and dynamics of food webs. It is a well-organized introduction of the topic and especially useful for graduate students. McCann builds the ideas from populations to small food webs and then whole systems. The chapter "A Primer for Dynamical Systems" (pp. 20–46) is very helpful to any student or researcher interested not only on ecological network theory but also on dynamics of any ecological or evolutionary system.

Moore, John C., and Peter C. de Ruiter. 2012. *Energetic food webs: An analysis of real and model ecosystems*. Oxford Series in Ecology and Evolution. Oxford: Oxford Univ. Press.

Traditionally, food webs are explored by researchers interested in community dynamics, such as species persistence in time, or ecosystem processes, such as energy flow across the species. This book integrates both research programs, exploring a myriad of topics on structure and dynamics of food webs.

Polis, Gary A., Mary E. Power, and Gary R. Huxel, eds. 2004. *Food webs at the landscape level*. Chicago: Univ. of Chicago Press.

This book addresses the relevance of large temporal and spatial scales, especially those between environments for ecological processes. Special attention is given to the way matter flows across ecological networks connecting distinct environments.

Reagan, Douglas P., and Robert B. Waide, eds. 1996. *The food web of a tropical rain forest*. Chicago: Univ. of Chicago Press.

This book reviews the natural history of the main players of a species-rich food web. Each chapter explores the natural history of one of these groups (e.g., termites, birds, litter invertebrates, and anoline lizards, among others) with special attention to the trophic interactions. At the end of the book, this impressive amount of information is synthetized in the description of the food web.

Terborgh, John, and James A. Estes, eds. 2010. *Trophic cascades: Predators, prey, and the changing dynamics of nature*. Washington, DC: Island.

Evidence is increasing that a few species—the apex consumers—are crucial to the organization of ecological communities in aquatic and terrestrial environments. This book explores several well-documented case studies on the impact of the extinction of top predators or large herbivores on the organization of natural communities. The last part of the book is devoted to a synthesis of what we know about the role of apex consumers in shaping communities, pointing out the importance of top–down effects on ecological communities.

Journals

The analysis of the structure and dynamics of ecological networks is currently a hot topic in ecology, with several articles published in the top-ranked journals such as Nature, Science, and Proceedings of National Academy of Sciences of the United States of America. Moreover, several ecological journals are now publishing influential and solid papers on ecological networks. Among them, theoretical and empirical papers published in Ecology Letters and Ecology focus primarily on the role of ecological processes in shaping ecological networks. Some of the papers published in Oikos often share a similar ecological view with papers published by the two former journals, but Oikos also publishes novel approaches and some more exploratory, conceptual work on the underlying processes shaping ecological networks. The evolutionary consequences and basis of ecological networks is explored theoretically and empirically in papers published in journals such as American Naturalist. New journals such as PLoS ONE, by allowing rapid publication based purely on technical reviewing of the work and online free availability, have an increasing role as repositories of significant contributions for the field.

American Naturalist. 1867–.

Many of the now-considered classic works on ecological networks were published in *American Naturalist*. This journal is published by the American Society of Naturalists and has an important impact on the field.

Ecology. 1920–.

This journal from the Ecological Society of America publishes both empirical and theoretical studies on the topic.

Ecology Letters. 1998–.

Currently the top-ranked journal in ecology, *Ecology Letters* is probably the most important avenue for publications of studies on ecological networks.

Nature. 1869–.

Together with Science, it is the most prestigious scientific journal. It publishes significant contributions on science and specifically on complex networks, including ecological networks.

Oikos. 1949–.

This journal from the Nordic Ecological Society publishes many papers on ecological networks, including both empirical and theoretical work as well as new methods to characterize network organization and provocative idea papers on the topic.

PLoS ONE. 2006–.

An open-access journal that publishes papers on all fields of science. It focuses on the evaluation of technical standards of submitted papers instead of on the perception of the importance of the field.

Proceedings of National Academy of Sciences of the United States of America. 1915–.

This journal, published by the National Academy of Sciences of the United States of America, is one of the most important scientific journals. It publishes papers on several aspects of ecological networks, and new approaches to the area are constantly introduced in this journal.

Science. 1880–.

This periodical is one of the most prestigious scientific journals; it publishes significant contributions on all topics of science.

Fundamentals of Networks

Networks are natural descriptions of systems formed by multiple elements connected by interactions. The elements of these systems can be depicted as nodes and the interactions connecting different elements can be represented by links. The mathematical object formed by a set of nodes and a set of links is called a graph, as reviewed in Harary 1969. For almost three hundred years the development of the graph theory was fueled by real-world problems, such as in Leonhard Euler's (b. 1707–d. 1783) 1741 classic "Solutio Problematis Ad Geometriam Situs Pertinentis" (*Commentarii academiae scientiarum Petropolitanae* 8:128–140), a work on the seven bridges of Königsberg, available from the Euler Archive. Tools directly derived from graph theory were used to characterize food webs in ecology, as reviewed in Pimm 2002 (cited under Foundational Works). In social sciences, the study of the interactions among individuals or among social organizations led to the development of an enormous set of tools to characterize the organization of networks formed by different types of social activities, as reviewed in Wasserman and Faust 1994. Additionally, tools derived from statistical mechanics, reviewed in detail in Costa, et al. 2007, allowed the characterization of the structure and dynamics of complex networks; see also Albert and Barabási 2002 and Barrat, et al. 2008. These approaches were at least partially motivated by the emergence of the Internet and very large databases of interactions among genes, proteins, and molecules within the cell. The striking similarity of structural patterns observed in networks describing complex systems in social, technological, and biological networks motivated the search for simple, unifying principles to explain the organization of complex networks, as seen in Newman, et al. 2006. Patterns that emerge in disparate, complex systems are a result of the interactions among the elements of the system. As pointed out in Amaral and Ottino 2004, the detection that minimal, similar processes may be operating in different systems and leading to similar network organizations is one of the key contributions of the theory of complexity. The combination of tools and ideas derived from graph theory, traditional food web theory, social sciences, statistical mechanics, and complex science are the core of the emergent field of ecological networks.

Albert, Réka, and Albert-László Barabási. 2002. Statistical mechanics of complex networks. *Reviews of Modern Physics* 74.1: 47–97.

A detailed, fifty-one-page review on the statistical mechanics of the structure and dynamics of empirical and theoretical networks. The authors explain network models in detail and how deviations from predictions of a given model led to development of new models. Available online for purchase or by subscription.

Amaral, Luís A. N., and Julio M. Ottino. 2004. Complex networks: Augmenting the framework for the study of complex systems. *European Physical Journal B* 38.2: 147–162.

This introductory review will help the reader to understand the basic aspects of the network approach. Special attention is given in explaining how the network approach fits into the broader area of the theory of complexity. It is especially useful for graduate students of all fields. Available online for purchase or by subscription.

Barrat, Alain, Marc Barthélemy, and Alessandro Vespignani. 2008. *Dynamical processes on complex networks*. Cambridge, UK: Cambridge Univ. Press.

This book describes the structure and dynamics of complex networks. The authors focus on how to model dynamics in systems characterized by networks, using multiple approaches in order to explore how perturbations and cascading effects affect and propagate across networks.

Costa, Luciano da F., Francisco A. Rodrigues, Gonzalo Travieso, and Paulino R. Villas Boas. 2007. Characterization of complex networks: A survey of measurements. *Advances in Physics* 56.1: 167–242.

A impressively detailed, seventy-seven-page catalog of measurements of network structural patterns and how they can be used to characterize the structure of complex networks. Different types of measurements are well explained, allowing the reader to understand the usefulness of each measure and how to apply it in a proper way to characterize networks. Available online for purchase or by subscription.

Harary, Frank. 1969. *Graph theory*. Reading, MA: Addison-Wesley.

A classical textbook on graph theory introducing several concepts of this area of discrete mathematics. *Graph Theory* has a rich body of concepts and a very particular jargon. This book provides a friendly starting point for the reader to get used to the basic concepts of this approach.

Newman, Mark, Albert-László Barabási, and Duncan J. Watts, eds. 2006. *The structure and dynamics of networks*. Princeton Studies in Complexity. Princeton, NJ: Princeton Univ. Press.

This book is a compendium of now classical papers on random graph theory and the structure and dynamics of real networks. It is very useful to researchers interested not only in the late-1990s–early-2000s explosion of works on complex networks but also in classical studies on random graphs.

Solutio problematis ad geometriam situs pertinentis.

The Euler Archive is an online resource with all works written by Euler. In addition to Euler's original paper on the Königsberg Bridge problem in Latin, this page also links to websites explaining it and current work related to the Königsberg Bridge problem.

Wasserman, Stanley, and Katherine Faust. 1994. *Social network analysis: Methods and applications*. Cambridge, UK: Cambridge Univ. Press.

Researchers interested in the organization of human societies originally developed some of the tools now used to characterize complex networks. This book is an impressive description of many measurements and approaches that allow a researcher to characterize not only social networks but ecological networks as well.

Types of Ecological Networks

Networks can describe any kind of interaction among elements in a system. In ecology the networks were first used to characterize the trophic relationships between species, the so-called food webs, as in Pascual and Dunne 2006. More recently, the network organization of other types of interactions has been explored. As reviewed in Bascompte and Jordano 2007, special attention has been given not only to terrestrial mutualisms, such as pollination and seed dispersal by animals, but also to mutualisms involving marine species, as in Ollerton, et al. 2007. Along the same lines, as in Lafferty, et al. 2008, parasite–host interactions are now being explored using the network approach. More recently, Verdu and Valiente-Banuet 2008 explores networks formed by interactions among plant species. Similarly, Vacher, et al. 2008 investigates the structure of networks formed by antagonistic interactions between fungus and their host trees, and Allesina and Levine 2011 explores the theoretical consequences of networks formed by competitive interactions to species persistence. One challenge ahead is to explore other levels of ecological organization, such as the structure of networks of individuals formed by patterns of overlap in resource use, as introduced in Araújo, et al. 2008.

Allesina, Stefano, and Jonathan M. Levine. 2011. A competitive network theory of species diversity. *Proceedings of the National Academy of Sciences of the United States of America* 108.14: 5638–5642.

This study introduces an explicit network approach to explore the coexistence in networks formed by competitor species. It combines the network approach with rock-paper-scissors models to suggest competition is not likely to lead to the extinction of co-occurring species in species-rich communities.

Araújo, Márcio S., Paulo R. Guimarães Jr., Richard Svanbäck, et al. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. *Ecology* 89.7: 1981–1993.

This study introduces the network approach to characterize individual-level variation in resource use. By combining experimental data, network analysis, geometric morphometrics, and optimal diet theory the authors were able to identify previously unknown effects derived from intraspecific competition on population niches. Available online for purchase or by subscription.

Bascompte, Jordi, and Pedro Jordano. 2007. Plant–animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology Evolution and Systematics* 38:567–593.

This review describes the major results from the study of structure and dynamics of mutualistic networks in a very clear way. It is a great start for the literature in mutualistic networks. Available online for purchase or by subscription.

Lafferty, Kevin D., Stefano Allesina, Matias Arim, et al. 2008. Parasites in food webs: The ultimate missing links. *Ecology Letters* 11.6: 533–546.

Although parasites are the dominant animal life on earth, they have been underrepresented in ecological networks for decades. This review illustrates the importance of parasites for food web structure and dynamics, describing the main challenges in the task of incorporating these organisms in current theories of ecological networks.

Ollerton, Jeff, Duncan McCollin, Daphne G. Fautin, and Gerald R. Allen. 2007. Finding NEMO: Nestedness engendered by mutualistic organization in anemonefish and their hosts. *Proceedings of the Royal Society B—Biological Sciences* 274.1609: 591–598.

Nestedness is a pattern that characterizes mutualisms among free-living species at community level. The authors show that even highly specialized mutualisms can show patterns of nestedness but at much larger spatial scales. Future studies should address the role of spatial scales on the structure of ecological networks.

Pascual, Mercedes, and Jennifer A. Dunne. 2006. *Ecological networks*. Oxford: Oxford Univ. Press.

This book is probably the best review of the current literature of ecological networks; it covers the historical foundations and empirical patterns to the mathematical modeling of ecological and evolutionary dynamics. The focus is on food webs, but networks describing other types of interactions, such as mutualisms, are described as well.

Vacher, Corinne, Dominique Piou, and Marie-Laure Desprez-Loustau. 2008. Architecture of an antagonistic tree/fungus network: The asymmetric influence of past evolutionary history. *PLoS ONE* 3.3: e1740.

Most of the studies in ecological networks focus on food webs, plant–animal interactions, and, more recently, parasite–host interactions. This is a very interesting example of how the network approach can be used to detect non-random patterns of interaction in other ecological systems. In this study the organization of antagonistic interactions, at regional level, among fungus and host trees are explored using the network approach.

Verdu, Miguel, and Alfonso Valiente-Banuet. 2008. The nested assembly of plant facilitation networks prevents species extinctions. *American Naturalist* 172.6: 751–760.

This study introduces the network approach on the facilitation of interactions. One key aspect of this study is that it moves from the analysis of facilitation between pairs of species or a single focal species toward a community-level analysis of this interaction.

This work suggests that the facilitation network studied is structurally similar to mutualistic, plant–animal networks. Available online for purchase or by subscription.

Pattern Description

One key aspect of ecological networks analysis is the description of patterns. Hence, one of the benefits of the network approach is that it allows the characterization of numerous aspects of the organization of ecological networks, as in Costa, et al. 2007 (cited under Fundamentals of Networks). For this reason, any attempt to summarize this enormous amount of possibilities in a few references would be prohibitive. The following readings summarize some of the key structural patterns that have guided some important discussions on the structure and dynamics of complex networks in general and particularly of ecological networks. Network measurements can be used to describe the patterns of interaction of a given species or of the network as a whole. At the species level, many distinct measurements were used to characterize the patterns of interaction of individual species within food webs, as in Luczkovich, et al. 2003, and mutualistic networks, as in Olesen, et al. 2007 (cited under Modularity). At the network level, as pointed out in Dunne, et al. 2002, the most basic aspect of the pattern of interaction described in ecological networks is connectance, which is the proportion of links observed in a network relative to the possible amount of links. Connectivity can also be characterized by distributions that describe the probability of finding a species with a certain number of interactions, the so-called degree distributions, as in Jordano, et al. 2003. As pointed out in Otto, et al. 2007, the statistical properties of degree distributions have important consequences for inferring the underlying processes organizing ecological networks as well as, in Montoya, et al. 2006, the fragility of ecological networks to perturbations. Taken together, these studies suggest that a few highly connected species often characterize ecological networks, linking multiple species. Consequently, ecological networks are frequently characterized by small paths that connect any random selected pairs of species, as in Williams, et al. 2002. Accordingly, the lengths of food chains connecting producers and apex consumers are often small and the degree of omnivory is often high, as in Hall and Raffaelli 1991. As Martinez 1994 shows, most of the structural aspects of ecological networks scale with network size, indicating that there might be some general rules for the assembly of ecological networks. The following subsections illustrate how the study of structural patterns has provided insights on the organization and fragility of ecological networks by citing some readings on three structural aspects that have been receiving considerable attention: modularity, nestedness, and interaction strength.

Dunne, Jennifer A., Richard J. Williams, and Neo D. Martinez. 2002. Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America* 99.20: 12917–12922.

It was not clear if ecological networks share the same structural properties observed in biochemical, technological, and social networks. This study shows that ecological and other complex networks often show similar structural organization. However, deviations observed in the structure of ecological networks are associated with the higher connectance and smaller size of ecological networks when compared with other complex systems.

Hall, Stephen J., and Dave Raffaelli. 1991. Food-web patterns: Lessons from a species-rich web. *Journal of Animal Ecology* 60.3: 823–842.

In addition to describing the network structure of a species-rich food web, this study illustrates the importance of a good characterization of interacting species when describing the structure of ecological networks. It illustrates how well-documented food webs differ in several ways from previously described food webs in which trophic aggregation of similar species was more common. Available online for purchase or by subscription.

Jordano, Pedro, Jordi Bascompte, and Jens M. Olesen. 2003. Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters* 6.1: 69–81.

This study uses degree distributions to explore the organization of mutualistic networks, describing these networks as often being characterized by a few supergeneralists and the majority of species establish just a few interactions. This pattern led to the discussion of the role of constraints in potential interactions in shaping mutualistic networks (see also Olesen, et al. 2011, cited under Biological Correlates). Available online for purchase or by subscription.

Luczkovich, Joseph J., Stephen P. Borgatti, Jeffrey C. Johnson, and Martin G. Everett. 2003. Defining and measuring trophic role similarity in food webs using regular equivalence. *Journal of Theoretical Biology* 220.3: 303–321.

This article introduces the idea of regular equivalence to the study of ecological networks, which allows one to identify species with similar patterns of interaction. For example, two species that are apex predators with the same number of prey are trophically equivalent, even if they do not share the same prey. Available online for purchase or by subscription.

Martinez, Neo D. 1994. Scale-dependent constraints on food-web structure. *American Naturalist* 144.6: 935–953.

The first studies on food web organization suggested that these networks exhibited invariant organization. This study challenges this view using two data sets, one composed by smaller food webs and a new data set composed by species-richer food webs. Most structural patterns in the smaller food webs scale with species richness. Notably, these scaling relationships were able to predict the structural patterns observed of species-richer food webs. Available online for purchase or by subscription.

Montoya, Jose M., Stuart L. Pimm, and Ricard V. Solé. 2006. Ecological networks and their fragility. *Nature* 442.7100: 259–264.

This article reviews the available information on basic aspects of the structure of ecological networks. The authors make inferences about the fragility of ecological networks to disturbances. Available online for purchase or by subscription.

Otto, Sonja B., Björn C. Rall, and Ulrich Brose. 2007. Allometric degree distributions facilitate food-web stability. *Nature* 450.7173: 1226–1229.

This article combines ratios on predator and prey masses and analysis of degree distributions to infer how stability can emerge in food webs. It is a good example on how to integrate data on the biology of the interactions with tools derived from complex networks. Available online for purchase or by subscription.

Williams, Richard J., Eric L. Berlow, Jennifer A. Dunne, Albert-László Barabási, and Neo D. Martinez. 2002. Two degrees of separation in complex food webs. *Proceedings of the National Academy of Sciences of the United States of America* 99:12913–12916.

This article explores the path length, in numbers of interactions, between pairs of species in a network. This study shows that the distance between species within food webs is surprisingly small, with less than three interactions needed to connect, on average, each pair of species. These results have important consequences to dynamics by suggesting cascading effects could spread across multiple species in the network.

Modularity

A modular or compartmentalized network is characterized by presenting groups of nodes that interact more among each other than with other groups in the network, the modules, or compartments. Pimm and Lawton 1980 suggests that compartments characterized only major transitions between environments, a view that was later challenged by works such as Krause, et al. 2003. Modularity can also emerge in some degree in mutualistic networks formed by plants and their pollinators, as shown in Olesen, et al. 2007. As investigated in Rezende, et al. 2009, different processes can generate modularity. For example, evolutionary constraints are likely to contribute to the emergence of highly modular organization, as illustrated by interaction between herbivores and their host plants, as in Prado and Lewinsohn 2004, and ant–plant mutualisms, as in Fonseca and Ganade 1996 (cited under Biological Correlates). As explored in Borrett, et al. 2007, one of the key implications of modularity is to affect the propagation of coextinction cascades. A central problem when characterizing the modular pattern in networks and making inferences on its implications for dynamics is how to estimate the degree of modularity of a given network. The identification of modules within a network is not an easy task, and most of the current approaches use optimized computational methods to estimate the value of a given modularity index, such as the one based on simulating annealing proposed in Guimerà and Amaral 2005.

Borrett, Stuart R., Brian D. Fath, and Bernard C. Patten. 2007. Functional integration of ecological networks through pathway proliferation. *Journal of Theoretical Biology* 245.1: 98–111.

One property of many networks is pathway proliferation. The number of pathways connecting two species increases with the distance between the species in number of links. This study demonstrates that path proliferation occurs in food webs. The interplay of path proliferation and modularity led to the suggestion that modules in food webs would behave as integrated, functional groups due to indirect effects. Available online for purchase or by subscription.

Guimerà, Roger, and Luís A. Nunes Amaral. 2005. Functional cartography of complex metabolic networks. *Nature* 433.7028: 895–900.

This study introduces the most popular approach for characterizing modularity nowadays. There is some inaccuracy in the ecological literature because this work is often referred to as the one proposing the index of modularity, *M* (also referred to as *Q*). However, this index existed previously in the complex network literature, and what this study demonstrates is that an optimization procedure—the simulated annealing—allows for a better estimation of the level of modularity in complex networks. Available online for purchase or by subscription.

Krause, Ann E., Kenneth A. Frank, Doran M. Mason, Robert E. Ulanowicz, and William W. Taylor. 2003. Compartments revealed in food-web structure. *Nature* 426.6964: 282–285.

This study exemplifies many of the qualities of network approach. The approach developed in other fields (social sciences) is used to characterize patterns of interaction (modularity) relevant to the ecological dynamics (stability). The study also illustrates some of the difficulties of detecting modules in ecological networks, namely, to define modularity, to identify the modules, and to the test whether the patterns observed are expected by chance. Available online for purchase or by subscription.

Olesen, Jens M., Jordi Bascompte, Yoko L. Dupont, and Pedro Jordano. 2007. The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America* 104:19891–19896.

This study introduces the approach described in Guimerà and Amaral 2005 to the study of ecological networks. It describes the patterns of modularity in pollination networks, showing that species-rich networks are often modular. In addition, this study uses two species-level measures to characterize the role of species within modular networks.

Pimm, S. L., and John H. Lawton. 1980. Are food webs divided into compartments? *Journal of Animal Ecology* 49.3: 879–898.

Stability analysis of community matrices predicts that compartmentalization should favor stability. In this classic study, Pimm and Lawton conclude that compartments are not likely to improve stability because compartments characterize major transitions between habitats and not the structure of interactions within habitats. Although later studies challenged this proposal (see other readings in this section), this article fired up the interest on modularity/compartmentalization of ecological networks. Available online for purchase or by subscription.

Prado, Paulo Inácio, and Thomas M. Lewinsohn. 2004. Compartments in insect–plant associations and their consequences for community structure. *Journal of Animal Ecology* 73.6: 1168–1178.

This study illustrates how modularity can markedly characterize interactions between herbivores and their host plants. Prado and Lewinsohn point out that modularity emerges in these interactions as a consequence of high specialization and phylogenetic conservatism on herbivores' host use.

Rezende, Enrico L., Eva M. Albert, Miguel A. Fortuna, and Jordi Bascompte. 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters* 12.8: 779–788.

This study explores the underlying factors generating the modular structure in food webs. By combining the network approach and phylogenetic methods to analyze a marine food web, the authors show that the modular structure is generated by a complex interplay of body mass, phylogeny, and spatial organization. The analyses also suggest that sharks are the most important species for the organization of this network. Available online for purchase or by subscription.

Nestedness

Nestedness occurs when the assemblage of interacting partners of one species is a subset of the assemblage of the interacting partners of another species. Patterson and Atmar 1986 uses this concept to describe patterns of species distribution across discrete habitat patches. Bascompte, et al. 2003 later introduced nestedness to the study of ecological networks, leading to the discovery that pollination and seed dispersal networks often show nested patterns of interaction. Currently, there is a considerable debate on the underlying causes of nestedness in ecological networks, as reviewed in Vázquez, et al. 2009. There is evidence indicating that interaction type matters: Thébault and Fontaine 2010 shows that mutualistic networks often show a higher degree of nestedness when compared to networks of interactions between plants and their natural enemies. In this sense, although nestedness and modularity are distinct, nonrandom patterns of interaction, a given network can be simultaneously nested and modular, as in Fortuna, et al. 2010. In addition, there is currently a hot debate on the implications of nestedness for the stability and persistence of species within networks, and studies using different approaches present contrasting results, with nestedness either promoting, as suggested in Bastolla, et al. 2009 and Thébault and Fontaine 2010, or imperiling species persistence, as suggested in Allesina and Tang 2012. Finally, although there are multiple ways to analyze the degree of nestedness of a given network, no matter the measure used, the inferences on the degree of nestedness are often based on the theoretical benchmark represented by null models, as reviewed in Ulrich, et al. 2009.

Allesina, Stefano, and Si Tang. 2012. Stability criteria for complex ecosystems. *Nature* 483.7388: 205–208.

This study uses analytical work and numerical simulations to generalize the analysis in May 2001 (cited under Foundational Works) on how complexity affects the stability of ecological networks. Special attention is given to analyzing how particular types of interactions and network structures, such as nestedness, affect the local stability of ecological communities. The conclusion is that nestedness often leads to more unstable networks. Available online for purchase or by subscription.

Bascompte, Jordi, Pedro Jordano, Carlos J. Melián, and Jens M. Olesen. 2003. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America* 100.16: 9383–9387.

One of the most influential studies on ecological networks, this article introduces the idea of nestedness in mutualisms. The detection of nestedness as a general pattern in species-rich mutualism networks among plants and their pollinators and seed dispersers challenged the view that these interactions present no organization. Emphasis is given to the potential consequences of nestedness for coevolutionary and ecological dynamics.

Bastolla, Ugo, Miguel A. Fortuna, Alberto Pascual-Garcia, Antonio Ferrera, Bartolo Luque, and Jordi Bascompte. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458.7241: 1018–1020.

In nested networks, species often present a strong overlap in their assemblages of interacting partners. By combining analytical work and numerical simulations this study addresses the role of nestedness in minimizing competition and favoring the maintenance of species-rich mutualisms. Available online for purchase or by subscription.

Fortuna, Miguel A., Daniel B. Stouffer, Jens M. Olesen, et al. 2010. Nestedness versus modularity in ecological networks: Two sides of the same coin? *Journal of Animal Ecology* 79.4: 811–817.

Modularity and nestedness are two distinct, non-random patterns of interaction. Nevertheless, this study points out that ecological networks can show evidence for both patterns of interaction simultaneously. It also shows that the relationship between nestedness and modularity depends on the connectance in complex ways.

Patterson, Bruce D., and Wirt Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* 28.1–2: 65–82.

In this classic study, Patterson and Atmar explore the changes in composition of mammalian assemblages across montane habitats. They record that the mammalian assemblages are more nested than expected by the theoretical benchmarks provided by two null models. This article is especially useful for researchers interested in the origin of nested concepts in ecology and the usefulness of null models in detecting significant patterns in ecological data. Available online for purchase or by subscription.

Thébault, Elisa, and Colin Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329.5993: 853–856.

Using empirical data and numerical simulations of sets of differential equations this study illustrates how distinct interaction types favor different network structures due to differential species loss. Antagonisms would favor the emergence of modular networks, whereas nestedness would emerge in mutualistic networks. Available online for purchase or by subscription.

Ulrich, Werner, Mário Almeida-Neto, and Nicholas J. Gotelli. 2009. A consumer's guide to nestedness analysis. *Oikos* 118.1: 3–17.

This article is the best available review of metrics used to characterize nestedness in matrices describing both ecological networks and species occurrence across habitats. The authors explain in detail for which types of question each nestedness measure is more appropriate. Available online for purchase or by subscription.

Vázquez, Diego P., Nico Blüthgen, Luciano Cagnolo, and Natacha P. Chacoff. 2009. Uniting pattern and process in plant–animal mutualistic networks: A review. In *Special issue: Plant-pollinator interactions*. Edited by Don Levin, Pat Heslop-Harrison, Mike Jackson, and David Frost. *Annals of Botany* 103.9: 1445–1457.

A review of the patterns observed in mutualistic networks and the processes that could be generating these patterns. Special attention is given to the underlying ecological and evolutionary processes that may generate nestedness.

Interaction Strength

Most of the descriptions of ecological networks are based on presence/absence patterns of interactions. However, there is a considerable amount of variation in the interaction strength, and to estimate it is a difficult task, as reviewed in Wootton and Emmerson 2005. Nevertheless, the increasing availability of detailed data sets describing the frequency of interactions in the field is now allowing researchers to explore how to characterize quantitative patterns within networks, as pointed out in Ings, et al. 2009. As Paine 1992 shows, food webs are characterized by weak links with low interaction strength. Bascompte, et al. 2006 shows weak links are also common in mutualistic networks, leading to asymmetries on the dependence between pairs of interacting species. Blüthgen, et al. 2007 introduces an approach to using the quantitative information on the strength of interactions to infer information about ecological specialization. Using this approach, Schleuning, et al. 2012 recently challenged the view that ecological communities are more specialized in the tropics. As in McCann, et al. 1998, the widespread distribution of weak links in nature may favor stability in ecological networks. In this sense, long loops formed by multiple weak links are likely to favor the stabilization of complex ecological networks, as in Neutel, et al. 2002.

Bascompte, Jordi, Pedro Jordano, and Jens M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312.5772: 431–433.

This study indicates that most mutualistic interactions are characterized by weak interaction strengths and that the interacting partners often show asymmetrical levels of mutual dependence between each other. Moreover, it uses an analytical approach to illustrate how these patterns may contribute to the stability of species-rich mutualisms.

Blüthgen, Nico, Florian Menzel, Thomas Hovestadt, Brigitte Fiala, and Nils Blüthgen. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology* 17.4: 341–346.

This article uses an approach derived from information entropy to characterize the degree of specialization in quantitative networks. By using this approach the authors are able to show that patterns of specialization vary across different types of mutualisms.

Ings, Thomas C., José M. Montoya, Jordi Bascompte, et al. 2009. Ecological networks—Beyond food webs. *Journal of Animal Ecology* 78.1: 253–269.

This important review discusses the main challenges for future research in ecological networks. One of the key, promising avenues is the incorporation of quantitative information in interaction strengths.

McCann, Kevin, Alan Hastings, and Gary R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395.6704: 794–798.

This study reports that weak links are likely to dampen oscillations in consumer-resource dynamical models, favoring the persistence of species. It also reports that real food webs are often characterized by weak links. Available online for purchase or by subscription.

Neutel, Anje-Margriet, Johan A. P. Heesterbeek, and Peter C. de Ruiter. 2002. Stability in real food webs: Weak links in long loops. *Science* 296.5570: 1120–1123.

This study explores the role of interaction strengths in the stability of food webs. The authors report that long loops formed by many weak links are a common feature in real food webs. By using mathematical modeling, they suggest these long and weak loops enhance the stability of food webs. These long and weak loops are likely to emerge as a consequence of the biomass pyramids that characterize several ecological communities. Available online for purchase or by subscription.

Paine, Robert T. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355.6355: 73–75.

Historically, interaction strengths are estimated in ecology by means of manipulation experiments. This study demonstrated through experimental manipulation that the per capita interaction strength varies widely across species within an ecological community, with the majority of species having weak interaction strengths. Available online for purchase or by subscription.

Schleuning, Matthias, Jochen Fründ, Alexandra-Maria Klein, et al. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology* 22.20: 1925–1931.

Theory predicts that species of tropical communities should be more specialized than temperate communities. By integrating information theory, network approach, and an impressive data set, this study challenges this view by showing that pollination and seed dispersal networks often decrease in the degree of specialization toward the tropics. Available online for purchase or by subscription.

Wootton, J. Timothy, and Mark Emmerson. 2005. Measurement of interaction strength in nature. *Annual Review of Ecology Evolution and Systematics* 36:419–444.

This review describes the interaction strength concept and the difficulty of estimating it. By comparing this review with other readings suggested in this section the reader will have a picture of two distinct views of interaction strength in current network literature. This review focuses on the per capita interaction strengths, whereas much of the current literature on ecological networks uses species-level measures of interaction strengths. Available online for purchase or by subscription.

Biological Correlates

A central issue in the study of ecological networks is to understand the underlying ecological and evolutionary processes shaping the observed structural patterns. In this sense, a key assumption for many studies of ecological networks is that the observed structure contains, at least on some level, clues about the processes that are shaping ecological interactions. One way to explore the candidate processes organizing networks is to search for correlations between structural patterns and biological attributes. We now have evidence that several biological attributes influence the organization of ecological networks. For instance, having knowledge of the differences in the abundances of interacting species is crucial to understand the patterns of interaction observed because it provides a template for estimating the probability of interaction between two species in a given community, as in Vázquez, et al. 2007. As Schleuning, et al. 2011 shows, habitat heterogeneity within communities is likely to generate modular organization in ecological networks; see also Pimm and Lawton 1980 (cited under Modularity). Other basic aspects of the natural history of these interactions can also affect network organization, such as the outcomes of the interactions, as in Blick and Burns 2009, and the degree of interaction intimacy of individuals of different species, as discussed in Fonseca and Ganade 1996. Furthermore, species traits are crucial to understanding network organization. For example, as discussed in Woodward, et al. 2005, in food webs the trophic interactions are always affected directly or indirectly by body size, and similar trends may occur in other interactions. More broadly, phenotypes are likely to shape the organization of ecological networks by modulating the likelihood of an interaction occurring, as in Stang, et al. 2006, or by constraining the interaction of otherwise potentially interacting species, as in Olesen, et al. 2011. Finally, because closely related species often show similar traits, phylogenetic information can be used to characterize and predict patterns of interaction in ecological networks, as in the approach introduced in Ives and Godfray 2006.

Blick, Ray, and Kevin C. Burns. 2009. Network properties of arboreal plants: Are epiphytes, mistletoes and lianas structured similarly? *Perspectives in Plant Ecology Evolution and Systematics* 11.1: 41–52.

This study analyzes the structure of commensal and antagonistic interactions among plant species. By combining numerical simulations and empirical data the authors report differences in structural patterns across distinct types of plant–plant interaction. Available online for purchase or by subscription.

Fonseca, Carlos R., and Gislane Ganade. 1996. Asymmetries, compartments and null interactions in an Amazonian ant–plant community. *Journal of Animal Ecology* 65.3: 339–347.

Several years before the explosion in the study of ecological networks, this study used empirical data on ant–plant interactions and analyses of matrices of interactions to explore in which ways the structure of highly intimate, ant–plant interactions differ from low-intimacy mutualisms characterized almost ten years before (see Jordano 1987, cited under Foundational Works). Available online for purchase or by subscription.

Ives, Anthony R., and H. Charles J. Godfray. 2006. Phylogenetic analysis of trophic associations. *American Naturalist* 168.1: E1–E14.

This study provides a method to explore the phylogenetic structure of interacting assemblages of species. The authors use a food web that includes leaf miners, their food plants, and their parasitoids, illustrating how the phylogenetic signal can be used to predict interactions in the absence of other data.

Olesen, Jens M., Jordi Bascompte, Yoko L. Dupont, Heidi Elberling, Claus Rasmussen, and Pedro Jordano. 2011. Missing and forbidden links in mutualistic networks. *Proceedings of the Royal Society B—Biological Sciences* 278.1706: 725–732.

This article introduces a new approach to exploring biological correlates of network structure. Instead of attempting to explain why some interactions occur, the study focuses on the role of biological attributes in limiting the occurrence of interactions, the so-called forbidden interactions.

Schleuning, Matthias, Nico Blüethgen, Martina Flörchinger, Julius Braun, H. Martin Schaefer, and Katrin Böhning-Gaese. 2011. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. *Ecology* 92.1: 26–36.

This study investigates interactions among plants and frugivores in an African tropical forest, reporting how patterns of specialization vary in the different forest strata, generating spatial heterogeneity in the specialization within the ecological community. Available online for purchase or by subscription.

Stang, Martina, Petter G. L. Klinkhamer, and Eddy Van Der Meijden. 2006. Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web. *Oikos* 112.1: 111–121.

This study investigates how variation in the abundance across species and the phenotypic traits of flowers and their visitors affect the organization of a plant-pollination network. Available online for purchase or by subscription.

Vázquez, Diego P., Carlos J. Melián, Neal M. Williams, Nico Blüthgen, Boris R. Krasnov, and Robert Poulin. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116.7: 1120–1127.

This article studies how the variation in species abundance explains the patterns of asymmetrical interactions observed in ecological networks. Available online for purchase or by subscription.

Woodward, Guy, Bo Ebenman, Mark Emmerson, et al. 2005. Body size in ecological networks. *Trends in Ecology and Evolution* 20.7: 402–409.

This article reviews the role of body mass in shaping ecological networks, including the interplay between body mass and other species attributes, such as abundances. Available online for purchase or by subscription.

Assembly Rules and Network Models

Since the seminal work of Cohen 1978 (cited under Foundational Works), ecologists have been interested in inferring the underlying ecological and evolutionary processes that organize ecological networks. One way to explore these processes is to explicitly build up matrices of probability incorporating distinct, potentially important, biological correlates and then use a likelihood approach for model selection, as in the approach used in Vázquez, et al. 2009. Another way is to build minimal models of network assembly inspired by models used in physics and random graph theory that incorporate some of the candidate processes organizing ecological networks. Williams and Martinez 2000 proposes the most popular of all models, the niche model, which incorporates basic aspects of niche overlap among species. Several, more complex food web models were proposed based on the niche model (Allesina, et al. 2008; Stouffer 2010), and recent work in Saavedra, et al. 2009 generalizes this approach to mutualistic interactions. One of the key issues with this approach is the inference of realistic parameters and how to select among the candidate models. In this sense, body size patterns are a natural candidate for estimating the parameters of the rules of interaction, as in Williams, et al. 2010. Finally, the incorporation of evolutionary processes is now allowing researchers to explore how evolution shapes the ecological network organization through speciation and extinction (Guill 2010, Loeuille and Loreau 2005).

Allesina, Stefano, David Alonso, and Mercedes Pascual. 2008. A general model for food web structure. *Science* 320.5867: 658–661.

In addition to incorporating the multidimensionality of previous, simpler models, this work also introduces a likelihood approach to select among the candidate, network models. Available online for purchase or by subscription.

Guill, Christian 2010. A model of large-scale evolution of complex food webs. *Mathematical Modelling of Natural Phenomena* 5.6: 139–158.

This article uses the niche model as a starting point (see Williams and Martinez 2000) adding extinction and speciation dynamics to reproduce macroevolutionary patterns in agreement with paleontological data. Available online for purchase or by subscription.

Loeuille, Nicholas, and Michel Loreau. 2005. Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America* 102.16: 5761–5766.

This study uses a simple model that incorporates ecological and evolutionary processes to illustrate how realistic food webs can emerge from simple rules of interaction based on niche width and the strength of competition.

Saavedra, Serguei, Felix Reed-Tsochas, and Brian Uzzi. 2009. A simple model of bipartite cooperation for ecological and organizational networks. *Nature* 457.7228: 463–466.

This work introduces a stochastic model inspired by food web models that reproduces both ecological mutualistic networks and organizational networks in economy. It illustrates the potential of generalization of the network approach. Available online for purchase or by subscription.

Stouffer, Daniel B. 2010. Scaling from individuals to networks in food webs. *Functional Ecology* 24.1: 44–51.

In this study the assembly models often used to model ecological networks are considered in a broader perspective. These models are contrasted with the population-level models that explicitly consider rules of interaction between pairs of species. Attention is given to what we can learn from the similarities and differences of both types of models of multispecies assemblages.

Vázquez, Diego P., Natasha P. Chacoff, and Luciano Cagnolo. 2009. Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology* 90.8: 2039–2046.

This study introduces a new approach that combines multiple biological correlates to reproduce the structure of ecological networks. The approach is based on the multiplication of probabilities associated with each biological factor. Available online for purchase or by subscription.

Williams, Richard J., Ananthi Anandanadesan, and Drew Purves. 2010. The probabilistic niche model reveals the niche structure and role of body size in a complex food web. *PLoS ONE* 5.8: e12092.

Recent literature on modeling the organization of ecological networks is now moving from randomly assigned parameter values toward parameter values estimated using biologically realist functions, such as the effects of body size on patterns of interaction. This study is a good example of this sort of work.

Williams, Richard J., and Neo D. Martinez. 2000. Simple rules yield complex food webs. *Nature* 404.6774: 180–183.

This work introduces the most popular food web model: the niche model, which inspired most of the models now used. It is a great example of how assembly models with minimal rules can reproduce the organization of ecological networks. Available online for purchase or by subscription.

Evolutionary Dynamics

As Thompson 2009 points out, evolutionary dynamics play a fundamental role in organizing interaction patterns within ecological networks. In fact, Gómez, et al. 2010 reports that even the analysis of the entire web of life shows that network structures have a phylogenetic signal. Models of network assembly that incorporate evolutionary processes start to shed light on how evolution may affect the organization of food webs, as in Loeuille and Loreau 2005 (cited under Assembly Rules and Network Models), and mutualistic interactions, as in Santamaría and Rodriguez-Girones 2007. Moreover, Ollerton, et al. 2003 reports empirical evidence on patterns of trait convergence, whereas asymmetrical dependences contribute to the role of selection on particular traits in shaping networks, as in Ramirez, et al. 2011. However, species interactions are not shaped only by the evolutionary dynamics. Rather, Kauffmann and Johnsen 1991 shows that the network structure may also dictate how natural selection acts on interacting populations and, consequently, the coevolutionary dynamics at the community level. By incorporating network structure in evolutionary analysis, it is possible to outline the modes of selection imposed by the organization of species-rich, interacting assemblages and start to explore how the structure of these assemblages affect evolution and coevolution, as in the approach introduced in Guimarães, et al. 2011. As in Loeuille 2010, the eco-evolutionary feedbacks are an important consequence of the evolutionary processes acting on ecological networks, and thus evolution is likely to be crucial for understanding the stability of species-rich ecological communities.

Gómez, José M., Miguel Verdú, and Francisco Perfectti. 2010. Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature* 465.7300: 918–921.

This work studies the phylogenetic signal across the entire web of life, encompassing various types of interactions. It is a wonderful example of how past evolutionary history can help us to understand current patterns of interaction among species. Available online for purchase or by subscription.

Guimarães, Paulo R., Jr., Pedro Jordano, and John N. Thompson. 2011. Evolution and coevolution in mutualistic networks. *Ecology Letters* 14.9: 877–885.

This study explores the role of coevolution and evolution in shaping traits in mutualistic networks. The analyses suggest that a particular lifestyle, the super-generalists, are organizing the emergence of trait similarity among interacting species and especially within species in the same trophic level. Available online for purchase or by subscription.

Kauffmann, Stuart A., and Sonke Johnsen. 1991. Coevolution to the edge of chaos: Coupled fitness landscapes, poised states, and coevolutionary avalanches. *Journal of Theoretical Biology* 149.4: 467–505.

This article uses a minimal model describing how the fitness landscape of a species changes due to the selection acting on species it interacts with. The analysis uses regular networks, in which all species have the same number of interactions, to explore the coevolutionary dynamics. It is a nice example of how variation in connectivity can lead to different coevolutionary dynamics in ecological networks. Available online for purchase or by subscription.

Loeuille, Nicolas. 2010. Influence of evolution on the stability of ecological communities. *Ecology Letters* 13.12: 1536–1545.

This study combines the ecological and evolutionary dynamics of ecological networks. The emerging eco-evolutionary dynamics led to provocative results, such as the role of evolution in destabilizing species-rich networks. Available online for purchase or by subscription.

Ollerton, Jeff, Steven D. Johnson, Louise Cranmer, and Sam Kellie. 2003. The pollination ecology of an assemblage of grassland asclepiads in South Africa. *Annals of Botany* 92.6: 807–834.

In this detailed empirical study on a pollination network the authors explore the role of evolutionary convergence of floral traits in shaping patterns of interaction within the network.

Ramirez, Santiago R., Thomas Eltz, Mikiko K. Fujiwara, et al. 2011. Asynchronous diversification in a specialized plant-pollinator mutualism. *Science* 333.6050: 1742–1746.

This study combines multiple lines of evidence, including network analysis, to show that asymmetries in the dependence between species characterize a textbook example of reciprocal specialization previously thought to be strong: the interactions between orchid bees and specialized orchids they pollinate. Available online for purchase or by subscription.

Santamaría, Luis, and Miguel A. Rodríguez-Gironés. 2007. Linkage rules for plant-pollinator networks: Trait complementarity or exploitation barriers? *PLoS Biology* 5.2: e31.

This study uses numerical simulations to explore how distinct trait-mediating rules of interaction affect the organization of mutualistic networks. Comparison with the structure of real networks leads to the conclusion that a combination of linkage rules are more likely to occur in nature.

Thompson, John N. 2009. The coevolving web of life. *American Naturalist* 173.2: 125–140.

This article explores the role of coevolution in shaping ecological networks. It points out the major challenges that we should address in our quest for understanding the role of evolutionary processes in shaping biodiversity. Also, it provides some basic information for new researchers in the field about what we know of the coevolutionary process. Available online for purchase or by subscription.

Ecological Dynamics

One of the long-lasting questions in ecology is whether complex, megadiverse ecological networks are stable, as discussed in McCann 2000. May 2001 (cited under Foundational Works), analyzes the local stability of community matrices, showing that the assumption "the richer the community, the higher its stability" is false, at least as a mathematical generality. These results contrast with the long-lasting belief that complexity favors stability. A possible solution for the complexity–stability debate may rely on addressing some simplifying assumptions that were severely criticized in empirical works, such as Polis 1991, and theoretical works, such as De Angelis 1975. For example, Kondoh 2003 shows that incorporating aspects of the biology of predators may be pivotal for the stability of food webs. The same is true for functional responses in mutualistic partners, as reported in Okuyama and Holland 2008. Along the same lines, Gross, et al. 2009 uses general modeling to incorporate the nonlinearities of species interactions. Accordingly, Fontaine, et al. 2006 shows that functional diversity of pollinators has positive effects on the diversity of plants. The complexity–stability debate is still a hot topic, and more recently some studies started to explore how stability is affected by the network organization by means of qualitative stability analysis, as in Allesina and Tang 2012 (cited under Nestedness). The results derived from this approach contrast with those derived from numerical simulations, as viewed in Thébault and Fontaine 2010 (cited under Nestedness), and analytical work with sets of differential equations assuming particular functional responses by interacting species, as in Bastolla, et al. 2009 (cited under Nestedness). These different conclusions are at least partially explained by the fact that approaches often focus on different aspects of the dynamics, from the local stability of unspecified equilibrium facing small perturbations to the consequences of species extinctions to species persistence in numerical simulations. A challenge ahead, as discussed in Melián, et al. 2011, is to understand the consequences of processes acting at different levels of organization (from individuals to communities) and the role of evolution on ecological dynamics.

De Angelis, Don L. 1975. Stability and connectance in food web models. *Ecology* 56.1: 238–243.

This study is an early attempt to reconcile the analysis introduced by May (see May 2001, cited under Foundational Works) with the idea that complexity can promote stability. It shows that under some conditions, complexity can in fact emerge in stable, species-rich communities. Available online for purchase or by subscription.

Fontaine, Colin, Isabelle Dajoz, Jacques Meriguet, and Michel Loreau. 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology* 4.1: e1.

The authors experimentally manipulate the diversity of pollinators in nature and analyze the effects on the diversity of plants. A higher diversity of pollinators led to a higher diversity of plants. This study is one good example of how to explore, with experiments, the effects of diversity on dynamics in networks.

Gross, Thilo, Lars Rudolf, Simon A. Levin, and Ulf Dieckmann. 2009. Generalized models reveal stabilizing factors in food webs. *Science* 325.5941: 747–750.

The authors use general modeling to explore the stability in food webs. General modeling allows them to incorporate the nonlinearities in the analysis and to avoid computational limitations to explore billions of theoretical networks. One of the main conclusions of the study is that stability emerges more easily in the presence of a generalist top predator. Available online for purchase or by subscription.

Kondoh, Michio. 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299.5611: 1388–1391.

Kondoh incorporates the adaptive behavior of foragers on the analysis of species persistence in food webs and shows that adaptive behavior favors the stabilization of complex food webs. Available online for purchase or by subscription.

McCann, Kevin S. 2000. The diversity–stability debate. *Nature* 405.6783: 228–233.

This article is a review of the complexity–stability debate. Special attention is given to ways by which one can address the problem of species-rich communities being intrinsically unstable.

Melián, Carlos J., César Vilas, Francisco Baldó, Enrique González-Ortegón, Pilar Drake, and Richard J. Williams. 2011. Eco-evolutionary dynamics of individual-based food webs. *Advances in Ecological Research* 45:225–268.

The authors introduce a model that incorporates the individual variation within species to investigate the contribution of individual variation to the structure and dynamics of food webs. The results suggest that intraspecific variation affects the degree of coupling between ecological and evolutionary dynamics. Available online for purchase or by subscription.

Okuyama, Toshinori, and J. Nathaniel Holland. 2008. Network structural properties mediate the stability of mutualistic communities. *Ecology Letters* 11.3: 208–216.

This article uses numerical analyses of sets of differential equations and the analyses of Jacobian matrices to explore the consequences of structure and diversity for the stability of mutualistic networks. This work challenges the view that mutualistic interactions are intrinsically unstable. Available online for purchase or by subscription.

Polis, Gary A. 1991. Complex trophic interactions in deserts: An empirical critique of food-web theory. *American Naturalist* 138.1: 123–155.

This article provides a critical assessment of several assumptions of stability analysis in food webs. Polis uses the natural history of a well-studied system in different sites to challenge many aspects of the food web theory. Available online for purchase or by subscription.

Conservation Biology

If the stability of populations and of the entire community is affected by the patterns of interaction among species, one central problem in the study of ecological networks is to infer how natural communities are responding to different forms of human impact, as reviewed in Tylianakis, et al. 2010. For example, as reviewed in Woodward, et al. 2010, we now have some evidence of how species within networks react to climate change. Along the same lines, studies such as Fortuna and Bascompte 2006 explore how the structure of ecological networks may affect species persistence due to habitat loss. In addition, simulations of species removal provide not only insights on the robustness of ecological networks to species extinctions, as discussed in Solé and Montoya 2001, but also give information on how co-extinctions erode the diversity, as in Rezende, et al. 2007. In recent years, the studies based on simulations of species removal have been incorporating more and more information about the biology of interacting organisms. For instance, Kaiser-Bunbury, et al. 2010 incorporates information on biological attributes, such as the behavior of interacting species, in the simulations of species extinction. Furthermore, evidence derived from empirical studies suggests that species loss does not occur randomly in ecological networks but depends on specialization and species-local abundances, such as in Aizen, et al. 2012. We are now starting to explore how different networks will respond to similar perturbations, and evidence reported in Pocock, et al. 2012 suggests that different types of interactions respond in distinct ways.

Aizen, Marcelo A., Malena Sabatino, and Jason M. Tylianakis. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science* 335.6075: 1486–1489.

This empirical study explores the effects of species loss on the organization of pollination networks. It indicates that low interaction frequency and high specialization between interacting partners contribute to the disruption of interactions. Available online for purchase or by subscription.

Fortuna, Miguel A., and Jordi Bascompte. 2006. Habitat loss and the structure of plant–animal mutualistic networks. *Ecology Letters* 9.3: 281–286.

This theoretical study generalizes previous work on metacommunity dynamics involving few species to complex, mutualistic networks. It shows that the structure of mutualistic networks favors persistence of species in landscapes facing habitat loss. Available online for purchase or by subscription.

Kaiser-Bunbury, Christopher N., Stefanie Muff, Jane Memmott, Christine B. Mueller, and Amedeo Caflisch. 2010. The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour. *Ecology Letters* 13.4: 442–452.

Analyses of the potential effects of species removal are always performed assuming static representations of ecological networks. This study incorporates pollinator behavior in the analysis by using empirical data on temporal variation of patterns of interaction to estimate the potential of pollinators to rewire their interactions in the absence of a specific interaction partner. Available online for purchase or by subscription.

Pocock, Michael J. O., Darren M. Evans, and Jane Memmott. 2012. The robustness and restoration of a network of ecological networks. *Science* 335.6071: 973–977.

A central question in the conservation of ecological networks is whether multiple networks of interacting species at the same area will respond similarly to perturbations. This study investigates the fragility of multiple ecological networks in an agroecosystem. The authors suggest that robustness varies across different ecological networks, with no significant covariation in the robustness of distinct networks. Available online for purchase or by subscription.

Rezende, Enrico L., Jessica E. Lavabre, Paulo R. Guimarães Jr., Pedro Jordano, and Jordi Bascompte. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448.7156: 925–928.

This study shows that the patterns of interaction in mutualistic networks present a significant phylogenetic signal. Consequently, extinction could be eroding the phylogenetic diversity faster than would be expected by chance, as indicated by simulations of species removal. Available online for purchase or by subscription.

Solé, Ricard V., and José M. Montoya. 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society B—Biological Sciences* 268.1480: 2039–2045.

This simulation study explores how species loss would affect the structure of food webs. It introduces approaches derived from the analysis of robustness of complex networks in physics into ecology. Available online for purchase or by subscription.

Tylianakis, Jason M., Etienne Laliberté, Anders Nielsen, and Jordi Bascompte. 2010. Conservation of species interaction networks. In *Special issue: Conserving complexity: Global change and community-scale interactions/tropical forest biodiversity in a human-modified world: A Multi-Region Assessment*. Edited by Edited by Teja Tscharntke, Jason Tylianakis, Toby A. Gardner, Jos Barlow, Navjot S. Sodhi and Carlos A. Peres. *Biological Conservation* 143.10: 2270–2279.

This review focuses on the aspects of network structure that are likely to confer robustness to ecosystem services. Special attention is given to the big challenges ahead, such as how to incorporate ecological networks in conservation biology. Available online for purchase or by subscription.

Woodward, Guy, Jonathan P. Benstead, Oliver S. Beveridge, et al. 2010. Ecological networks in a changing climate. In *Special issue: Ecological networks*. Edited by Guy Woodward. *Advances in Ecological Research* 42:71–138.

A detailed review of the role of climate change in changing different aspects of ecological networks. The analysis includes multiple levels of ecological organization and focuses on detailed consequences of climate change for aquatic food webs. Available online for purchase or by subscription.