From Small to Large Ecological Networks in a Dynamic World

Mercedes Pascual
Jennifer A. Dunne

Food webs are one of the most useful, and challenging, objects of study in ecology. These networks of predator-prey interactions, conjured in Darwin's image of a "tangled bank," provide a paradigmatic example of complex adaptive systems. While it is deceptively easy to throw together simplified caricatures of feeding relationships among a few taxa as can be seen in many basic ecology text books, it is much harder to create detailed descriptions that portray a full range of diversity of species in an ecosystem and the complexity of interactions among them (fig. 1). Difficult to sample, difficult to describe, and difficult to model, food webs are nevertheless of central practical and theoretical importance. The interactions between species on different trophic (feeding) levels underlie the flow of energy and biomass in ecosystems and mediate species' responses to natural and unnatural perturbations such as habitat loss. Understanding the ecology and mathematics of food webs, and more broadly, ecological networks, is central to understanding the fate of biodiversity and ecosystems in response to perturbations.

Ecological Networks: Linking Structure to Dynamics in Food Webs,
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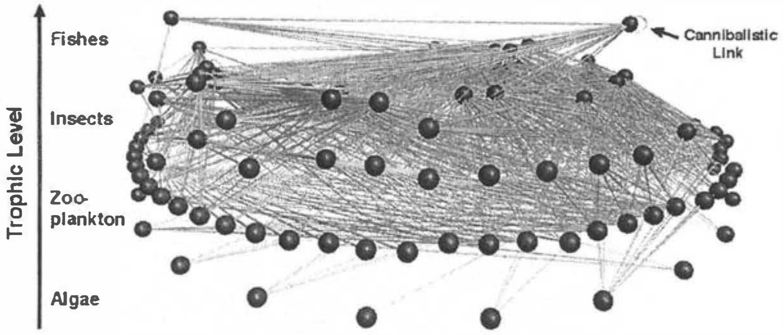

FIGURE 1 A detailed food web of Little Rock Lake, WI, with 997 feedings links among 92 taxa (Martinez 1991). Ecosystems are complex networks consisting of many species that interact in many different ways with each other and their environment. Food webs focus on the feeding relationships among co-occurring species in a particular habitat. In this image, each node represents a "trophic species" that may be a biological species, a group of species, a life-history stage of a species, or organic matter such as detritus (Briand and Cohen 1984). Each trophic species in a food web is functionally distinct; i.e., has a set of predators and prey that differ, even if only by one predator or prey item, from those of other trophic species. This image was produced using FoodWeb3D software written by R. J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab (www.foodwebs.org).

Research on ecological networks is also important for understanding the consequences of biodiversity itself for ecosystem function. Much theoretical and empirical food-web research, as well as other ecological research, has oriented itself around various notions of stability (Box 1). Ultimately, stability properties matter to the functioning of ecosystems and to the all-to-often unacknowledged services they provide to humans (Box 2). While a large body of research addresses the relationship between biodiversity and ecosystem functions such as primary productivity, the ecological networks considered in those studies are generally restricted to one or two trophic levels, and usually focus on interactions among competitors for one or a few resources (Kinzig et al. 2002; but see Montoya et al. 2003). The importance of extending studies of biodiversity-ecosystem function to include multiple trophic levels and complex predator-prey interactions has been recently emphasized (Dobson et al. in press; Worm and Duffy 2003). A better understanding of dynamics in large, complex networks is an important intermediate step in addressing how the functioning of ecosystems is influenced by structural properties of the underlying network.

Box 1: Different definitions and concepts of "stability" used in ecology

- **Local Asymptotic Stability (LAS):** An equilibrium is said to be locally stable if arbitrarily small perturbations away from this steady state always decay. Close to equilibrium, nonlinear systems can be approximated by a linear set of equations, $d\mathbf{x}/dt = \mathbf{A}\mathbf{x}$, that govern the dynamics of perturbations (with the vector $\mathbf{x}$ specifying the deviations from equilibrium). Written in this form, the system is specified by a matrix $\mathbf{A}$, the so-called community matrix in the case of ecological networks, whose dominant eigenvalue rules the exponential decay or growth of perturbations in the long term (May 1973; Pimm 1982). Local stability technically refers to asymptotic or long-term behavior, thus providing no information on the short-term or transient response to perturbations (Neubert and Caswell 1997; Chen and Cohen 2001b). For nonlinear systems, it is well known that the possible coexistence of multiple equilibria (and other attractors) further limits the relevance of this form of stability.
- **Resilience:** Resilience is closely related to the concept of local asymptotic stability and measures how fast a stable system returns to equilibrium following a perturbation away from it. Resilience is quantified as the absolute magnitude of the largest real part of any of the eigenvalues of the community matrix (Pimm and Lawton 1977; Pimm 1982). Ecosystem resilience has also been defined as the magnitude of perturbation that can be tolerated before a change in system control and structure (Holling and Gunderson 2002), but this definition is better described by the terms resistance or robustness.
- **Reactivity:** Reactivity is one of the measures characterizing the short-term transient response of a locally stable system to a perturbation away from equilibrium. It specifies whether perturbations can initially grow and be amplified, in spite of the eventual return of the system to equilibrium. Reactivity is calculated as the maximum instantaneous rate at which perturbations away from equilibrium can be amplified (Neubert and Caswell 1997; Chen and Cohen 2001b; Ruiz-Moreno et al. Chapter 7). Other relevant quantities characterizing the "stability" of transients are the size and time of the maximum amplification of perturbations (Neubert and Caswell 1997). The following measures move away from an emphasis on small perturbations in an arbitrarily small neighborhood of equilibria, and in some cases, away from the focus on equilibrium behavior altogether, allowing for stability concepts related to more complex nonlinear dynamics, such as cycles and chaos.

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In the rest of this introduction we provide a brief sketch of the historically central problem in trophic ecology, the relationship between species diversity and community stability. This points the reader to a few of many key books and papers in food-web research (see also Box 3), and sets the stage for outlining how the chapters in this book further develop issues of complexity and stability and

Box 1 continued

- **Qualitative Global (Asymptotic) Stability (QGAS):** Qualitative stability refers to the tendency of a system to return to equilibrium when interaction coefficients are specified only by their sign and not by their magnitude. It is global in the sense that this return is also independent of initial conditions. Thus, QGAS can evaluate responses to large perturbations. The qualitative theory of nonlinear differential equations has been applied to the QGAS of food webs (Cohen et al. 1990; Chen and Cohen 2001a).
- **Permanence and persistence:** These measures do not rely on the existence of any single specific type of attractor but focus instead on whether species remain in the system. Thus, permanence measures whether the system's variables remain bounded and positive. More technically, a system is said to be permanent if the boundary of the positive quadrant of state space is a repellor (Hofbauer and Sigmund 1998; Chen and Cohen 2001a). One way to determine permanence is by numerical invasibility analysis, in which the species are deleted one at a time to examine if they can reinvade from arbitrarily small numbers. For more technical criteria (i.e., sufficient conditions for permanence) applied to Lotka-Volterra systems, see Jansen (1987), Law and Morton (1993), and Chen and Cohen (2001a). Persistence is in turn determined via numerical simulation, by examining the trajectories of the dynamical system for a large number of initial conditions and for a prescribed window of time (e.g., Martinez et al. Chapter 6). For the possible discrepancies between permanence and persistence, see Law and Morton (1993) or Chen and Cohen (2001).
- **Invasibility:** Invasibility measures the likelihood that new species are able to invade an established community of interacting species. It is generally evaluated in assembly models of ecological networks (e.g., Kokkoris et al. 1999).
- **Variability:** Variability measures the magnitude of fluctuations in species' numbers. For a given species, it is computed as the coefficient of variation (standard deviation divided by the mean) of its abundance over time (Pimm 1984).
- **Robustness:** Robustness focuses on the persistence of features of interest in a system's response to perturbations, particularly those the system does not normally experience in its development or history (Jen 2003). It has been measured in a variety of ways depending on the system being studied, for example the likelihood of cascading secondary extinctions resulting from primary biodiversity loss in ecological networks (e.g., Dunne et al. 2002b).

expand into new areas of structure and dynamics, especially within the context of broader theory related to networks and complex systems.

The nodes of Darwin's "tangled bank" are species, whose identity, abundances, and biomasses provide means of measuring biological diversity. The links between the nodes (fig. 1) represent feeding relationships, and potentially other interactions, that account for the connectivity of ecological networks. Species richness and connectance, the proportion of possible interactions that actually occur, have often been used in food-web research as basic measures of complexity. These simple measures are highlighted in the influential work of May (1972, 1973) on the relationship between complexity and ecosystem stability. In this and other early theoretical food-web research, dynamical stability was equated with the mathematical concept of local stability, measured as the tendency of an arbitrarily small perturbation to grow or contract in the proximity of an equilibrium point. Much has been said about the relevance of this concept in ecology (e.g., McCann 2000; Dunne et al. 2005), and other interpretations of ecosystem stability have been used, including resilience, invasibility, persistence, permanence, and robustness (e.g., Holling 1973; Pimm 1984; McCann, 1998; Kokkoris et al. 1999; Chen and Cohen 2001a; see also Box 1).

Connectance and species richness provide simple characterizations of ecological network structure by describing global properties of an entire network of interacting species. A much larger set of properties that describe other aspects of global structure as well as more local characteristics of species and links quickly accumulated to address the existence of regularities in the structure of food webs (Lawton 1989; Cohen et al. 1990a; Pimm et al. 1991). More recently, the explosion of research on network topology as a fundamental aspect of the study of complex systems (Strogatz 2001; Albert and Barabási 2002) has stimulated new efforts to unravel regularities of ecological network structure (e.g., Camacho et al. 2002; Dunne et al. 2002a; Garlaschelli et al. 2003; Jordano et al. 2003).

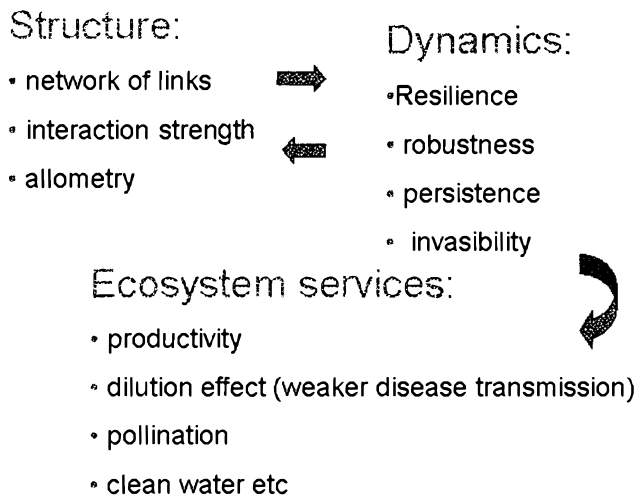
Species richness and connectance thus provided an early, and continuing, point of contact and integration between quantitative assessments of both dynamics and structure. Such integration has even deeper roots, since it emerged out of May's challenge to prior claims that complexity should enhance stability of ecosystems (e.g., Odum 1953; MacArthur 1955), which in turn emerged out of the very early recognition of the fundamental connection between ecological structure and function (Elton 1927). This core ecological notion continues to inform much current research. Interestingly, one of the most challenging problems across many scientific fields today is the relationship between the structure of complex networks and their nonlinear dynamics (Strogatz 2001). Complex networks are characterized not only by numerous components that interact, but by interactions that are nonlinear, are distributed non-randomly, and are adaptive, i.e., changing continuously in response to the state of the system itself. These characteristics obviously apply to food webs, and more broadly, to ecosystems. Ways that ecologists come to understand the interplay between structure and dynamics of ecosystems can, and should, influence research in other fields, as well as the reverse.

Within ecology, even though complex webs of many interacting species are widely observed in nature, understanding their persistence remains puzzling. This is largely due to methodological limitations. It is basically impossible to manipulate diverse assemblages of species in natural systems in a controlled, replicated, ethical fashion; experimentation using microcosms is limited in the diversity it can embrace; simple models may not be scalable to more complex systems or may oversimplify biology; and conducting nonlinear dynamical simulations of "virtual ecosystems" that are diverse and incorporate plausible biological processes is only now becoming computationally tractable, but presents its own challenges such as how to sensibly explore giant parameter spaces. Earlier complexity-stability research has generally focused on simple dynamical models such as linear approximations close to equilibrium and Lotka-Volterra equations; these early models often suggested that complexity gets in the way of stability (e.g., May 1972; Pimm and Lawton 1977, 1978). Since then, the inclusion of plausible structural elements, nonlinearities, and/or variable interaction strengths (De Angelis 1975; Yodzis 1981; Pimm 1982; de Ruiter et al. 1995; McCann and Hastings 1997; McCann et al. 1998) in simple models provide some glimpses at constraints that might lead to stability or persistence of diverse, complex systems. Understanding stability and persistence, in turn, can help us understand how and why ecosystems are robust or sensitive to human-related perturbations, the central concern of conservation biology.

The interplay between ecological structure and dynamics has many nuances. For example, the notion of incorporating not only the presence or absence of links between species but the strength of those interactions is clearly important for dynamical modeling (starting with De Angelis 1975), and there may be general patterns of how interaction strengths are distributed in ecological networks that relate to stability (Neutel et al. 2002). A different issue concerns how ecological network structure is studied. Most structural studies focus on "snapshots" of ecological networks, by compiling a master list of species and their observed interactions integrated over some sufficiently inclusive, albeit somewhat arbitrary, temporal and spatial scale. This strategy allows researchers to go beyond the contingent details of local dynamics of a few interacting species to look for a bigger, simpler picture where coarse-grained patterns, ideally with governing processes, may (or may not!) emerge (Brown 1995; Lawton 1999). However, structure is clearly dynamic at many scales, changing in time and space as the result of the plasticity of ecological interactions, environmental variation, and assembly processes that occur at both ecological and evolutionary time scales. Dynamic aspects of structure may also prove crucial for our understanding of stability and persistence.

While most observations and theory pertain to webs of trophic interactions, recent efforts that focus on parasites and mutualistic relationships underscore the importance of extending the scope of ecological network studies to embrace other kinds of interactions. Furthermore, the large and increasing body of ecological literature on higher-order interactions such as phenotypic plasticity (see review by Bolker et al. 2003) demonstrates that the strength of interactions between species is not constant but varies in response to various indirect effects that extend beyond the densities of directly interacting species (Peacor and Werner 2001). Consequences of such plasticity and other types of indirect effects, which can play as important a role as direct effects (Menge 1995), need to be explored

Box 2. Linkages among structure, dynamics, and ecosystem services



Structure:

- network of links
- interaction strength
- allometry

Dynamics:

- Resilience
- robustness
- persistence
- invasibility

Ecosystem services:

- productivity
- dilution effect (weaker disease transmission)
- pollination
- clean water etc

systematically with regard to their impact on the dynamics and structure of high-dimensional systems.

The first section of this book focuses on the history of and recent advances in uncovering regularities and universal patterns in the structure of complex ecological networks, with a focus initially on food webs that is followed by work on other types of interactions (parasitism, mutualism). The second section moves to the explicit coupling of structure and dynamics, and is followed by a set of chapters that address various aspects of adaptation at ecological and evolutionary time scales. The importance of an ecological network approach to conservation and restoration is emphasized in the final section, which includes an outline of a series of open empirical and theoretical questions. More challenges for the future are raised in the concluding chapter. A brief roadmap of these sections follows below.

STRUCTURE OF COMPLEX ECOLOGICAL NETWORKS

Within the study of complex systems, one pervasive subject is the characterization of the structure of biotic and abiotic networks that include dozens to millions of nodes. From studies of the structure of the internet and the World Wide Web, to those of the social links that underlie the transmission of innovation as well as infectious disease, network research is becoming omnipresent across disciplines, spawning thousands of papers and a number of popular books (e.g., Watts 1999, 2003; Barabási 2002; Buchanan 2002; Strogatz 2003). Well before the current re-popularization of research on the non-random, non-regular structure of "real-world" networks (Watts and Strogatz 1998), as informed by earlier graph theory (Erdös and Rényi 1960), ecologists were starting to characterize apparent generalities in the non-random structure of food-web networks (Cohen 1978) and to develop models inspired by graph theory to explain observed generalities (Cohen and Newman 1985). There is a rich and stormy history of empiricism and modeling related to complex food-web structure, with important ecological and graph-theory contexts that extend to the present day (Dunne Chapter 2; Cartozo et al. Chapter 3). Just as other kinds of network structure research have undergone a renaissance, there has been a recent renewed interest in potential generalities and simple models relating to the structure of food webs. This interest has resulted in a number of novel studies that are building on a new generation of improved food-web data (Dunne Chapter 2; Cartozo et al. Chapter 3).

For the most part, the links typically considered in the literature are conventional "predator-prey" interactions. Recent work has begun to expand this view to include other kinds of interactions. One important example is parasitism (Dobson et al. Chapter 4). The unintended introduction of parasites into ecosystems, such as rinderspest in the Serengeti and lampreys into the Great Lakes, provide some dramatic examples of the important role parasites can play in the dynamics of food webs (Dobson Chapter 4, Box C). While a few excellent studies have explicitly considered or focused on the role of parasites and parasitoids in ecological network structure (Huxham et al. 1996; Martinez et al. 1999; Memmott et al. 2000; Leaper and Huxhman 2002), more are needed. A recent study on coastal salt marshes (Lafferty et al. in press) illustrates the enormous field efforts required to obtain the data on both trophic and parasitic interactions. More importantly, it demonstrates the critical role played by parasites in both the structure and the biomass flow of ecosystems. Recent analysis of these data demonstrates that parasitic links are not distributed randomly upon the underlying trophic network (Warren et al. in prep). Instead, a clustering structure is apparent with measures that extend the concept of clustering coefficient (Dunne Chapter 2; Cartozo et al. Chapter 3) to networks with two types of links, trophic and parasitic ones. Because parasites are typically smaller than their hosts, their consideration is also likely to illuminate the role of size in determining network structure.

Research on ecological network structure is also being expanded to include plant-animal mutualisms (Bascompte and Jordano Chapter 5). While these are also a type of consumer-resource interaction, their consequences include positive effects that go far beyond classic "negative" feeding effects. For example, an animal feeds on the fruit of a plant, and then benefits that plant by acting as a dispersal vector for its seeds. These types of not-strictly-feeding interactions are revealing fascinating nonrandom network patterns that reflect coevolutionary dynamics likely to have important consequences for conservation. Those consequences (e.g., Memmott et al. 2004) are largely unexplored, and represent an important future area of research (Bascompte and Jordano Chapter 5; Memmott et al. Chapter 14).

INTEGRATING ECOLOGICAL STRUCTURE AND DYNAMICS

Two challenges are immediately obvious in addressing the dynamics of large networks. The first one concerns the need to specify appropriate non-random structures consistent with empirical patterns. The second one is that predator-prey and therefore food-web models are prototypical examples of nonlinear systems, capable as such of generating a variety of non-equilibrium behaviors including cycles and chaos (Hastings and Powell 1991; Fussman and Heber 2002). While mathematical analysis is difficult for low-dimensional nonlinear systems and usually impossible for large ones, the alternative of numerical exploration of parameter space through computer simulation is quickly limited by the size of the system being explored.

Static (probabilistic) models to generate the non-random trophic structure of ecological communities (Dunne Chapter 2) provide a starting point to investigate the dynamics of more realistic network models. For example, the niche model of Williams and Martinez (2000) successfully generates a network of links that shares many properties with empirical food webs. A dynamical model for trophic interactions can then be built upon the resulting structure (Martinez et al. Chapter 6). This set of differential equations for the nonlinear population dynamics of the interacting species is based on a bioenergetic model (Yodzis and Innes 1992) describing realistic biology with relatively simple parameters. The resulting hybrid model, which couples structure and dynamics, allows for the persistence of a surprisingly large number of species, as demonstrated with numerical explorations of parameter space and comparisons to the corresponding models for less realistic structures, including random ones. Such hybrid models provide a promising way to address feedbacks between structure and dynamics. An earlier example is found in the Lotka-Volterra cascade model (LVCM) which generates network structure via the cascade model, a predecessor of the niche model (Cohen et al. 1990b). Interestingly, the qualitative global stability (Box 1) of this hybrid model was studied analytically in the limit of a large number of species and long time sequences. Analytical results on these high-dimensional nonlinear systems are rare, if almost non-existent, and focus on ecological networks in which the signs and not the numerical values of the interaction coefficients are considered. They provide stability conditions that can be evaluated numerically (e.g., Chen and Cohen 2001a). As an alternative, numerical simulations of the dynamical system itself must be performed, but these still require a number of simplifying assumptions, such as similar values for specific parameters across species, to reduce the enormous size of parameter space (Martinez et al. Chapter 6).

Genetic algorithms (GAs; Holland 1975; Mitchell 1996) provide one possible numerical approach to explore the large space of parameters specifying the dynamics of networks (e.g., Sporns and Tononi 2002). They further allow the exploration of the large "network" space of possible structures, where the links between species are not predefined. Instead of specifying a structure and asking what are its dynamic consequences, one can address the opposite question of which structures exhibit particular dynamical properties of interest. Network space is explored by an "evolutionary" process that selects for those networks with the desired dynamical properties. Ruiz-Moreno et al. (Chapter 7) provides an example of an application to the local stability of food webs, and explores the relationship between network modularity and the response of the system to perturbations. Although this first application to food webs considers only linear dynamics close to equilibrium, the nonlinear case can also be explored but is computationally more taxing (see Sporns and Tononi [2002] for an example in neurobiology). While earlier work had considered the effect of compartments on long-term stability, results in this chapter indicate that modularity may be critical in short-term transient responses. The importance of considering short-term transient responses when evaluating the stability of food webs has also been recently emphasized by Chen and Cohen (2001b).

Another approach to reduce the size of network and parameter space consists of constraining parameters or structure based on empirical findings (e.g., Yodzis 1982: Emmerson and Raffaelli 2004). One potential avenue for realistic parameterizations is given by allometric scalings describing how specific parameters vary as a power-law function of the size of organisms (e.g., Raffaelli and Hall 2004). This approach is not new to biological oceanographers and plankton ecologists, but a substantial part of their work in this area concerned ecosystem models, and targeted steady-state dynamics and explanations for observed power-law distributions of biomass in pelagic ecosystems (e.g., Platt and Denman 1978). The few studies of the nonlinear behavior of plankton food-web models constructed with allometric scaling showed a striking propensity for unstable equilibria and pronounced fluctuations, raising questions about their applicability to nature (e.g., Moloney and Fields 1991). In the last decade, through a separate route not directly connected to trophic interactions, terrestrial ecologists have become increasingly fascinated by allometric scalings in both physiological and community patterns (e.g., Enquist and Niklas 2001; West et al. 1997; Williams 1997). While much elegant theory has focused on explanations of these patterns, steady-state (often linear) considerations have been the norm. The use of the patterns themselves in the formulation of dynamical models for ecological networks has not been pursued. Gillooly et al. (Chapter 8) begin to explore the connection of allometry to food web theory, with regard to the use of the two different ecological currencies of numbers and energy. The final chapter on challenges for the future (Pascual et al. Chapter 15) returns to allometry and emphasizes the importance of considering deviations from both steady-state conditions and simple power laws in community patterns, to understand responses to perturbations.

Finally, the daunting size of network space can be tackled with theoretical approaches on the assembly of communities (Yodzis 1982; Post and Pimm 1983; Law and Blackford 1992; Solé et al. 2002; see also the section on "Community Assembly" in the review by Hall and Rafaelli 1993). Species are allowed to sequentially invade a previously established local community from a predefined regional pool; parameter space is thus restricted by the trajectory of the assembly process itself for persistent local networks. This is a powerful approach but one in which properties of the regional pool can exert important constraints on the local assembly process. One avenue to define those constraints within the model itself is to incorporate explicitly the evolutionary time scale.

ECOLOGICAL NETWORKS AS EVOLVING, ADAPTIVE SYSTEMS

A number of theoretical studies are beginning to address how co-evolutionary processes shape the structure of the resulting food webs (McKane and Drossel Chapter 9), and through this structure, their response to perturbations. Evolutionary processes can also influence dynamical properties by modifying interactions over ecological time scales if sufficiently fast, as has been shown with a predator-prey model formulated at the individual level (Hargvigsen and Levin 1997). The central issue of "how evolution shapes ecosystem properties, and whether ecosystems become buffered to changes (more resilient) over their ecological and evolutionary development or proceed to critical states and the edge of chaos" (Levin 1998; see also Kauffman 1993) could have been explicitly written for the ecological networks that underlie ecosystems. In fact, the view of ecosystems as "prototypical examples of complex adaptive systems" (Levin 1998) is very much based on properties of ecological networks, namely the nonrandom distribution and nonlinear nature of interactions between species, and levels of selection that are below that of the whole structure. Different chapters in this book (Ruiz-Moreno et al. Chapter 7; Peacor et al. Chapter 10; Wilke and Chow Chapter 11) illustrate approaches from CAS. In addition, computational approaches centered on the concept of digital organisms begin to provide the tools to explore the assembly and dynamics of ecological networks *in silico* (Peacor et al. Chapter 10; Wilke and Chow Chapter 11). Several chapters (McKane and Drossel Chapter 9; Martinez Chapter 12; Pascual et al. Chapter 15) outline a series of open questions at the interface of ecology and evolution. The concept of instability boundaries, and the related idea of "self-organized instabilities" (Solé et al. 2002) are discussed, emphasizing the need to better understand under what conditions ecological networks converge to these boundaries (Pascual et al. Chapter 15).

Besides evolutionary and ecological time scales, the dynamics of ecological networks are influenced by changes that are behavioral and modify the structure of interactions. Phenotypic plasticity and other forms of higher-order interactions underscore the adaptive nature of food webs at shorter, behavioral, time scales (Peacor et al. Chapter 10). The structure itself must now be viewed as dynamic, continuously changing as a function of the state of the system. It is increasingly recognized that interaction strength varies not just as a function of the two species directly involved in the interaction, but with the abundance of other species in the network. Well-known examples of these so-called higher-order interactions are given by predator switching, in which predation on any one prey is also a function of the relative abundances of the other prey, and by predator (or pathogen) regulation of herbivores (Packer et al. 2003). For example, predator switching was incorporated in plankton ecosystem models, where its stabilizing effect on equilibria has been well known for a long time (e.g., Fasham et al. 1990). It was also considered in a recent theoretical study of large food webs to reexamine the question of complexity and stability (Kondoh 2003). Another suite of examples is provided by phenotypic plasticity. Changes in behavioral or physiological traits of a prey, driven by the presence of a predator, affect in turn its own ability to forage and therefore its own predation rate (e.g., Peacor et al. Chapter 10; Peacor and Werner 2001). Indirect interactions of this sort are not mediated by density but by traits, and contrast with the lethal effects of predators typically represented in graphs of food webs. On the dynamic front, experiments and models have shown that phenotypic plasticity can have significant effects, although only low numbers of species have been considered so far (see review by Bolker et al. 2003). These studies have also represented phenotypic plasticity with a prescribed functional form at the population level (e.g., Ives and Dobson 1987). Because these functional forms are not really known, there is significant scope for formulating models at the individual level and using the models themselves to examine representations at the more aggregated population level (Bolker et al. 2003; discussion in Peacor et al. Chapter 10).

STABILITY AND ROBUSTNESS OF ECOLOGICAL NETWORKS

Although the relationship between complexity and "stability" is a fascinating theoretical question that continues to prove mathematically and computationally challenging after many decades, it is important to recognize that a main motivation behind the early thoughts on this subject was to address applied issues in the conservation and management of ecological systems. For example, in his still cited masterwork "The Ecology of Invasions by Animals and Plants," Elton (1958) wrote that "the enormous problem still is to manage, control, and where necessary alter the pattern of food-chains in the world, without upsetting the balance of their populations. It is this last problem that has not by any means been solved, and which is exacerbated every year by the spread of species to new lands." On a more, if not overly, optimistic tone he added, "Once the notion is grasped that complexity of populations is a property of the community, to be studied and used in conservation, there is hardly any limit to the ways in which it could be introduced."

The last section of this book treats the subject of ecological networks and their robustness to perturbations within the realm of conservation and restoration. The effects of habitat destruction and fragmentation are addressed, as well as the collapse of ecological networks following spatial perturbations and species' extinctions. One way of thinking about these issues is in the context of ecosystem "robustness," where robustness is a type of stability that focuses on the persistence of features of interest in a system's response to perturbations, particularly those it does not normally experience in its development or history (Jen 2003). Thus, robustness is a useful way to think about ecosystem response to perturbations such as species loss. Memmott et al. (Chapter 14) outline a series of open questions for future theory but also empirical work. The case is convincingly made for the importance of a network, multi-trophic, approach to conservation and restoration. Solé et al. (Chapter 13) emphasize spatial considerations from a network perspective.

Ultimately, a significant proportion of the quality and possibly even the persistence of human life is dependent upon the conservation of natural ecosystems. The conservation of functioning ecosystems will only benefit from a deeper understanding of the robustness and resilience of ecological networks, and of the structural features that underlie their dynamical responses to perturbations. It is one of the defining scientific problems of the twenty-first century as only now do we have the computing power to examine problems which involve evolving nonlinear interactions among large numbers of different components whose sizes, rates of birth-death, interaction strengths, and other factors vary over many orders of magnitude. The problems have daunting scales of complexity, yet their solution will not only contribute to the development of the mathematics of complexity, they may also enhance our ability to preserve the invaluable diversity of nature.