

# Challenges for the Future: Integrating Ecological Structure and Dynamics

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The visual tension between the orderly representation of the *tocapu* designs in the *pallai* and the apparent scattering of elements in the *pampas* reflects an important Inca's aesthetic principle: a chaos and order that is analogous to the relationship between nature and culture.

—The Colonial Andes: Tapestries  
and Silverworks, 1530–1830  
(Metropolitan Museum, NY, 2004).

## 1 INTRODUCTION

The tapestries of the Incas, particularly the large areas of those tapestries called “pampas” that include a myriad of animals and plants, provide one example of humans’ understanding of the complexity of nature. Remarkably, a sense of order emerges from these apparently chaotic representations because of their interplay with the more regular patterns included in the whole. Standing in front

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of one of these marvelous representations of the natural world, one is reminded of the enormous complexity of ecological systems and of the past and present efforts to unravel the order behind it. The presence in the pampas of human figures and hybrid deities, with more and more apparent elements of outside influences, is a reminder of the importance of uncovering the critical properties of ecological networks that confer robustness to change. A better understanding of the properties that sustain the persistence of diverse ecosystems and their functions is crucial at this time of rapid environmental change and habitat loss, when perturbations of structure are unavoidable.

We started this book with a reference to Darwin's famous "tangled web," one of the earliest scientific images of the complexity of food webs and ecological networks, and one that continues to be relevant today. The challenging subject of food-web structure and its relationship to dynamics and stability has fascinated ecologists for a long time and has stimulated heated debates (Box 3, Pascual and Dunne Chapter 1; Dunne Chapter 2). In our view, the recurrent tensions regarding evidence for the existence of generalities in network structure and for valid theoretical approaches to address the dynamics of high-dimensional nonlinear systems have played an essential role in the development of the field. Pimm et al. (1991), in a review of an earlier period of intense research on food webs, argued for the existence of generalities in structure and for their relevance to dynamics. While improved data have challenged the generality of these early patterns, new regularities are emerging as are new approaches for investigating the interplay between structure and dynamics and their relationship to different aspects of ecosystem stability. In this book, we return to the subject at a time when network research has become a fundamental focus of the study of complex systems across many fields. While considerable advances have been made in the description of network structure for many types of systems, modeling the nonlinear dynamics of large networks remains a challenge for now and the future (Strogatz 2001).

The first section of this book reviewed what we know about food-web structure in light of these advances, as well as recent extensions to ecological networks that encompass other interactions, including parasitism and mutualism. The second and third sections illustrated recent and incipient efforts to tackle the full nonlinear dynamics of large networks in connection to structure, as well as recent theoretical advances in models for the evolution, assembly, and dynamics of ecological networks. Several chapters introduced computational approaches from the theory of complex adaptive systems, such as genetic algorithms and digital organisms, to highlight their potential utility for food-web research. The final section discussed issues at the intersection of ecological network research and more applied issues, for example, the importance of a multitrophic level perspective for conservation and restoration, with particular emphasis on the impact of habitat loss and fragmentation. In spite of all of the recent and ongoing research on networks in general and food webs in particular, a new synthesis of the relationship between structure and dynamics of complex networks remains premature. For

that reason, we focus here on some areas we consider key for future theory to achieve such a synthesis in ecological network research. The sections that follow touch on three basic properties of complex systems that make the study of their dynamics especially difficult: their adaptive character, the nonlinearity of their interactions, and their large number of components. We emphasize a dynamic view of whole-system robustness that is consonant with, and can emerge from, instability at smaller scales.

## 2 WEAK INTERACTIONS AND THE NONLINEAR DYNAMICS OF LARGE NETWORKS

One aspect of structure likely to be particularly important to the dynamics of large networks is the distribution of variable “interaction strengths” of the links in the web. The theoretical finding that interaction strength is one key property that promotes persistence in nonlinear models of food webs has attracted considerable attention. Weak interactions have been proposed as the “glue” that binds large networks together (McCann et al. 1998), with ramifications for the value of biodiversity itself, and in particular for the potential importance of the many species in nature whose low abundances and weak per-capita consumption rates might otherwise be taken as evidence of a negligible role (McCann 2000). The potentially important functional role of weak interactions resonates with criticisms that studies of food-web structure are based on overly simplified binary link networks, and there have been strong pleas for experimental measurements of interaction strength in the field (Paine 1992; Lawton 1992). Much research on interaction strength followed those criticisms and built on earlier pioneering empirical (e.g., Paine 1980) and theoretical (e.g., Yodzis 1981) work. However, in almost all cases there remains a significant gap in how field- and model-based inquiries define and measure interaction strength, which slows progress (Berlow et al. 2004). We focus here primarily on theoretical work, but acknowledge that such approaches need to be thoughtfully connected to field-based experimentation (e.g., Brose et al. ms.).

The influential theoretical work of McCann et al. (1998) relied on dynamical models of low-dimensional food webs consisting of two to three species and a basal resource. This approach made possible detailed numerical simulations examining how the strengths of particular interactions affect the degrees of temporal variability in species abundances. In particular, the amplitude of population fluctuations and the likelihood of low population abundances were considered to be determinants of extinction. The main working hypothesis, that inhibiting strong interactions within a food web would promote persistence, was based on the detailed studies of another low-dimensional system, a three-species food chain in which a basal resource is consumed by an herbivore, and the herbivore is, in turn, consumed by a top predator (Hastings and Powell 1991). Chaotic dynamics with large population fluctuations were shown to occur in this system from the inter-

play of two coupled oscillators. It followed that the stabilization of the individual oscillators, obtained by either reducing their amplitudes or by promoting equilibrium behavior, should, therefore, eliminate chaos or large amplitude cycles at the level of the whole system, reducing the likelihood of population extinction. This hypothesis on the inhibition of strong interactions was addressed by studying a number of different configurations for low-dimensional food webs (McCann et al. 1998). The extrapolation from these theoretical findings to properties of real food webs, particularly from a small to a large number of species, is an obvious but non-trivial step, as demonstrated by the study of large nonlinear systems of coupled oscillators, which remains a challenge across physics and biology (Strogatz 2001). In ecology, only a handful of theoretical studies have tried to tackle the role of interaction strength in the dynamics of large communities (e.g., Wilmer et al. 2002; Kokkoris et al. 1999). The stabilizing role of weak links is at least in part consistent with the earlier finding that donor-controlled predator-prey interactions have a stabilizing role in Lotka-Volterra models of communities (Pimm 1982).

One such recent study on weak interactions in large networks assembled a web recursively through a random process (Wilmer et al. 2002). It demonstrated that communities with weaker mean interaction strength support a larger number of species than those with strong mean interaction strengths. In their model, species are allowed to sequentially invade the previously established community. The strengths of their interaction links are then drawn at random from a prescribed probability distribution whose variance provides a measure of interaction strength. Local stability is then evaluated as the criterion for the addition or subtraction of the species in the assembly process. Thus, although no explicit nonlinear dynamics are considered, the long-term number of species in the persistent communities fluctuates around a stationary stochastic equilibrium, whose mean can be quite large (e.g., approximately 200). Furthermore, as the number of species increases, the communities appear more robust, in the sense that fluctuations in species numbers relative to the mean abundance decrease in amplitude. Another theoretical study considered randomly assembled communities of competing species using Lotka-Volterra equations (Kokkoris et al. 1999). Mean competition strength falls as the assembly process develops and most established interactions are weak. However, close examination of the reported distribution of interaction strengths shows that this effect is not very pronounced, with a mode at 0.5 (values range between 0 and 1) and most values falling between 0.3 and 0.6. A key observation here is that communities become refractory to further invasion once their mean interaction strength is below that of the species pool from which invaders are drawn. It is apparent from these examples that the role of interaction strength in large ecological networks remains an open subject, as only local stability close to equilibria, and simple (type I) functional responses inherent in Lotka-Volterra formulations have been considered (but see Brose et al. in review). Nevertheless, these studies produce results that may be directly compared with long-term studies of community and food-web assembly, such

as have been collected from Krakatau (Memmott et al. Chapter 14; Dobson in press).

More importantly, recent work indicates the limitations of just looking at the presence of weak interactions per se. With a generalized Lotka-Volterra model, Jansen and Kokkoris (2003) proposed that the variance, and to a lesser extent the mean, of interaction coefficients can be used to understand the local stability of ecosystems. In particular, an increase in the variance (for a constant mean) tends to decrease the probability that an equilibrium is both stable and feasible (i.e., positive equilibrium population densities). They argue that connectance per se, a basic measure of complexity in May's early work, is not a critical determinant of stability. Instead, they proposed an explanation for the U-shaped relationship between connectance and stability as described in Rozdilsky and Stone (2001). Their work indicates that the presence of weak interactions cannot be evaluated without consideration of the statistical distribution of interaction coefficients.

Ultimately, the emergent properties of food-web structure are likely to go beyond the properties of the statistical distribution of interaction strengths; this is apparent in recent findings by Kokkoris et al. (2002) on the impact of correlations between coefficients and in the combined theoretical and empirical work of Neutel et al. (2002) on soil food webs. For example, Neutel et al. (2002) showed that long loops of interactions in soil food webs contain relatively many weak links and suggested that this structure is a natural consequence of the biomass pyramid of ecosystems. In the absence of weak links, long loops would be destabilizing in the mathematical sense of requiring strong intraspecific regulation to achieve local stability. One critical implication is that it is not the statistical distribution of interaction strength that matters, but instead the distribution of such weights among the links of the webs. A similar message arises from an earlier and very different type of analysis by Haydon (2000), in which the linkage between weakly and strongly self-regulated elements appears critical to the local stability of community matrices. Thus, structure involves not just the presence and absence of the links, but also the distribution of interaction strengths across these links. These features are inseparable and cannot be evaluated independently. One challenge is to identify key properties of this distribution and develop ways to characterize them in network data. Dynamical consequences for large nonlinear systems remain an open issue.

### 3 ALLOMETRIC SCALING: A BRIDGE TO REALISTIC STRUCTURES?

Another major challenge in the study of the structure and dynamics of large food webs is the large number of parameters typically required for modeling studies. Given that the analysis of their nonlinear behavior is typically restricted to numerical simulations, the choice of realistic ranges of parameters becomes critical. The problem is exacerbated as we move away from simple linear func-

tional responses for consumption. One potential avenue for realistic, simplified parametrizations is given by allometric scalings describing how specific parameters vary as functions of the size of organisms. A recent study shows that consideration of allometric relationships greatly increases the apparent stability in the dynamics of a well-described estuarine food web (Emmerson and Raffaelli 2004). By contrast, plankton ecosystem models that incorporate allometry to parametrize key rates show a striking propensity for unstable equilibria and pronounced fluctuations, raising questions about their realism. On the terrestrial side, remarkable allometric scalings have been described in both physiological and community patterns, conforming to power law patterns over many orders of magnitude (e.g., Enquist et al. 1998; West et al. 1997; Williams 1997). Much elegant theory has focused on explanations of these patterns but not on the use of the patterns themselves in the formulation of dynamical models for ecological interactions and associated networks. Consideration of deviations from both steady-state conditions and power-law patterns is likely to be important in understanding the dynamical properties that characterize the response of ecosystems to perturbations.

Regularities in the size structure of pelagic marine ecosystems were first described by Sheldon et al. (1972) who examined the distribution of particulate matter in different size classes for the upper ocean. He discovered that there are roughly equal amounts of material in logarithmically equal size intervals. Similarly, the size distribution for the living component of particulate matter in these systems conforms to a power-law relationship (of slope  $-1$  when normalized by the nominal biomass of each class; Chisholm 1992). Theoretical efforts to explain this pattern of the biomass size spectrum were closely linked to properties of trophic interactions such as predator-prey size ratios and efficiency of biomass conversion (Borgmann 1987), and to allometric scalings at the physiological level (Platt and Denman 1978). Platt and Denman (1978) considered, for example, the biomass size spectrum as continuous and described the flow of biomass up this spectrum based on the weight dependence of growth and metabolism. Although the literature on the subject is enormous, the theory is rooted for the most part in steady-state assumptions and does not address nonlinear dynamics explicitly. In one exception, Silvert and Platt (1980) discuss potential consequences of nonlinear feedbacks, including the possibility that “small oscillations in food supply can drive large resonant swings in population,” with a continuous biomass flow model that incorporates predation.

Separate from theory on biomass size spectra, plankton ecologists have more recently considered the nonlinear dynamics of size-based food webs (e.g., Moloney and Field 1991). Simple food chains with a single compartment per trophic level (i.e., phytoplankton and zooplankton) were deemed insufficient to represent the dynamics of plankton ecosystems. However, additional compartments result in additional parameters. This problem was circumvented by specifying parameters based on empirically determined body-size relationships from the literature. The resulting model was applied to three different ecosystems off the west coast of

southern Africa (Moloney et al. 1991). From a more theoretical perspective, Pahl-Wostl (1993) built similar food-web networks with trophic levels subdivided into size classes. One general property of the models was the propensity for unstable equilibria, with rapid and pronounced fluctuations of the size classes including chaotic behavior. Interestingly, stability properties in these models are a function of hierarchical scale. Thus, at the trophic level, the total biomass obtained by aggregating the component size classes exhibited much more regular dynamics with equilibrium behavior. The realism of the fast oscillations at the lower levels has been controversial. For particular size classes representing specific taxonomic groups, the fluctuations were considered pathological in their short time scales (Moloney and Field 1991; Armstrong, 1999). However, field data appear to support the “dynamic, rapidly fluctuating plankton community” simulated for the summer season at one of the sites (the Agulhas bank; Moloney et al. 1991). The mathematical origins of the within-chain instabilities have been analyzed by Armstrong (1999), using particular symmetric structures of the food web in which functional forms and parameters within classes of a given trophic level were assumed to be equal. This work further examined and proposed modifications to the structure of the basic model that dampen the instabilities and are consistent with the observed ecosystem patterns of biomass size spectra.

These examples from plankton ecology provide only a glimpse at the fascinating potential for merging allometry and food-web dynamics. The model used by Martinez et al. (Chapter 6), based on the bioenergetic framework of Yodzis and Innes (1992), provides a natural framework within which to incorporate allometric scalings and consider the dynamical consequences in large networks. This type of formulation can specifically incorporate taxonomic diversity while using a currency of relevance to biogeochemistry, ecosystem science, and evolutionary studies (see also Gillooly et al. Chapter 8). The resulting theoretical predictions are also relevant to the recent characterizations of ecosystems that consider both trophic structure and biomass distribution within a single descriptive framework (e.g., Cohen et al. 2003).

## 4 VARIATIONS ON REPRESENTATIONS OF STRUCTURE

The graphical representation of food webs as networks of nodes and links (e.g., fig. 1, Pascual and Dunne Chapter 1) pervades our perception of “structure” as a tangible and fixed object of study. This perception is supported by an extensive body of work that revealed network-structure regularities in early collections of food-web data (e.g., Cohen et al. 1990a; Pimm et al. 1991) as well as in more recent and better-sampled data sets (see review by Dunne Chapter 2). Additional types and aspects of ecological interactions may greatly complicate our view of structure and open avenues for novel characterizations.

For example, the addition of parasitic links will require extensions of the analysis of networks to account for different types of links explicitly. This is

fairly straightforward within a network structure framework (e.g., Huxham et al. 1996; Memmott et al. 2000), but it is more challenging and thus far less explored within a dynamical framework. The limiting step for assessing parasitic interactions within ecological networks is still the lack of detailed data, but new datasets continue to be compiled (e.g., Dobson et al. Chapter 4; Lafferty et al. in press; Thompson et al. 2005). Data for coastal salt marsh ecosystems (Lafferty et al. in press) reveals that the parasitic links are not distributed randomly upon the predator-prey part of the network but exhibit a higher degree of clustering (Warren et al. in prep.). This pattern is well captured by an extension of the structural niche model (Williams and Martinez 2000) developed by Warren et al. (in prep.). The analysis of data on other types of interactions, for example between plants and their mutualists such as pollinators and seed dispersers, has revealed patterns of nestedness clearly distinguishable from random patterns (Bascompte and Jordano Chapter 5). As with parasites, implications for dynamics remain to be examined. For example, do mutualistic interactions of this type have similar implications to those described for cooperative links in catalytic networks (Jain and Krishna 2001)? The relevance of mutualistic interactions for conservation is highlighted by Bascompte and Jordano (Chapter 5) and Memmott et al. (Chapter 14), with a suite of important open questions regarding the impacts of habitat destruction.

Another source of open questions on how we represent and analyze structure is the recognition 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 (see Bolker et al. 2003 for a review). One important example is phenotypic plasticity: changes in behavioral or physiological traits of a prey species that are driven by the presence of a predator, that in turn affect its own ability to forage (e.g., Peacor and Werner 2001). Because indirect interactions of this sort are not mediated by density but by traits, appropriate functional forms to represent them in typical equation-based models of food webs are not well understood. One promising theoretical approach is the use of individual-based models to derive functional forms at the population level. Peacor et al. (Chapter 10) describe a computational framework based on digital organisms that could be used for this purpose. As they demonstrate, a simple formulation of this “adaptive” approach reveals two novel mechanisms for a stabilizing role of phenotypic plasticity on dynamics. Interestingly, the model was not formulated to test specific a priori hypotheses, but instead served as a tool to explore the emergence of persistence mechanisms from individual-based assumptions. Experiments and other models typically formulated at the population level have also demonstrated the influence of phenotypic plasticity on dynamics (e.g., Ives and Dobson 1987; Kondoh 2003), but so far there is no consensus on its stabilizing role. Regardless of the modeling approach, the challenge of large systems remains.

With regard to structure, the modifications that result from phenotypic plasticity contrast with the lethal outcomes of predation typically represented in graphs of food webs. We can, therefore, think of structure as composed of not

only the direct links between nodes but also the additional links that modulate their strength. Plastic interactions in both data and models may require a fundamental reexamination of structure.

## 5 NETWORKS AND FLOWS

Properties of structure will also change in networks that more accurately represent the flow of energy in the system. The importance of currency, specifically energy vs. population numbers, has been raised by Gilooly et al. (Chapter 8). Martinez et al. (Chapter 6) also discuss some of the pathways that should be added to their “bioenergetic” food web model for further realism, including detrital pathways. These extensions would close the gap between food-web models in community ecology that describe interactions between species and those in ecosystem science that incorporate detrital compartments and nutrient pools.

The view of food webs as flow networks goes back to the early “trophic-dynamic viewpoint” of Lindeman (1942) and is found in more recent food-web studies that use energy as the basic currency (Ulanowicz 1986; Christian and Luczkovich 1999; Heymans et al. 2002). The characterization of cycles is explicitly the core focus in flow networks, but for large systems requires enormous computational time, as it increases more than exponentially with the number of nodes. Another interesting element of structure related to cycles that is basic within graph theory but is only beginning to be applied to food webs (Allesina 2004; Allesina et al. in press) is that of strongly connected components (SCCs) (Skiena 1990; Read and Wilson 1998). SCCs apply only to directed networks and are defined as subsets of vertices that are connected through cycles: two species or vertices belong to the same SCC if we can find paths that connect them in both directions. In this way, SCCs define subsets of species connected through cycles, but their identification is much faster than that of cycles because computational time grows only linearly with system size (Tarjan 1972; Allesina et al. in press). These subsets are intriguing in that they provide one type of ecological compartment associated with flows (see also Krause et al. 2003) whose dynamical consequences in ecological networks are thus far unknown. A recent study of generic directed networks in the physics literature (Variano et al. 2004) raises the possibility that SCCs influence local stability and other aspects of robustness. Consideration of other types of subgraphs, such as those composed of species with the same number of links to all other species in the subgraph (Melián and Bascompte 2004), is also warranted.

## 6 FROM DETERMINISTIC TO STOCHASTIC MODELS OF NETWORKS

The high-dimensional food-web model of Martinez et al. (Chapter 6) achieves persistence for a large number of species for the full nonlinear dynamics of the system. This model is a hybrid in which the structure is determined by a static stochastic model that draws the links between species using different distribution rules (i.e., niche, cascade, random), while the dynamics are specified with a set of ordinary differential equations based on the bioenergetic model of Yodzis and Innes (1992). Numerical simulations show that the niche model, which best reproduces a set of structural properties of real food webs (Williams and Martinez 2000; Stouffer et al. in press), also confers higher dynamical persistence. Thus, structural properties of real food webs appear critical to dynamical properties of nonlinear food webs (see also review by Jordán and Scheuring 2004). Using an opposite approach, McKane and Drossel (Chapter 9) develop a dynamic and stochastic model of food-web evolution and assembly to produce ecological networks (McKane and Drossel Chapter 9; Drossel et al. 2001). In their “webworld” model, ecological time scales are considered to be much faster than evolutionary ones, with population dynamics treated deterministically allowed to reach an attractor between periods of evolutionary stasis. The two approaches are complementary and provide useful frameworks for more detailed investigations of the connection between structure and dynamics. In particular, the evolutionary-assembly approach can inform our understanding of how the relative temporal scales of ecology and evolution influence relationships uncovered with the structure-dynamics approach. It can also help to define relevant regions of parameter space, and allows investigation of a variety of interesting questions, including: Do evolutionary trajectories produce transient communities with longer persistence times as structure develops? Do communities become more robust to perturbations along this trajectory? Is robustness at the level of the system as a whole obtained by variability at the level of component species, as discussed below?

More extensive numerical explorations of parameter space are possible for dynamical systems that are still high-dimensional but have fewer species than the model of Martinez et al. (Chapter 6). Fussman and Herber (2002) provide an interesting example using parallel computation to address the likelihood of chaos in a deterministic model, similar to that of Martinez et al., as complexity, including species richness, increases. They show that chaotic dynamics become less likely, occurring in a more restricted region of parameter space, while the frequency of equilibria also decreases. These findings indirectly imply that cyclic behavior should become more common. It is unclear whether such conclusions extend to larger systems, but the question is clearly important for the relevance of the many studies that consider stability properties and linear approximations close to equilibria (see review by Dunne et al. 2005).

An earlier study using a hybrid model (Cohen et al. 1990b; Chen and Cohen 2001) provides one of the few examples of analytical results on the stability of large nonlinear networks. Lotka-Volterra equations were built upon a network of links produced by the cascade model. Their mathematical analysis tackles the global qualitative stability of the system, related only to the signs and not the strength of interactions. They demonstrated the existence of a phase transition that divides stable from unstable networks as a function of three stochastic parameters determining the type of predator-prey interactions. The possibility of extending this type of analysis to other nonlinear models of ecological networks opens many challenging, and interesting mathematical problems for the future. Analytical approaches would provide powerful tools to establish general results in spite of high dimensionality.

Much more work remains to be done to develop a general dynamical theory that explains within one framework not only structural properties of ecological networks (Dunne Chapter 2; Cartozo et al. Chapter 3) but also macroscopic community patterns. A number of macroscopic patterns have an important place in the description of ecological communities; examples include the well-known species-area curves and species-rank abundance curves. In a theory where these patterns emerge in a dynamic context, we can also hope to understand the implications of those patterns for instability. Stochastic assembly models are perhaps the best candidates to build such a theory. They are a powerful tool to capture the stochastic nature of immigration/colonization and extinction via species interactions, and have a venerable tradition in ecology (e.g., Post and Pimm 1982; Law and Blackford 1992). Hubbell's neutral theory of biodiversity (Hubbell 2001) uses this type of formulation, but does not incorporate multiple trophic levels and other aspects of trophic and non-trophic interaction networks. The stochastic assembly model by Solé et al. (2002) does encompass in an abstracted representation predator-prey interactions. In this model, structure emerges and continuously changes as the result of innovation (colonization) and extinction (Solé et al. 2002; McKane et al. 2000; Solé et al. 2000). Macroscopic (statistical) patterns at the level of the whole community, including species-area and rank abundance curves, emerge from processes at the level of interacting populations and individuals. Another emerging pattern, relevant to food-web structure, is given by the following relationship between species richness  $S$  and connectance  $C$  which sets a limit to diversity:

$$S \sim C^{-1+\varepsilon}, \quad (1)$$

where  $\varepsilon^{-1} = \ln(1-\mu)/\mu$  and  $\mu$  denotes the immigration probability of new species (Solé et al. 2002; McKane et al. 2000). Note that eq. (1) encompasses a wide array of curves depending on the specific value of the parameter  $\mu$ . For a small immigration parameter,  $\varepsilon$  is close to zero and eq. (1) becomes the hyperbolic relationship previously proposed by May (1973) from the local stability analysis of a community of interacting species near equilibrium. The history of this earlier relationship and empirical evidence supporting considerable deviations from it,

are reviewed in detail elsewhere (Dunne Chapter 2). Here, we note that eq. (1) is equivalent to the following expression relating the number of links to the number of species

$$L \sim S^{2 - \frac{1}{1-\epsilon}}, \quad (2)$$

where the definition of connectance  $C = L/S^2$  has been used. Thus, depending again on the strength of immigration, eq. (1) is consistent with the power-law dependence of links with species observed in real food webs, including in the limit of high immigration, the hypothesis of constant connectance (see fig. 1 in Chapter 2). More importantly, eq. (1) sets a dynamic limit to diversity: communities in the model are set at this boundary by the dynamic tension between innovation (immigration, speciation) and species interactions. Thus, at the macroscopic level of the whole community, this curve functions as an “attractor” and macroscopic quantities such as species richness reach a stationary state, while at the microscopic level instability is rampant, with recurrent species extinctions and unpredictable population fluctuations (Solé et al. 2002). The idea that the stability of systems at aggregated, higher levels of organization are sustained by instability at lower levels has already been recognized as important in ecology (Tilman 1999; May 2001). We return to it below in the context of ecosystem robustness.

Assembly models are also a natural framework for incorporating evolution, an important area for the future. A number of formulations that couple evolutionary and ecological dynamics in a network context are beginning to emerge (see McKane and Drossel Chapter 9; Martinez Chapter 12 for a brief summary). Although it is still too early, a major goal of future theory should be to establish generalizations, which are closely connected to empirical network patterns from the results of multiple models. Abstract formulations (e.g., Solé et al. 2002) can play an important role in synthesizing and interpreting aspects of the behavior of more detailed models (e.g., McKane and Drossel Chapter 9; Peacor et al. Chapter 10). Comparisons should not be limited to theory within ecology, as similar types of questions on the emergence of complex structures, the existence of critical boundaries, and the associated dynamics of large systems are being asked in a variety of other fields with models of evolving networks.

One remarkable example concerns the evolution of an idealized chemical system with both “catalytic” and “inhibitory” interactions in a model that couples the dynamics of “species’ populations” (at fast time scales) and of links between them (at slow time scales) (Jain and Krishna 2001). A selection process results in the extinction of populations with small abundances as the result of interactions between “species.” Innovation occurs through the immigration of new types to the system. The model demonstrates the emergence of cooperation as a small autocatalytic set appears by chance but inevitably, providing the seed for the rapid growth of a complex network dominated by cooperative interactions (Jain and Krishna 2001). The differential equations used for the population dynamics are not immediately transposable to ecological interactions, but analogies for

systems that include mutualistic as well as antagonistic interactions are intriguing. Questions on possible functional similarities between autocatalytic sets and other types of cycles in ecological networks that include energy flows also arise. Furthermore, one interesting property seen in the dynamics of this model is the intermittent collapse of the system, with the rapid loss of a “keystone” species that “plays an important organizational role in the network despite its low population” (Jain and Krishna 2001). The system loses a large number of species and reorganizes again, with periods of relative stasis in diversity punctuated by intermittent catastrophic events. Thus, self-organization in this system leads to a complex structure poised in a state of apparent stability that is nevertheless susceptible to unpredictable and intrinsic catastrophic events.

Instability boundaries take many forms in models of network evolution and dynamics, including concepts of self-organized criticality (SOC) and phase transitions (see Solé and Goodwin 2000 for examples); they are described in the literature by different images including the well-known “edge of chaos” (Kauffman 1993). In an ecological framework, Solé et al. (2002) argue that SOC is too restrictive in its assumptions to fully encompass the type of critical boundaries relevant to ecological systems. They propose the more general concept of *self-organized instability* to describe a critical boundary in diversity generated by the tension between immigration and extinctions in the self-organization of communities. The questions of whether ecological networks function near instability boundaries and what their implications are for species’ extinctions, population fluctuations, and responses to specific perturbations, can only be addressed by further theory in order to develop a general understanding of which processes underlie different types of boundaries, and which properties are key for differentiating empirically among these types. In a similar but much simpler context, Pascual and Guichard (2005) review the conditions leading to different types of criticality in spatial ecological systems with disturbance, including predation, disease, and abiotic perturbations. The temporal and spatial scales of recovery and disturbance appear key to the type of critical behavior observed, with clear implications for responses to perturbations and the occurrence of large shifts in system state. Are there similar organizational principles for types of “self-organized instabilities” in ecological networks? If so, what patterns and properties of specific processes should be measured to empirically identify a particular type in nature? The relative temporal and spatial scales of the different evolutionary and ecological processes are likely to play an important role.

## 7 SOME SPATIAL CHALLENGES

The spatial dimension is largely missing from studies of large networks (see review by Brose et al. in press), although it is a key component of the most serious current threats to ecological systems. Memmott et al. (Chapter 14) outline a series of critical questions on the effects of habitat destruction and fragmenta-

tion, and emphasize the importance of a multi-trophic perspective to pressing problems in conservation and restoration. Solé and Montoya (Chapter 13) illustrate the importance of a multi-trophic perspective with a network model that addresses habitat destruction. A spatial scaling theory of species diversity and their trophic interactions has been proposed by Brose et al. (2004). Their theory accurately predicts how trophic links scale with area and species richness across scales from microcosms to metacommunities. However, the issue of space is missing from most dynamical models of complex food webs.

Lotka-Volterra equations and their descendants used so far to address deterministic dynamics of ecological networks with many species are “mean-field” models. In these models, space is not treated explicitly because individuals are assumed to be well mixed and to interact at mean densities as a result of fast movement or long dispersal distances relative to the rate of interactions and their spatial extent, respectively. Local interactions among individuals are well known to be capable of dramatically affecting the dynamics of ecological models (e.g., Durrett and Levin 1994) and can also play a role in “adaptive” or plastic responses of prey (Peacor et al. Chapter 10). Clearly, however, tracking individuals for a large number of species would quickly become computationally prohibitive, and generate results difficult if not impossible to interpret. Some recent findings on individual-based models for a single predator and its prey indicate that simpler, low-dimensional models in which space is represented implicitly apply at the population level (Pascual et al. 2001; Pascual et al. 2002). Thus, although individual predators and prey interact locally in a spatial lattice, the aggregated dynamics of “global” abundances at the level of the whole lattice are well approximated with a simple “modified mean-field” model. Specifically, the predator-prey dynamics at the population level can be modeled as if space did not matter by modifying the functional forms of the mean-field equations. Additional parameters are introduced in the functional forms describing how the per-capita predation rate and prey growth rate vary with population abundances. The resulting equations exhibit dynamics that are more stable than their mean-field counterparts: permanent cycles become transient oscillations that approach equilibria, and transient cycles exhibit smaller amplitudes and faster convergence to equilibria. Although this type of scaling approach, from the local (or individual) to the global (or population) scale, is still under investigation for the case of only two interacting species, its potential application to the study of food webs should be considered.

In the same spirit, higher-dimensional numerical models for a large number of species’ trophic interactions also do not treat space explicitly, but use different nonlinear functional responses to implicitly represent spatial and other non-trophic effects. Changing the form of the response (for example, from Type II to Type III) can be used to reflect the existence of prey refuges, or behavior modification of prey in the presence of predators (Martinez et al. Chapter 6). Dynamics can change dramatically with shifts in the functional response (e.g.,

Williams and Martinez 2004), yet another indication that spatial effects can be critical.

## 8 ROBUSTNESS AND SCALE

As will be clear from the discussion so far and from the papers in this volume, fundamental to the consideration of networks is the relation between structure and dynamics. How do the microscopic interactions among individuals lead, over ecological and evolutionary time, to the range of topological structures that are observed at higher levels of organization, and what are the implications for stability and robustness of macroscopic features of webs? Key features or robust systems relate to their heterogeneity and functional diversity, as well as levels of redundancy and modularity (Levin 1999). We have already seen, for example, that weak links can make food webs more robust by introducing a degree of modularity that limits the spread of catastrophic disruptions. But food webs are not systems that have been designed for robustness; their features are emergent. Is there any reason then to expect food webs to be maximally robust to disturbances at any scale? Such questions are rich areas for research.

Indeed, even when designing a web as a robust structure, issues of scale assume importance. What makes a system robust on short time scales may be at the cost of increased fragility on longer time scales; this concept of “robust, yet fragile” is indeed a central theme in recent advances in control theory (Carlson and Doyle 2002). Similarly, as already mentioned, robustness at higher levels of organization or broader spatial scales may be in spite of the fact, or indeed possibly because of the fact, that there is a lack of robustness at lower levels or at smaller scales. That very lack of robustness at the lower levels provides the capacity for the network to “adapt” in response to perturbations. This is not to imply that adaptive capacity is an evolutionary response to change; the focus of selection, of course, is at levels well below that of the whole food web. Indeed, food webs, by their diffuse nature, are clearly not evolutionary units. This, however, only makes more interesting a comparison of emergent properties with what would be expected were these designed systems.

## 9 IN CLOSING

In the concluding chapter of his inspiring book *SYNC*, Strogatz (2003) brings forward both the current excitement and the limitations of the studies of complex systems. He writes, “I hope I’ve given you a sense of how thrilling it is to be a scientist right now. It feels like the dawn of a new era. After centuries of studying nature by teasing it into smaller and smaller pieces, we’re starting to ask how to put the pieces back together again.” But after referring to a

number of problems in a variety of fields on the emergence of order and self-organization, he also writes “we’re still waiting for a major breakthrough in understanding, and it could be a long time in coming. I think we may be missing the conceptual equivalent of calculus, a way of seeing the consequences of myriad interactions that define a complex system.” He refers here to breakthroughs in the mathematical analysis of qualitative dynamical properties, but more broadly perhaps to the emergence of a general theory of complex systems.

The dynamics of ecological networks are one particularly important challenge whose relevance and urgency cannot be overemphasized. From a theoretical perspective, we believe that general principles can result from the synthesis of many parallel efforts in the types of models discussed here. Given the enormous difficulties and time involved in empirical studies, more consideration should be given to the types of data required to assess specific hypotheses on stability, robustness, and the consequences of perturbations.

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