

Network Evolution: Exploring the Change and Adaptation of Complex Ecological Systems Over Deep Time

Neo D. Martinez

1 INTRODUCTION

One of the most exciting new directions in research on food webs and ecological networks is network evolution or, in other words, the development of the structure and function of ecological networks over time scales long enough for node selection and speciation to occur (Caldarelli et al. 1998; Drossel and McKane 2002; Worden 2003; Yoshida 2003; Cattin et al. 2004; Rossberg 2004; Anderson and Jensen 2005). Most food-web studies focus on shorter-term snapshots of network structure and time series of network dynamics. The difference between long-term evolution over “deep time” and short-term structure and dynamics is a familiar one. Hutchinson distinguished the two by suggesting that we “view the natural world as the ecological theater, serving as a stage for the evolutionary play” (Hutchinson 1965). Following this suggestion, research on network evolution goes well beyond contemporary topology, theatrical population booms and busts, and more staid equilibria. That is, network evolution encompasses a broad

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spectrum of studies, from the dynamics of intra-node stocks and inter-node flows to the evolutionary play of node survival, adaptation, and speciation over time.

Though the distinction between network dynamics and network evolution may be familiar, much research occupies a kind of gray area in between these two ends of a spectrum. For example, in adaptive prey preference and feeding behavior models (Post et al. 2000; Brose et al. 2003; Kondoh 2003), network topology changes and species can be lost but the most fundamental traits of nodes do not change. Similarly, network structure changes during the assembly of local communities from regional species pools. Such assembly (Holt et al. 1999; Fox and McGrady-Steed 2002) and also disassembly (Holt et al. 1999; Fox and McGrady-Steed 2002) informs network evolution by exploring how networks respond to species gain and loss but again, without adaptive change in intrinsic properties of nodes.

The difference between network evolution and network dynamics is that network evolution describes changes in the more fundamental properties of nodes, such as which species potentially interact with a node, the functional form of these interactions, and even species' metabolic, assimilation, and maximum ingestion rates. These properties typically remain constant in the context of network dynamics even though species' biomasses, feeding rates, and presence or absence can change. The invasion by, and extirpation of nodes, which drives network and community assembly and disassembly, belongs to the intermediate scale between shorter-term network dynamics and longer-term evolution. While these changes occur simultaneously in nature, they are still somewhat distinguishable by their frequencies or rates of variation that decrease from food-web dynamics through assembly/disassembly to evolution.

In their chapter of this book, Drossel and McKane (chapter 9) review recent research on network evolution. This chapter discusses a range of other outstanding questions about network evolution, focusing on the effects of different types of evolutionary rules including the networks that emerge from implementation of the rules. Then, different approaches for evaluating emergent networks are discussed. With these basic concepts in place, the chapter subsequently describes more specific modeling approaches that implement rules in ways that facilitate the evaluation of their results. The chapter concludes by pointing toward the development of new evaluation criteria and by connecting the study of evolving networks to other areas of ecology.

2 EXPLORING NETWORK EVOLUTION

The first question one might ask is, "What sorts of rules for network evolution lead to the networks that we see in nature?" Typically, "rules" represent formalizations of biological mechanisms thought to be responsible for network evolution, but could represent any formalized process for constructing networks. An important caveat is that the empirical networks we see in nature should not

be taken completely literally due to limitations of the data (May 1983; Paine 1988; Martinez 1991; Polis 1991; Cohen et al. 1993; Martinez 1993b; Borer et al. 2002; Dunne chapter 2). In particular, there is a frequent mismatch between the larger spatiotemporal scale of evolution and the much smaller spatiotemporal scales at which food webs are currently being documented (Martinez and Lawton 1995; Martinez and Dunne 1998). Still, overall generalities that appear to survive methodological variation (Winemiller 1990; Martinez 1991; Goldwasser and Roughgarden 1993; Martinez 1993b; Martinez et al. 1999; Thompson 2000; Banašek-Richter et al. 2004) and empirical variation (Martinez 1992, 1993a, 1994; Warren 1994; Williams and Martinez 2000; Dunne et al. 2002b; Williams et al. 2002) are more likely to represent robust regularities that do warrant attention. For example, in no case with which I am familiar has *connectance*, defined as the fraction of all possible network links realized (Martinez 1992), exceeded 50%; food-web connectance is almost always much closer to 10%. Rules that create networks exceeding 50% should be treated skeptically. Other generalities go beyond statistical patterns in the data to indicate sets of rules that successfully predict the complete structure of food webs (Williams and Martinez 2000; Dunne et al. 2004), including rules that explicitly attempt to capture evolutionary aspects of food-web structure (Cattin et al. 2004). Such relatively comprehensive models generate networks that can be evaluated using increasingly many network properties (Dunne et al. 2002a; Garlaschelli et al. 2003; Cattin et al. 2004; Dunne et al. 2004) instead of restricting evaluations to one or two properties such as connectance or mean food-chain length. Perhaps the most exciting empirical development relevant to network evolution is paleofoodweb research that reconstructs food webs over “deep” time, stretching back over a half billion years before the present (Dunne and Erwin unpublished data). As this research progresses to the point of describing series of food webs from different times and habitats, it will provide both new tests of hypotheses (e.g., trophic specialization increases with time following major extinction events) and new empirical patterns that should inspire yet more hypotheses and theories.

Two of the most central questions that network studies aim to answer are, “How do networks come into being?” and, “How do networks vary over time scales within which species originate, invade, and go extinct?” Answers to these questions seek to uncover the evolutionary plot concerning the *players*, or nodes, and their mechanistic interactions that are responsible for network evolution. Such interactions are likely to involve well-known evolutionary mechanisms such as natural selection, less well-articulated constraints on network structure (e.g., plants must exist before herbivores can evolve), and newly emerging dynamical constraints that restrict the number and types of species that can persist and interact as nodes within a variable environment. A productive strategy for answering these questions would be to uncover a minimal set of rules that create networks consistent with empirical patterns. An important issue involves the environment within which species and their interactions evolve, such as en-

environmental and demographic stochasticity (Cushing et al. 2003) and spatial heterogeneity.

3 RULES FOR NETWORK EVOLUTION

There is a wide range of mechanisms whose formalizations can provide important and useful rules for implementing network evolution. One of the most fundamental mechanisms with respect to species and the individuals that comprise their populations concerns the metabolic rates determining energetic maintenance cost of staying alive long enough to reproduce. Much if not most of the significance wrapped around the structure of the archetypal ecological networks called food webs is the need for this network to supply species with their metabolic requirements. Formalization of metabolic rules needs to take into account the degrees of constraint and flexibility associated with the body sizes and metabolic types of: (a) autotrophs including vascular plants, phytoplankton, and microbial chemoautotrophs; (b) animals including ectotherms, endotherms, invertebrates and vertebrates; and (c) microbes including bacteria, fungi, and protozoa. Closely associated with metabolic rates are the maximum rates of ingestion and assimilation that indicate potentially important variability among different types of animals and microbes (Yodzis and Innes 1992). One may want to relate these rates to trophic generality and specialization, trophic level, and omnivory. It is also important to consider rules that determine whether species are strong interactors such as keystone species or weak interactors whose removal less dramatically impacts their communities (Berlow et al. 2004). The emergence of such species would appear to depend on generating variation in resource consumption efficiencies and preferential predation upon the most efficient consumers.

Other rules relate more directly to the interactions themselves as opposed to the interactors, though the two are not completely separable. For example, there are many different types of functional responses that determine how consumption varies with the abundance of resources and other species in ecological networks (Gentleman et al. 2003; Skalski and Gilliam 2001). Few if any interactions are thought to be “Holling type I” interactions, which lack thresholds and in which feeding rates continually increase without satiation, regardless of food availability. Some interactions with thresholds are thought to be “Holling type II” responses in which feeding rates quickly accelerate as rare resources become more abundant. “Holling type III” responses are characterized by a much slower acceleration of feeding on rare resources, and are thought to occur in the presence of either limited refuges for resources or more intelligent consumers. Intelligent consumers avoid expending energy to hunt and feed unless resources are at a high enough density to provide more energy than is needed for consumption. Other “Beddington-Holt” functional responses address whether consumers are likely to interfere with each other’s feeding rates as their densities increase (Skalski and Gilliam 2001). While the variation of these responses is known to greatly

alter the dynamics of both low-dimensional (species < 5) and high-dimensional ($10 \leq \text{species} \leq 30$) networks (Williams and Martinez 2004b,c), their evolutionary stability and other evolutionary consequences are not well understood. Another important issue regarding interactions and network development concerns the hypothesis, based on non-ecological networks, that new nodes preferentially attach to existing highly connected nodes when joining established networks (Albert et al. 2000; Newman 2003). If relevant for ecology, this may suggest that speciation is more likely to either generate prey species that are eaten by generalists or generate predator species that eat prey with the most consumers. However, the ecological probability, dynamic effects, and evolutionary stability of such issues as attachment preference are poorly known (Dunne et al. 2002b).

Several other rules that may be implemented during network evolution are common to both nodes and interactions. For example, might there be tradeoffs between different properties such as the generality of nodes and the functional responses of their interactions, or between the assimilation efficiency of an interaction and the maximal ingestion rate of the node possessing that interaction? Still more general questions concern the directionality of evolution, i.e., whether or not any system's or component's traits tend to evolve in a consistent direction, either increasing or decreasing. For example, do networks evolve based on selection for nodes with high assimilation efficiencies or does such evolution lack any such directional selection? Such rules could emerge from network evolution rather than being implemented during network evolution as emphasized in this section. Still, implementing well-chosen rules can locate selection at genetic, individual, population, or network levels. How do networks differ when selection operates at these different levels? A similar question of scale involves exploring the effectiveness of immediate payoffs (e.g., quick biomass gain) compared to nodes that achieve long-term success at the evolutionary scale.

Many other questions concern environmental effects on network evolution. How is evolution altered by a stochastic versus stable environment? When evolution occurs in a stochastic environment, how does dominance by low frequency variation, known as *red noise*, alter network evolution in comparison to dominance by high frequency variation, known as *blue noise*? Also, what are the evolutionary effects of episodic versus gradual environmental change? How are resulting networks and their evolution altered when played out in a spatially explicit environment? Such spatial considerations could be examined at an individual level or at a meta-network level in which networks are connected in a landscape by inter-network migrations of different species.

This focus on the network is quite different from the usual focus of evolutionary theory on individuals, populations, and species. Still, these entities evolve within a network that Darwin described as a "tangled bank" of interactions. How does the evolution of nodes such as populations and species within a network differ from evolution within simpler contexts? Evolution of nodes within networks allows the consequences of a myriad of indirect interactions to influence the outcome of each species' evolution (e.g., Worden 2003). Additionally,

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networks or graphs can provide structure to evolutionary interactions such that nodes only directly interact with nodes that are connected with a link or edge to other nodes (Lieberman et al. 2005). Such evolution within or “on” networks is quite interesting apart from the evolution “of” networks emphasized here.

4 EVALUATING NETWORKS USING EVOLUTIONARY RULES

Beyond explorations of how the many factors mentioned above alter the evolution of networks, one needs criteria for evaluating those effects. Of course, matching networks generated using rules with empirical data is the most obvious criterion to employ. Less obvious are the aspects of network data on which to focus, and what priority to ascribe to the numerous quantifiable aspects of network structure. Of course, aspects of network nodes (e.g., total number and distribution among trophic levels) and interactions (e.g., link density and degree distribution) warrant attention, but also notable are statistical (e.g., regressions) and more mechanistic models of larger sets of empirical data. An important example is a recent comparison between the niche model (Williams and Martinez 2000; Camacho et al. 2002a,b; Dunne et al. 2004) and the nested hierarchy model (Cattin et al. 2004). The nested hierarchy model actually predicts less accurately a suite of increasingly common network properties (Martinez and Cushing Box A). However, unlike the niche model, the nested hierarchy model uses evolutionary rules to make networks that are non-interval, similar to most reasonably-sized food webs (Bersier et al. Box B). How is one supposed to balance such disparate success and failure (Stouffer et al. 2005)? There are also more general criteria to be addressed such as the robustness to disturbance and evolutionary trajectory of networks over deep time.

One place to start an empirically based evaluation of ecological network evolution is to focus on the network nodes, ideally meant to represent species or populations. What kinds of nodes emerge during network evolution? For example, when allowed to evolve, do metabolic rates assume empirically observed values? Do they assume uni-modal, bi-modal, or multi-modal distributions, as appears to be the case in nature given the presence of several metabolic types? Do the body sizes implied by “evolved” metabolic rates assume empirically observed ratios between predators and prey, herbivores and plants, or parasites and hosts? Does generality (number of species a node consumes) or vulnerability (number of species that consume a node), assume empirically observed distributions? For example, generality appears much more variable and widely distributed than does vulnerability (Williams and Martinez 2000). However, narrow vulnerability distributions may relax when consumption is coupled with mutualism such as pollination (Memmott 1999; Bascompte et al. 2003; Vazquez 2005).

If such patterns are robust, they may have profound evolutionary implications. What about the distribution of nodes among trophic levels and degrees of om-

Box 1.

A variety of criteria can be used to evaluate ecological networks in terms of their evolution and assembly, as indicated by the following questions:

1. How does network evolution differ from network assembly?
2. Does network evolution attain adaptive peaks?
3. How does the evolved network vary with time and over various spatial scales?
4. Are there consistent transient or asymptotic states?
5. How do the spatial scales of observations or mechanisms (e.g., local interaction with few species vs. regional interaction with many species) alter evolved networks in terms of bioenergetics or speciation?
6. How are non-trophic species traits (e.g., dispersal ability, mobility, tracking efficiency, and tracking ability) impacted by trophic network evolution?
7. How does the evolution of agent-based models differ from the evolution of ODE-based models of population biomass?

nivory (Williams and Martinez 2004a)? If we turn our focus to interactions rather than nodes, do we see empirically observed distributions of type II and type III functional responses, or degrees of predatory interference (Skalski and Gilliam 2001; Sarnelle 2003) when functional responses are allowed to evolve in terms of recently introduced control parameters (Williams 2004b,c)?

Beyond focus on the node and interaction components of networks, one can evaluate ecological network evolution based on the network as a whole. For example, different habitats generally have different networks. Pelagic networks are characterized by extremely small planktonic autotrophs and larger, though still small, herbivores such as zooplankton. Terrestrial networks are characterized by relatively large autotrophs including vascular plants and trees, along with much smaller herbivores such as insects, with the significant exceptions of less speciose larger-bodied mammalian herbivores such as ungulates (Hairston et al. 1960). During network evolution, do such characterizations represent different basins of attraction? While it is tempting to evaluate this question based on network architecture, recent claims that, for example, marine food webs are structurally quite different from non-marine food webs (Link 2002) appear to be overstated (Dunne et al. 2004) and there is little evidence that overall food-web structure reveals the profound differences seen in the distributions of body sizes among different trophic groups. However, perhaps research on paleofoodwebs will reveal structural variation over time rather than among habitats that will provide more useful, empirically-based criteria for evaluating network evolution.

Once empirically based criteria are chosen to evaluate network evolution, another question arises as to which data to use for comparison. Early food-web data were criticized for numerous methodological inconsistencies both among and within webs (Winemiller 1989; Martinez 1991; Polis 1991). Some nodes would be

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resolved to subspecies while others would aggregate entire kingdoms (e.g., microbes). The early data were also criticized for unacceptably low sampling effort that misrepresented empirical food-web structure (Tavares-Cromar and Williams 1996; Goldwasser 1997; Martinez et al. 1999; Thompson 2000). More recent data have reduced but not eliminated such inconsistencies and low sampling effort. However, such problems still require focused attention when empirical networks are used to evaluate network evolution. One needs to balance the abundance of older webs with more problems against the paucity of newer webs with fewer problems. One aspect of empirical webs that can help guide their use is the purpose for which they were constructed. For example, smaller less-complete webs that were constructed to illustrate the distribution of interaction strengths among a few species (Paine 1992) should be applied in different ways than larger, more complete webs that were constructed to illustrate overall network structure (Martinez 1991).

Beyond using network data to evaluate network evolution, one can compare hypotheses of ecological network evolution against models of network structure. For example, there are several statistical models that characterize the variation of food-web structure with scale in terms of species diversity (Martinez 1992, 1993a, 1994), space (Brose et al. 2004), and taxonomic resolution and trophic similarity (Martinez 1991, 1993b; Solow and Beet 1998; Thompson and Townsend 2000; Williams and Martinez 2000). As evolution adds and eliminates species, one would want to know whether or not the variation of network structure follows the variation specified by these statistical models. Similarly, other network models are based on degree distribution (Barabasi and Albert 1999) and assortative linking (Newman 2003). One would like to know how variation characterized by these statistical models compares to variation seen both during network evolution and within a collection of networks that result from some evolution-based rules. More mechanistic models characterize variability due to randomness (Erdős and Renyi 1960; Bollobás 1985; Williams and Martinez 2000), trophic hierarchy (Cohen 1990, Williams and Martinez 2000), niche structure (Williams and Martinez 2000; Cattin et al. 2004), phylogenetic structure (Cattin et al. 2004) and preferential attachment (Newman 2001). Again, how do evolved networks compare to these network models? If hypothesized mechanisms for network evolution give rise to networks that are generally consistent with accurate statistical and more mechanistic models of network structure, then such hypothesized evolutionary processes can be claimed to be generally consistent with the data. On the other hand, consistent differences between initial networks and those that result from longer-term evolution may point towards patterns to search for among paleofood-webs extracted from the fossil record. For example, specialists that eat only one or a very few species may be very rare during early simulated network evolution, increasing in abundance in later evolutionary stages. While current food-web data seem to have many specialists, paleofoodwebs may have lacked specialists both early in their history and shortly after major extinction events. Perhaps significant numbers of specialist species only occur well after such events. Such

an empirical finding could provide important support for evolutionary models that match this pattern and also illustrate as-yet unknown general differences between current and ancient ecological networks.

In addition to specific criteria for evaluating hypotheses of network evolution such as empirical patterns and statistical and mechanistic models of current food-web structure, one can use much more general criteria. One example includes robustness that occurs when food webs stop changing during evolution. What sorts of webs achieve such robustness? Beyond robustness to evolution, one would like to know which evolutionary mechanisms give rise to networks that resist invasions by other species or that contain keystone species whose exclusion precipitates dramatic changes to the rest of the network. More subtly, does network evolution generally give rise to particular kinds of qualitative population dynamics?

Other general sets of criteria involve the concept of directionality at the node, link, and network levels. Is there any directional progression of, for example, the degree or omnivory of nodes (Williams and Martinez 2004), the compartmentalization of links (Girvan and Newman 2002; Krause et al. 2003), or the amount of connectance (Martinez 1992; Dunne et al. 2004)? Network evolution dynamics could also be directional. For example, network evolution might progress towards species that have particular assimilation efficiencies, or particular levels of generality and vulnerability. Whole networks could progress through different qualitative types of dynamics from chaotic fluctuations to equilibria.

5 IMPLEMENTING EVOLUTIONARY RULES AND EVALUATING RESULTS

Most of the discussion of approaches to implementing rules and evaluating the results, based on the criteria described above, focuses on different aspects of simulations. However, network evolution can also be explored by other approaches such as analytical modeling (Camacho et al. 2002b; Cameron 2002; Stouffer et al. 2005) and microcosm experiments (Bohannan and Lenski 2000; Morin 2004). Still, such approaches and computer simulations can all pursue a general approach of building and exploring models that synthesize a wide range of fundamental components of ecological networks. For example, bioenergetic models of trophic interactions can be coupled with models of shared resource consumption among plants and detrital models of deposition of biomass, microbial consumption of non-living biomass, and mineralization of nutrients. Another approach could be to link abstract analytical models (Harte and Kinzig 1993) with more detailed computational models (Brose et al. 2003; Martinez et al. Chapter 6) and agent-based models (Pfister and Peacor 2003). Successful linking would show that synthetic models can be phenomenologically accurate at both individual and system levels. Agent-based models could also be used to explore the accuracy of functional responses that model feeding behavior of larger undifferentiated

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stocks of biomass containing many individuals. This could test whether, and to what degree, there is consistency between differential equation approaches and agent-based models, especially with respect to functional responses and their consistency with allometric scaling (Economo et al. 2005), optimal feeding, and other behavior by agents.

Ideally, one might like to explore hybrid dynamics-evolution models which incorporate time scales relevant to both ecological and evolutionary dynamics. While much of such dynamics involves nutrient flows and living and dead biomass, it is also important to develop non-trophic and quasi-trophic interaction models involving ecosystem-engineering interactions. Such interactions are common to ecosystems, biofilms, and pollination and dispersal systems in which strong mutualisms overlap and interact in different than strictly trophic interactions (Martinez 1995). For example, while pollinators and seed dispersers often benefit from consuming plant nectar, pollen, and fruit, plants can benefit from using animals' metabolic energy to disperse propagules (Bascompte et al. 2003). Additionally, early colonizers of biofilms can both exclude competitors and provide food for later colonizers. Additional interactions include mimicry, camouflage, and phenotypic plasticity in models of network evolution. Pursuing these approaches will require increased sophistication of models (e.g., adding detrital pathways, engineering, and selection). Such sophistication may be made more tractable by focusing on simpler or earlier systems (e.g., bacteria and plants) that provide insight into how many more species evolve within more complex networks. Explorations of how the first ecosystems functioned and what they looked like, or how population cycles and size structure influence ecosystem dynamics, could provide the foundation for explaining the rich complexity apparent today.

6 CONCLUSION

While much of the focus of this chapter is to develop theories, approaches, and criteria for modeling ecological network evolution, such modeling should also lead to suggestions or specifications of observational (e.g., in the fossil record) and manipulative (e.g., in microcosms) experiments that rigorously test models. Such tests should attend to both means and variation of models and empirical data. Evaluations are typically more compelling when they involve parameters within models that can be empirically measured. In developing models, dialog with field biologists is critical in order to assess which parameters and patterns appear most important in the natural world. As an iterative process, such dialogue with empiricists will facilitate comparison between high-quality snapshots of real ecosystems and longer-term development of ecosystems over deep time. Beyond the inherent interest in network evolution in its own right, exploring network evolution with approaches developed for ecological networks should also greatly

elucidate the rich, yet still opaque, relationship between the ecology and evolution of complex natural ecosystems.

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