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Abstract: We discuss theoretical aspects of the broader food-web research agenda, particularly the background and various approaches used for modeling food-web dynamics in abstract systems with more than two taxa. Much of this type of modeling has oriented itself around the classic and enduring complexity-stability debate in ecology, especially those aspects which relate to the theoretical and associated empirical food-web research into the relationships between ecosystem complexity, often characterized as number of links and/or number of species in a community, and various aspects of ecosystem stability. “Stability” in ecology is a catch-all term that has been variously defined to reflect aspects of population and/or system equilibrium, persistence, resilience, resistance, and robustness. In some cases stability refers to the outcome of internal dynamics while in other cases it reflects the response of a population or system to a perturbation. The very notion of what is a plausible definition of ecosystem stability has driven some of the fundamental shifts in modeling methodology that will be described.

Introduction

Understanding the structure and dynamics of ecological networks is critical for understanding the persistence and stability of ecosystems. Determining the interplay among network structure, network dynamics, and various aspects of stability such as persistence, robustness, and resilience in complex “real-world” networks is one of the greatest current challenges in the natural and social sciences, and it represents an exciting and dramatically expanding area of cross-disciplinary inquiry (Strogatz 2001). Within ecology, food-web research represents a long tradition of both empirical and theoretical network analysis (e.g., Elton 1927, Lindeman 1942, MacArthur 1955, Paine 1966, May 1973). All aspects of ecological network research have increasing relevance (McCann 2000) for a world facing biodiversity and habitat loss, invasive species, climate change, and other anthropogenic factors that are resulting in the drastic reorganization of many ecosystems, and in some cases may lead to the collapse of ecosystems and the vital, underappreciated services they provide human society (Daily 1997).

Most theoretical studies of trophic dynamics have focused narrowly on predator-prey or parasite-host interactions, and have thus ignored network structure. In natural ecosystems such interaction dyads are embedded in diverse, complex food webs, where many additional taxa and their direct and indirect effects can play important roles for both the stability of focal species as well as the stability of the broader community. Moving beyond the one- or two-species population dynamics modeling paradigm, other research has expanded the focus to include 3 to 8 species, exploring dynamics in slightly more complex systems. However, these interaction modules still present a drastic simplification of the diversity and structure of natural ecosystems. Other approaches have focused on higher diversity ecological networks, but have either left out dynamics altogether (e.g., network topology and carbon-budget studies) or ignored network structure in order to conduct analytically tractable dynamical analyses. The nature of modeling requires judicious simplifications (Yodzis and Innes 1992), but such choices can leave empirical ecologists suspicious and theoretical ecologists perplexed, both wondering how to bridge the gap between simple mathematical models and complex natural systems. At worst, theoreticians and empiricists end up ignoring or deriding each other’s work, dismissing it as irrelevant for being too abstract or too particular, never the twain shall meet.

In this paper, we focus on theoretical aspects of the broader food-web research agenda, particularly the background and various approaches used for modeling food-web dynamics in abstract systems with more than two taxa. Much of this type of modeling has oriented itself around the classic (May 1972) and enduring (McCann 2000) complexity-stability debate, especially those aspects which relate to the theoretical and associated empirical food-web research into the relationships between ecosystem complexity, often characterized as number of links and/or number of species in a community, and various aspects of ecosystem stability. “Stability” is a catch-all term that has been variously defined to reflect aspects of population and/or system equilibrium, persistence, resilience, resistance, and robustness (see McCann 2000 for some broad, but not exhaustive, stability definitions). In some cases stability refers to the outcome of internal dynamics while in other cases it reflects the response of a population or system to a perturbation. The very notion of what is a plausible definition of ecosystem stability has driven some of the fundamental shifts in modeling methodology that will be

described in following sections. We do not address the more empirically and experimentally based “diversity-stability” debate of recent years (e.g., Naeem et al. 1994, Hector et al. 1999, Tilman et al. 2001), which mostly focuses on the relationship between plant species richness and primary productivity.

This chapter discusses how three approaches to dynamical modeling of ecological networks try to strike a balance between simplifying and embodying aspects of the complexity of natural systems to gain a better understanding of aspects of ecosystem stability. In particular, the degree to which the different approaches incorporate diversity, network structure, nonlinear dynamics, and empirically measurable parameters will be recurring themes. We do not address spatial heterogeneity, metapopulation dynamics, age-class structure, environmental variability, or stoichiometry. Inclusion of those important factors in dynamical food-web models may well alter many of our notions about the interplay between ecosystem complexity and stability. While we do not explicitly review studies focused on food-web structure or topology (e.g., Cohen et al. 1990, Williams and Martinez 2000, Dunne et al. 2002a, Garlaschelli et al. 2003), we do refer to them to the degree that they have influenced dynamical approaches. A fundamental message of this chapter is that the insights from studies on the network structure of complex food webs need to be merged with dynamical approaches if we are to make serious headway regarding issues of the stability of complex networks and the potential for using dynamical models in a conservation and management context.

We focus on one end of a spectrum of modeling (Holling 1966), the use of abstract models to elucidate general qualitative insights about ecosystem structure, dynamics, and stability. We do not discuss more explicitly applied approaches for simulating particular ecosystems, a strategy which has been used for many aquatic systems (e.g., mass-balance, carbon-budget models such as EcoPath/EcoSim: Christensen and Walters 2004). Such approaches are presented elsewhere in this book (Christian et al., Morris et al.). These researchers have often referred to their work as “network analysis.” However, in our view, “network analysis” is a very broad term that encompasses all types of research that treat a system as a network of nodes and “edges,” or links, regardless of how those nodes and links are defined or their relationships are analyzed (Strogatz 2001). In ecology, there has often been a tension between research focused on abstract models versus that focused on applied simulation models of particular ecosystems. We shall see that as abstract models seek to represent greater ecological complexity, they take on some of the characteristics of applied simulation modeling, hopefully narrowing the gap between theoretical and empirical work by carefully integrating characteristics and goals of the two modeling extremes. In this spirit, we will end by reviewing a recent application of a multispecies non-linear dynamical food-web model to the issue of how culling a top predator is likely to affect the hake fishery yield in the Benguela ecosystem (Yodzis 1998, 2000, 2001).

Background

In the first half of the 20th century, many ecologists believed that natural communities develop into stable systems through successional dynamics. Aspects of this belief developed into the notion that complex communities are more stable than simple ones. Odum (1953), MacArthur (1955), Elton (1958) and others cited an array of empirical evidence supporting this hypothesis. Some popular examples included the

vulnerability of agricultural monocultures to calamities in contrast to the apparent stability of diverse tropical rainforests, and the higher frequency of invasions in simple island communities compared to more complex mainland communities. It was thought that a community comprised of species with multiple consumers would have fewer invasions and pest outbreaks than communities of species with fewer consumers. This was stated in a general, theoretical way by MacArthur (1955), who hypothesized that “a large number of paths through each species is necessary to reduce the effects of overpopulation of one species.” MacArthur concluded that “stability increases as the number of links increases” and that stability is easier to achieve in more diverse assemblages of species, thus linking community stability with both increased trophic links and increased numbers of species. Other types of theoretical considerations emerged to support the positive complexity-stability relationship. For example, Elton (1958) argued that simple predator-prey models reveal their *lack* of stability in the oscillatory behavior they exhibit, although he failed to compare them to multispecies models (May 1973). The notion that “complexity begets stability,” which already had great intuitive appeal as well as the weight of history behind it, was thus accorded a gloss of theoretical rigor in the mid 1950’s. By the late 50’s it took on the patina of conventional wisdom and at times was elevated to the status of ecological theorem or “formal proof” (Hutchinson 1959). While some subsequent empirical investigations raised questions about the conclusiveness of the relationship (e.g., Hairston et al. 1968), it wasn’t until the early 70’s that the notion that complexity implies stability, as a theoretical generality, was explicitly and rigorously challenged by the analytical work of Robert May (1972, 1973), a physicist by training and ecologist by inclination.

May’s 1972 paper and his 1973 book “Stability and Complexity in Model Ecosystems” (reprinted in a 2nd edition in 1974 with an added Preface, Afterthoughts, and Bibliography; most recently reprinted in an 8th edition in 2001 as a “Princeton Landmarks in Biology” volume) were enormously important on several fronts. Methodologically, May introduced many ecologists to a much-expanded repertoire of mathematical tools beyond Lotka-Volterra predator-prey models, and also set the stage for major ecological contributions to the development of theories of deterministic chaos (e.g., May 1974, 1976). Analytically, May used local stability analyses of randomly assembled community matrices to mathematically demonstrate that network stability decreases with complexity. In particular, he found that more diverse systems, compared to less diverse systems, will tend to sharply transition from stable to unstable behavior as the number of species, the connectance (a measure of link richness—the probability that any two species will interact with each other), *or* the average interaction strength increase beyond a critical value. We describe his analyses in more detail in the next section. May (1973) also pointed out that empirical evidence is not conclusive with regard to a particular complexity-stability relationship (e.g., there are a number of highly stable, productive, and simple natural ecosystems such as east coast *Spartina alterniflora* marshes; complex continental communities have suffered the ravages of pests such as the Gypsy Moth; etc.).

May’s analytical results and his conclusion that in “general mathematical models of multispecies communities, complexity tends to beget instability” (p. 74, 2001 edition) turned earlier ecological “intuition” on its head and instigated a dramatic shift and refocusing of theoretical ecology. His results left many empirical ecologists wondering

how the astonishing diversity and complexity they observed in natural communities could persist, even though May himself insisted there was no paradox. As May put it, “In short, there is no comfortable theorem assuring that increasing diversity and complexity beget enhanced community stability; rather, as a mathematical generality, the opposite is true. The task, therefore, is to elucidate the devious strategies which make for stability in enduring natural systems” (p. 174, 2001 edition). Most subsequent work related to food webs was devoted to finding network structures, species’ strategies, and dynamical characteristics that would allow complex communities to persist. In some cases, the research was undertaken to corroborate May’s findings, and other research sought to reanimate what many now felt to be the ghost of positive complexity-stability past. Whatever the motivation, important pieces of this ongoing research agenda include examining the role of omnivory, the number of trophic levels, weak interactions between species, adaptive foraging of consumers, and complex network structure on various measures of ecosystem stability. However, substantially differing methodologies, stability definitions, and a variety of sometimes apparently conflicting results have somewhat muddied the original question of whether complexity begets stability. Instead, the question is becoming more usefully recast along the lines of May’s notion of “devious strategies” —what are the general characteristics of complex ecological networks that allow for, promote, and result from the stability and persistence of natural ecosystems.

Local Stability Analyses of Community Matrices

In his seminal studies on food web stability, May (1972, 1973) measured local or neighborhood stability. In this analysis, it is assumed that the community rests at an equilibrium point where all populations have constant values (Fig. 1a). The stability of this equilibrium is tested with small perturbations. If all species return to the equilibrium – monotonically or by damped oscillations – it is stable (Fig. 1a). In contrast, if the population densities evolve away from the equilibrium densities – monotonically or oscillatory – they are unstable (Fig. 1b). Neutral stability represents a third possibility, in which the perturbation neither grows nor decays as the population densities either reach an alternative equilibrium or oscillate with a constant amplitude in limit cycles (Fig. 1b).

In a community of n species, this approach is based on an $n \times n$ Jacobian community matrix of species interaction coefficients that describe the impact of each species i on the growth of each species j at equilibrium population densities. In food webs, these coefficients may be positive (i.e., i is eaten by j), zero (no interaction) or negative (i.e., i eats j). To describe interactions by single coefficients it is necessary to assume linear interactions. The n eigenvalues of the community matrix characterize its temporal behavior (see May 1973 for a detailed description how these eigenvalues are calculated). For every population, positive real parts of the eigenvalues indicate perturbation growth, negative real parts indicate perturbation decay, and zero real parts indicate neutral stability. Accordingly, if any of the eigenvalues has a positive real part the system will be unstable, i.e., at least one of the species does not return to the equilibrium. Stability may be measured either as a binary variable – return to equilibrium or not – or as a metric variable in form of the return time needed by the population densities to settle back to the equilibrium.

May (1972, 1973) used community matrices in which species were randomly linked with random interaction strength to show that the local stability decreases with

complexity (measured as connectance), diversity, and average interaction strength among the species. The use of such random community matrices has attracted much criticism. It was shown to be extremely unlikely that any of these random communities even remotely resembles ecosystems with a minimum of ecological realism such as containing at least one primary producer, a limited number of trophic levels and no consumers eating resources that are two or more trophic levels higher (Lawlor 1978). The non-randomness of ecosystem structure has been demonstrated in detail by more recent food-web topology studies (e.g., Williams and Martinez 2000, Dunne et al. 2002a, 2004, Morris et al. this volume). Accordingly, subsequent work added more structural realism to those random community matrices by including empirical patterns of food web structure and interaction strength distributions.

Varying connectance in 10 species food webs, De Angelis (1975) tested May's (1972) results within a more realistic model environment and found three conditions for positive complexity-stability relationships: (1) the biomass assimilated by consumers is a small fraction (<50%) of the amount of biomass removed from the resource population, (2) the consumers are subject to strong self-dampening (up to 20 times the maximum growth rate of primary producers) which restricts their population growth, and (3) a bias towards bottom-up control of the interactions (i.e., resource biomass has a stronger influence on the interaction strength values than consumer biomass), which also means that consumers have very little influence on the dynamics of their resources. The realism of these conditions, however, is questionable as assimilation efficiencies for carnivores should generally be higher (~85%, Yodzis & Innes 1992) and such extreme self dampening or low influence of consumers on resources appear unlikely. Nevertheless, for a long time the results of De Angelis (1975) remained the only mathematical models showing positive complexity-stability relationships.

In a more structural approach, Pimm and Lawton (1977, 1978) used community matrices of four interacting species. They systematically varied food chain length and introduced omnivory by letting one of the species consume resources of multiple trophic levels. They found that the stability of the community matrices decreases with the number of trophic levels. The results for omnivory, however, varied, as omnivory decreases stability in terms of the fraction of stable models that return to equilibrium but at the same time increases stability of these stable models by decreasing their return time. Nevertheless, they concluded that the number of trophic levels in natural communities is limited by the stability of population dynamics (Pimm & Lawton 1977), and they predicted that omnivory should be a rare phenomenon in natural food webs (Pimm & Lawton 1978). In particular the latter prediction was not found to be consistent with empirical data as more detailed food webs were compiled (e.g. Martinez 1991, Polis 1991). In a further approach to analyze the relationship between food-web structure and dynamics, Yodzis (1981) showed that empirical community matrices corresponding to 40 real food webs are more stable than randomly assembled community matrices. This clearly indicated that natural food webs are structured in a way that stabilizes the internal population dynamics, but the question remained open as to which particular structural properties were important. Interestingly, Moore and Hunt (1988) showed that in those 40 food webs species are blocked into smaller subwebs of high connectance with only a few links connecting the subwebs. Based on analyses of May (1972), they argued that such

compartmentalization may increase network stability and thus be responsible for the comparatively high stability of empirical food webs.

Evidence for clustering or compartmentalization in more detailed natural food webs has been suggestive, but scant. Krause et al. (2003), using food-web network data with unweighted links as well as with links weighted by interaction frequency, carbon flow, or interaction strength, identified significant compartments in 3 of 5 complex food webs. However, out of 17 versions of the 5 food webs examined, only 6 versions revealed significant compartmentalization. Girvan et al. (2002) found ecologically meaningful compartments based on unweighted topology for a Chesapeake Bay food web (Baird & Ulanowicz 1989), but had difficulty identifying compartments in other more highly resolved food webs (Girvan pers. com.). Topological analysis of 16 diverse, well-resolved food webs showed that their clustering coefficient (Watts & Strogatz 1998) is low in comparison to other types of networks (Dunne et al. 2002a). The low clustering coefficients of food webs is in part attributable to their high connectance (links/species²) compared to other real-world networks (Dunne et al. 2002a)—in effect, there is such a high concentration of links in most food webs that the possibility of compartmentalization, at least from a purely topological perspective, is drowned out. In addition to being based on unweighted links, which may obscure compartmentalization, the clustering coefficient misses compartments of non-omnivorous species based on a single basal species. In sum, the issue of whether and how food webs are compartmentalized, and the impacts of compartmentalization on stability, remains an open question that requires more research.

Extending the approach of adding empirical realism to local stability analyses, de Ruiter et al. (1995) parameterized the general community matrix model with empirical food-web structures and interaction strengths among the species. In their empirical data, they found a pattern of strong top-down effects of consumers on their resources at lower trophic levels in food webs and strong bottom-up effects of resources on their consumers at higher trophic levels. Adding empirical interaction strength patterns to the community matrices increased their local stability in comparison to matrices with random interaction strength values. Most importantly, these results demonstrated that natural food-web structures as well as the distribution of interaction strengths within those structures contribute to an increased local stability of the corresponding community matrices. Neutel et al. (2002) explained this finding with results that showed that weak interactions are concentrated in long loops. In their analysis, a loop is a pathway of interactions from a certain species through the web back to the same species, without visiting other species more than once. They measured loop weight as the geometric mean of the interaction strengths in the loop and showed that loop weight decreases with loop length. Again, when applied to the community matrix, this empirically documented pattern of interaction strength distributions increased its local stability in comparison to random interaction strength distributions.

Thus, over the last 30 years, studies of the local stability of community matrices have contributed to our understanding of the relationship between complexity and stability. De Angelis (1975) indicated some specific conditions for positive complexity-stability relationships, whereas none of the subsequent studies has inverted the negative complexity-stability relationship demonstrated by May (1972). Nevertheless, other studies consistently suggested that local stability increases when ecological realism is

added to the community matrix. In this sense, stability is gained by a limited number of trophic levels (Pimm & Lawton 1977), natural food-web structures (Yodzis 1981, Ulanowicz 2002) and interaction strength distributions (de Ruiter et al. 1995, Neutel et al. 2002). However, to gain mathematical tractability, the community matrix approach, with or without the addition of more plausible ecological structure, makes several assumptions that may restrict the generality of its results. First, community equilibrium is assumed, which excludes chaotic population dynamics that may characterize many natural systems (Fig. 1c, Hastings et al. 1993). Second, only small perturbations are tested. Larger perturbations might yield alternative equilibria. Only addressing local or neighborhood stability does not necessarily predict global stability, although they can coincide. Third, linear interaction coefficients are only a rough approximation of species' dynamics that will only hold for arbitrarily small variances in population densities. For any larger population variances, non-linear species' interactions will be poorly approximated by linear coefficients. This assumption of small population variances, however, is likely to hold once the analyses are restricted to slightly perturbed populations at equilibrium. However, that case is a rather small slice of a much broader ecological pie.

Non-Linear, Non-Equilibrium Population Stability in Food-Web Modules

To overcome the limitations of the equilibrium assumption and linear interactions included in community matrix analyses, an alternative approach to analyzing food-web stability emerged in the early 1990s (e.g., Hastings & Powell 1991, Yodzis & Innes 1992, McCann & Yodzis 1994a,b). Giving up those assumptions prohibited the use of community matrices. Instead, these studies defined less analytically tractable, but more ecologically plausible models of non-linear species' interactions to study the population dynamics in species-poor food-web modules such as three-species food chains. In effect, one aspect of ecological plausibility was traded for another: nonlinear, nonequilibrium dynamics were embraced, but diversity was lost. Most of these non-linear dynamical studies have used an allometric bioenergetic consumer-resource model of species biomass evolution that developed by Yodzis & Innes (1992). It defines for every species how much biomass is lost due to metabolism or being consumed and how much biomass is gained due to primary production or feeding on other species. In this approach, primary producer growth is based on logistic growth equations, and consumer growth is based on non-linear functional responses of consumption to resource densities (Skalski & Gilliam 2001). Another aspect of ecological plausibility is added through the basis of most of its parameters on species body-size and metabolic categories (i.e. endotherm, ectotherm vertebrate, invertebrate, primary producer). Specifying this bioenergetic model for every species in a food web yields a set of ordinary differential equations (ODEs). The numerical integration of the ODEs results in time series of species' biomass evolution that may be used to characterize population dynamics (e.g., stable equilibria, limit cycles, chaotic cycles, Fig. 1). Furthermore, if species extinction is defined as falling below a threshold of biomass density (e.g., 10^{-30}) the persistence of the populations in the food web can be studied. This approach led to the identification of persistent chaos in three species food chains where the population minima are bounded well away from zero (Hastings & Powell 1991, McCann & Yodzis 1994a, Fig. 1c). However, on a longer time scale, persistent chaos may transform into transient chaos due to sudden catastrophic population crashes (McCann & Yodzis 1994b). Together, these

results demonstrate that species and community persistence is not restricted to equilibrium dynamics (Fig. 1a,b), with the potential for chaotic population dynamics (Fig. 1c) that may or may not be persistent over short and long time scales.

Exploring another aspect of ecological complexity, McCann & Hastings (1997) investigated the impact of omnivory on dynamics by altering the network structure so that the top species of the food chain consumed both the herbivorous and basal species. They found that this type of omnivory stabilizes population dynamics by either eliminating chaotic dynamics or bounding their minima away from zero. In contrast to the earlier community matrix work of Pimm and Lawton (1978), this suggests that omnivory is a stabilizing feature of complex networks. It has to be cautioned, however, that these results were obtained under the assumption that the omnivore has a higher preference for the intermediate species than for the basal species, which rarely appears in natural food webs (Williams & Martinez 2004a). Furthermore, the consequences of omnivory in a comparable simple experimental system are highly dependent on nutrient enrichment, since coexistence of both consumers is restricted to intermediate nutrient saturations (Diehl & Feissel 2001).

In an extended study of food-web modules, McCann et al. (1998) showed that weak interactions might generally dampen population oscillations and thus stabilize dynamics in ecological networks. They suggested that such weak interactions among species might be the key for understanding the existence of complex communities, if most interactions in such communities are weak. Post et al. (2000) demonstrated that a set of two three-species food chains linked by the same top consumer can be stabilized when the top consumer can switch its preferences between the two intermediate species. Such preference switching appears likely whenever consumers migrate between different habitat compartments, such as the pelagic and littoral food webs of lakes (Post et al. 2000). This suggests a potentially important role of spatial patterns on food-web stability that remains to be elucidated. Extending the size of the food web modules, Fussmann and Heber (2002) demonstrated that the frequency of chaotic dynamics increases with the number of trophic levels, but decreases with other structural properties that cause higher food web complexity. Interestingly, these results indicate that – dependent on which process dominates in a particular food web – population stability might increase or decrease with food web complexity.

Overall, the numerical integration of non-linear population dynamic models of food-web modules has added a great deal to our understanding of dynamical stability of multispecies systems. While not as simple, abstract, and analytically tidy as community matrix analyses, these models appear to capture more faithfully some centrally important aspects of natural ecological communities—aspects which appear very relevant to issues concerning complexity and stability. Most importantly, this modeling approach has clarified that non-equilibrium population dynamics do not prevent species' persistence (Hastings & Powell 1991, McCann & Yodzis 1994a). Further results suggest how omnivory (McCann & Hastings 1997, Diehl & Feissel 2001), weak interactions (McCann et al. 1998), and spatial processes (Post et al. 2000) may stabilize food webs. Being restricted to species-poor food web modules, however, none of these studies can adequately explore or test complexity-stability relationships in diverse networks that reflect more of the complexity of natural systems. While it has been suggested that results from interaction module studies can be generalized to more diverse, complex

networks, that notion is based on two potentially problematic assumptions: (1) population dynamics respond similarly to independent variables in food-web modules and complex networks, and (2) population stability coincides with community stability. It has been shown that species' persistence does not coincide with population equilibria (McCann & Yodzis 1994a) and that the frequency of chaotic dynamics is influenced by food-web complexity (Fussmann & Heber 2002). I

Species Persistence in Complex Food Webs

More recently, the numerical integration approach has been extended to complex food-web models (Williams & Martinez 2004a, ms.). In this approach, bioenergetic models are applied to a diverse assemblage of species in complex trophic networks. The structure of these complex networks is defined by a set of simple topological models: random, cascade or niche model food webs (Williams & Martinez 2000). The niche model has been found to successfully predict the general structure of complex food webs, while the cascade model (Cohen et al. 1990) predicts some aspects and the random model predicts almost no aspects of food-web structure (Williams & Martinez 2000, Dunne et al. 2004). Dynamics based on the Yodzis and Innes (1992) approach are run on each of the three types of food-web structures, and the ensuing short- and long-term population dynamics are investigated. The explicit integration of complex network structure with non-linear, non-equilibrium bioenergetic modeling allows for the exploration and testing of complexity-stability relationships in more plausibly complex food webs, while retaining certain aspects of modeling simplicity. The topology models, which are analytically solvable (e.g., Camacho et al. 2002), use two readily estimated parameters, species richness (Brose et al. 2003a) and connectance (Martinez et al. 1999), and a few simple rules for assigning links. The dynamics model (Williams and Martinez 2004b), modified and generalized from Yodzis and Innes (1992), while not analytically tractable, is defined by a narrow set of parameters that can be measured relatively readily (e.g., allometric data), simple rules governing biomass gain and loss, and interaction dynamics that have been studied extensively in empirical settings (e.g., functional response). As described in the previous section, the bioenergetic dynamics model has the additional benefit of having been studied extensively in a simple module setting.

In these integrated structure-dynamics networks, global stability can be measured as persistence, i.e., the fraction of species with persistent dynamics (which includes equilibrium, limit cycle, and chaotic dynamics). Using such food-web models, Williams and Martinez (ms.) found that persistence decreases linearly for communities of 15 to 50 species and connectance values between 0.05 and 0.3, thus qualitatively replicating the results of May (1972) in a completely different model environment. Also, they found that food webs with random topology display very low persistence, while adding some network structure in the form of the cascade model increases persistence by an order of magnitude. Use of the niche model structure improves persistence yet again over the cascade model (Williams & Martinez ms.). Given that this coincides with a decrease in empirical adequacy of the structural models, the results strongly suggest that the complex network structure of natural communities provides a higher probability of species persistence. Interestingly, the structure of the persistent food webs that remained after species extinctions was more consistent with empirical data than the original structural models, even in the case of the niche model (Williams & Martinez, ms.). These results

suggest a tight relationship between food-web structure, dynamics, and stability, since network structure influences the population dynamics that in turn determine persistent food-web structures. In addition to the important role of complex network structure for persistence, Williams and Martinez (2004b, ms.) showed that small variations in the functional response of consumption to resource and/or predator density can have dramatic effects on stabilizing the dynamics of particular species, as well as overall species persistence. One important stabilizing variation in functional response is the slight relaxation of consumption at low resource densities. Prior dynamical models have typically assumed Type II functional responses (Holling 1959) which lack this type of feeding relaxation, or have looked at stabilizing aspects of strong versions of relaxation-type responses (e.g., strong Type III) in model systems with only two species (Murdoch et al. 1975, Hassell 1978, Yodzis & Innes 1992). The relaxation of feeding at low resource density is evocative of a variety of well-documented ecological mechanisms (Skalski & Gilliam 2001) including predator interference, prey switching, and refuge seeking. These types of trophic and non-trophic behaviors allow rare or low-biomass resource species to persist in both natural and model ecosystems, increasing overall community persistence.

In another approach to integrating complex structure and dynamics, and in contrast to most prior dynamical studies, Kondoh (2003a,b) allowed consumer preferences for resources to adaptively vary in diverse random and cascade model food webs. He found positive complexity-stability relationships in many of these adaptive networks. However, the results are confounded due to inclusion of implausible linear non-saturating species interactions and internal growth terms that allow consumers to persist without resources. A stability re-analysis of adaptive networks using the Williams-Martinez framework revealed that positive complexity-stability relationships require an arbitrarily high fraction of adaptive consumers (>50%) with a high adaptation rate in simple cascade model food webs, and do not occur in the more empirically well-corroborated niche model food webs (Brose et al. 2003b). Together these results indicate that positive complexity-stability relationships due to adaptive foraging are unlikely to be found in natural systems.

Integrating speciation events and assembly into dynamical food-web models has shown that – despite a high species-turnover – communities may assemble into persistent diverse networks (Caldarelli et al. 1998, Drossel et al. 2001). However, the food-web network structures that evolve are at best loosely comparable to empirical food webs, and appear less complex in some fundamental ways. For example, the connectances (the number of potential feeding links that are actually realized, links/species², as calculated using unweighted links) of 8 example webs are very low ($C = 1$ to 6%, mean of 3%, Drossel et al. 2001, Tables 1 & 2) and connectance decreases with species richness. In comparison, a set of 18 recent empirical food webs have much higher connectances ($C = 3$ to 33%, mean of ~14 %, Dunne et al. 2004, Table 2) and display no significant relationship between species richness and connectance (see also Martinez 1992). Nevertheless, this evolutionary food-web model gives rise to qualitatively interesting patterns, such as periods of high community diversity and complexity followed by catastrophic extinction events leading to periods of lower diversity and complexity. The community evolution approach has yet to be analyzed in terms of complexity-stability relationships, and it remains unclear what causes the extinction events (Drossel et al.

2001). While the integration of evolutionary and population dynamics in a food-web assembly model is intriguing, this formulation is severely hampered by its extraordinarily large number of parameters, rendering the interpretation of results as well as their relevance to natural systems difficult, if not impossible.

In summary, the recent extension of the numerical integration approach to diverse model ecosystems with complex, ecologically plausible network structure offers an approach for exploring conditions that give rise to, and hinder the stability of individual populations within a complex ecosystem, as well as the stability of the whole system (Williams & Martinez 2004b, ms., Brose et al. 2003b). Interestingly, many results from the integrated network structure and dynamics models are consistent with prior local stability analyses: a generally negative complexity-stability relationship and an increased stability of empirically consistent food-web structures in comparison to random webs (Williams & Martinez ms.). Integrating adaptive or evolutionary processes in complex community models may lead to further insights regarding how diverse, complex natural ecosystems may persist (Caldarelli et al. 1998, Drossel et al. 2001, Kondoh 2003, Brose et al. 2003b). It remains a disadvantage in comparison to the local stability approach that resource competition among basal species is generally not included in the non-equilibrium models, but it can be readily added. In general, the utility of current and future applications of these more complex dynamical approaches will depend to a great degree on a careful balancing act between implausible abstraction associated with fewer parameters and model clarity versus greater biological plausibility associated with more parameters and the increased danger of model obfuscation.

Application to an Aquatic Ecosystem

The various approaches to modeling previously described have been used to explore the conditions for and limitations upon stability and persistence in idealized ecosystems. However, aspects of the models may also lend themselves to more applied implementation, allowing assessment of stability of natural ecosystems in the face of actual or anticipated perturbations. This issue is of particular, immediate concern in aquatic ecosystems that contain fisheries. While the use of single-species models, which have dominated fisheries research and management, is generally acknowledged as inadequate and is slowly giving way to analysis of simple food-web modules (Yodzis 2001), those modules may still be inadequate for discerning the likely outcome of perturbations that occur in a diverse multispecies context. Yodzis (1998, 2000) has examined this fundamentally important issue for both theory and practice in the context of whether culling (removing or killing) fur seals is likely to have a negative or positive impact on the hake fishery in the Benguela ecosystem.

Within a fisheries context, one view of Benguela food-web dynamics is that people harvest hake, fur seals eat hake, and therefore if people reduce the fur seal population there will be more hake for people to harvest without a net decrease in the hake stock. However, this is obviously an extraordinary oversimplification of a much more complex ecosystem. Instead, Yodzis (1998) considers a more realistic food web that contains 29 taxa including phytoplankton, zooplankton, invertebrates, many fish taxa, and several other vertebrate taxa (modified from Field et al. 1991). While still a simplification of the diversity and complexity of the system, this 29-taxa web better captures the variety of pathways that can link components of the network. There are over

28 million paths of potential influence from seals to hake in this food-web configuration. While many of those pathways may have negligible impacts on the hake-seal interaction, it cannot be assumed *a priori* that scientists can ignore most of those pathways of influence when assessing the interaction between the two species (Yodzis 1998).

Yodzis (1998) utilizes this more realistic food web as the framework for studying multispecies dynamics determined by the nonlinear bioenergetic consumer-resource model discussed previously (Yodzis and Innes 1992). Parameter values for this model were set for the Benguela ecosystem in one of three ways: using field data estimations (e.g., population biomasses, average body mass), through allometric and energetic reasoning, and by allowing unknown parameters to vary randomly. The use of some randomly varying parameters means that probability distributions, rather than particular solutions, were calculated for the outcome of interest: “What the impact of reducing fur seal biomass on the biomass of hake and other commercial fishes?” In effect, Yodzis is simulating an experimental press-perturbation—an experiment that cannot be done in a scientific or ethical way on the actual ecosystem. This framework and question requires two further simplifications: Yodzis assumes local perturbations (e.g., small culls) and equilibrium dynamics (e.g., constancy in parameter values and dynamics). While we have already seen that there can be problems with these sorts of assumptions, they allow the use of the analytically tractable Jacobian matrix (used by May 1972, 1973) to determine the outcome of small, long-term perturbations in a complex system, which is a reasonable approach to use for this particular question. Thus, the analysis combines elements of all three approaches to multispecies dynamical modeling we have discussed, including local stability analyses of community matrices, nonlinear bioenergetic dynamics, and complex food-web structure. These modeling elements, in conjunction with empirical data on trophic interactions and various characteristics of taxa in the Benguela ecosystem, form a plausible framework in which to simulate a cull of fur seals and its likely effects on commercial fishes in the context of a complex ecosystem.

Using this modeling framework, Yodzis (1998) found that if fur seals are culled, there is a significant probability that two of three commercial fishes (hake, anchovy, and horse mackerel) will have negative responses, and that across all of the commercial stocks it is more likely that there will be a loss than a gain. Perhaps even more importantly, Yodzis’ analyses (1998, 2000) underscore the dangers of relying on overly simplistic models to make predictions. One important issue is how sensitive the model is to inclusion of apparently unimportant trophic links—i.e., can trophic links that reflect some relatively small percentage of a predator’s consumption be ignored without affecting the outcome of the model? The answer is “no” for most trophic links. As the cutoff level (of percentage of diet) for inclusion rises above 10%, results start to vary drastically from outcomes seen on the complete web, thus showing that “taxonomic completeness and resolution, detailed foodweb structure, does make an enormous difference in predicting the outcomes of generalized press perturbations, such as culling fur seals in the Benguela ecosystem” (Yodzis 1998). The interaction between hake and fur seals within the Benguela food web is highly influenced by many other species in the web (Yodzis 2000), and it is very likely that those types of influences are found in many, if not most ecosystems. The presence of these potentially strong diffuse effects in complex food webs renders the use of small modules as a means of simplified community analysis highly suspect for many ecosystems and many types of questions (Yodzis 2000).

Conclusions

We have reviewed three dynamical modeling approaches for studying complexity-stability relationships in abstract food webs, and some of their central characteristics are compared in Table 1. This type of modeling has its roots in linear, equilibrium dynamics research. Some studies continue to utilize equilibrium assumptions, which may be appropriate for certain kinds of questions, as discussed in the previous section. However, since the early 1990's alternative approaches have taken advantage of increasing computing power and advances in nonlinear dynamics to explore population dynamics in detail, using nonlinear and nonequilibrium assumptions which are more likely to reflect the types of dynamics that occur in natural systems. Rather than being restricted to the binary stable/unstable outcomes that typify local stability analyses, researchers can now explore a wider range of types of population and whole-system stability. This is especially the case with the extension of nonlinear, nonequilibrium dynamical analysis to food webs with complex, plausible network structure. For example, one new measure of stability is the percentage of species in a model food web that displays persistent dynamics (Martinez & Williams *ms.*), which can be further broken down into the percentages of species that display different types of persistent dynamics (e.g., stable equilibria, limit cycles, chaos) (Figure 1). Some of the promising new directions for this type of research include explorations into evolutionary and adaptive dynamics, nutrient dynamics, spatial heterogeneity, and non-trophic interactions. However, adding new layers of ecological plausibility to models carries with it the risk of generating a parameter space so large and uncontrolled that interpretation of model outcomes is rendered an exercise in creative tale-spinning, and the links to empiricism that may have motivated the addition may be rendered worthless. Any elaborations need to be carefully justified, made as simple as possible, and explored in detail.

Rather than being shackled just to questions of whether species richness and connectance “beget” stability or instability, researchers are expanding their search for the “devious strategies” that promote different aspects of population and ecosystem persistence and robustness. Regardless of the methodology used, there are some emerging, consistent results indicating that natural food webs have non-random network structures and interaction strength distributions that promote a high degree of population stability and species persistence. As recently pointed out by McCann (2000), the model and empirical evidence (e.g., Berlow 1999) that many weak interactions can buffer a few strong, unstable consumer-resource interactions, thus stabilizing the whole community, is consistent with MacArthur's (1955) hypothesis that having more feeding links acts to dampen large population swings. Non-random network structure, regardless of interaction strength, also appears to buffer against population extinction, and the more realistic the food-web structure, the greater the species persistence. From a purely topological perspective, increasing connectance may buffer against the probability of cascading extinctions (Dunne et al. 2002b) partly because middle and high connectance webs have more uniform link distributions (the distribution of trophic links per species) than low connectance webs, which tend to have power-law distributions (Dunne et al. 2002a). Power-law networks appear especially vulnerable to loss of highly connected nodes (e.g., Albert et al 2000, Dunne et al. 2002b).

It should be clear that there is still an enormous amount of work to be done to elucidate May's "devious strategies," and in the face of widespread biodiversity loss and ecosystem perturbation, there is an increasingly compelling set of reasons to do that research. Food-web research has proven to be a useful vehicle for many theoretical and empirical questions in ecology, and some of the most heroic work will be accomplished by people who are willing to try to integrate the lessons from abstract models with real-world applications (e.g., Yodzis 1998). Beyond ecology, the analyses and results that emerge from the study of complex food webs are likely to reverberate back outwards to influence our understanding of other types of biotic and abiotic networks.

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Table 1: Summary of the stability analysis methodologies

	Local stability	Food-web module stability	Complex food-web persistence
interactions	linear	non-linear	non-linear
equilibrium assumption	yes	no	no
small perturbations	yes	no	no
chaotic dynamics allowed	no	yes	yes
community size	small to diverse	small	diverse
population dynamics analyses	stable / unstable	yes	yes
community stability analyses	yes	no	yes
community persistence	yes	no	yes
competition among primary producers	yes	no	no
nutrient dynamics	no	no	no

Figure 1: Population dynamics in time series.

