

Evolution of Food-web Networks in Fluctuating Environments

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ABSTRACT

We use a network-theoretic approach to address questions about the evolution of food-web characteristics under fluctuating environments. Our model is a weighted, directed graph with nodes representing populations and edges the interactions between them. The dynamics of the network are driven by stochastic generalized Lotka-Volterra equations. Networks evolve by extinction due to inter- and intra-specific density effects, followed by probabilistic recolonization and speciation. We use numerical simulations and analytical calculations to understand the effects of different kinds of stochasticity on network evolution. The results provide multiple insights about the relationship between environmental uncertainty and food-web evolution as well as the structural and dynamical properties of emergent food-webs. In particular, we show that demographic and environmental stochasticity can have unpredictable and sometimes counterintuitive effects, that stability and certain topological features can be associated with the environmental conditions in which food-webs assemble and persist, and that food-webs can achieve stability by selection for specific life history distributions of component populations. We discuss the implications of these results for food-web theory.

INTRODUCTION

Biological communities, food-webs and ecosystems that are more complex with respect to number of individuals and the connections among them, such as tropical rainforests or coral reefs, often appear more stable than comparatively less complex systems. The persistence of such complex systems suggested many to posit some general relationship diversity and stability (Hutchinson 1959; Elton 1958). However, May (1974) demonstrated that the probability of an interactive multi-population systems being mathematically stable rapidly falls with increasing complexity (both in terms of number of species' populations and interactions between them). To many biologists this poses a paradox, because real communities and food-webs are often very large and complex, yet temporally stable at observable time scales. This has lead to a number of related debates about the relationships between stability and complexity of such systems, with very little consensus.

Much research has since been devoted to resolving this apparent paradox, with mixed success (Johnson et al. 1996; Cottingham et al. 2001). Currently, it appears that the best solution that can be offered is either to make restricted models that yield stable persistence (Ives and Hughes 2002), or accept that real systems are indeed a small subset of all possible configurations and observe the structure of the few model systems that are complex and stable (Haydon 2000). In doing so, these later studies echo the views expressed by May (1974, p. 3-4) in his seminal work: *“That stability may usually go with complexity in the natural world, but not usually in general mathematical models, is not really paradoxical. In nature we deal not with arbitrary complex systems, but rather with ones selected by a long and intricate process. The emergent moral is that theoretical work should not try to prove any general theorem that “complexity implies stability”, but instead should focus on elucidating the very special sorts of complexity, the singular strategies, which may promote such mathematically atypical stability”*. Pimm (1982, p. 62) expresses similar sentiment: *“interactions in real food-webs are not random in either sign or magnitude...most randomly assembled communities are ecologically unreasonable”*.

Here, we model the evolution of food-webs with the objective of finding conditions for, and the rate at which, stable systems emerge using a relatively simple mathematical framework. In particular, we focus on an aspect that is fundamentally important, but has been somewhat overlooked until recently: the effects of stochasticity on food-web evolution and persistence. All real world food-webs are assembled and persist with intrinsic stochasticity due to errors in birth-death processes in component populations, and extrinsic perturbations due to temporal stochasticity in the environment, both in terms of resources and living conditions. The former is termed “demographic stochasticity” or “ecological drift”, and the latter “environmental stochasticity” (May 1974; Lande et al. 2003; Hubbell 2001). Given that the majority of community, food-web, and ecosystem-ecology research is motivated by questions about the temporal

stability and resilience of these systems, it is perhaps surprising that relatively few studies have looked at the effects of fluctuating environments on long-term dynamics and equilibrium characteristics of food-webs. A search of papers on the ISI Web of Knowledge™ shows that since 1975, out of 215 theoretical papers on food-web and community ecology theory, only 10 have addressed the issue of demographic or environmental stochasticity in some way, six of these being restricted primarily to small, purely competitive systems (Namba 1984; Ives et al. 1999; Ives and Hughes 2002; Ripa and Ives 2003; Norberg et al. 2001; Bastolla et al. 2005; Anderies and Beisner 2000; Chesson and Huntly 1997; Pimm and Lawton 1977; Chesson 1994). A search for empirical papers also shows a similar trend, with only 8 of 172 papers having anything to do with environmental stochasticity (Floder et al. 2002; Gonzalez and Descamps-Julien 2004; Litchman and Klausmeier 2001; Litchman 2003; Litchman et al. 2003; Petchey et al. 2002; Romanuk and Kolasa 2002; Jennings and Warr 2003; Girvan et al. 2005).

The effects of environmental stochasticity on food-web dynamics and stability were explicitly addressed by May (1974) in his seminal treatise. Not long after, Pimm and Lawton (1977) argued that environmental variability acting as perturbations on a system decrease the probability of persistence of long food chains if resilience (which we define below as “return time” below) is too low. This means that stochasticity places constraints on the length of chains in the web, because in randomly assembled systems, longer chain lengths increase return time. These are interesting results with obvious implications for understanding the relationship between topology and stability of food-webs. However, in most of the research that followed, the role of stochasticity took a backseat until recently (most papers on stochasticity in food-webs have appeared in the last five years). It should also be noted that we are not referring here to robustness or “keystoneness”, measured by species (i.e., node) removal, a related feature that has traditionally received more attention in food-web research (Solé and Montoya 2001; Paine 1995; Ebenman et al. 2004).

Thus, the neglect of the role of stochasticity on food-web assembly could account for some of the controversy surrounding the theoretical results and empirical observations from the burgeoning body of food-web research. For example, although empirical data suggests that certain web properties such as connectance, average path lengths and clustering coefficients appear to be consistent across terrestrial and marine food-webs (Dunne et al. 2002a; 2004; Montoya and Sole 2002; Stouffer et al. 2005), other small-world topological properties are not, and the universality of food-web topology remains unresolved (e.g., Camacho and Arenas 2005; Stouffer et al. 2005; Garlaschelli et al. 2003). One of the questions we will address is whether such universality need at all be expected, given that there is considerable variation in the conditions under which food-webs evolve. Moreover, stochasticity apart, very little is known about the relationship between topological and non-topological features such as stability, biomass storage, and power (energy flux) in food-webs.

METHODS

We adopt a network-oriented approach to model food-web evolution and structure (See Proulx et al. 2005). To a large extent, network-based modeling and analyses of food-webs have focused on topological aspects such as degree distributions and connectance, yielding many interesting insights and revealing possible generalities in network architecture (Dunne et al. 2002b; Dunne et al. 2002a; Jordan and Scheuring 2002; Montoya and Sole 2002; Sole et al. 2002; Newman 2003; Allesina and Bodini 2004; Proulx et al. 2005; Quince et al. 2005; Stouffer et al. 2005). While such studies of strictly topological features are insightful, the study of ecological networks requires an emphasis on dynamical evolutionary processes (Allesina and Bodini 2004; Barabasi and Albert 1999; Proulx et al. 2005; Williams and Martinez 2000). This study will provide insights into how dynamical forces and evolution shape network structure. We address the following questions in this study:

1. Given a set of biological and environmental features, what kind of steady states do dynamical species-interaction networks evolve to; do certain topological and dynamical features emerge consistently?
2. Are there consistent associations between structural and dynamical features of emergent networks (e.g. between resilience, biomass storage, and topology)?
3. Do fluctuating environments affect such relationships?

To address these questions, we use directed-graph networks structured by General Lotka-Volterra (GLV) equations evolving under extinction immigration-speciation dynamics. We model different regimens of demographic and environmental stochasticity to understand the effect of temporal uncertainty on food-web evolution and emergent properties. In the following sections, we first outline the basic model, its extensions, and analytical techniques. We report preliminary results, discuss them, present our conclusions, and propose future directions and extensions of the study framework.

Deterministic model:

Consider a community (or ecosystem) of n interacting non-evolving populations (or species). This system can be represented as a network with nodes as species and edges the interactions between them. Each species' population X is assumed to grow according to the generalized Lotka-Volterra inter-specific interaction model (GLVM) given by the following difference equation for the i^{th} species:

$$N_{i,t+1} = N_{i,t} + r_i N_{i,t} \left(1 + \frac{\sum_{j=1}^n (a_{ij} N_{j,t})}{K_i} \right) \quad (1)$$

where X_i is population size of the i^{th} species (node value), r_i its per-capita intrinsic or maximal (r_{max}) growth rate and K_i its carrying capacity, which determines the strength of intra-specific density dependence and equilibrium population sizes in the absence of interspecific interactions. The a_{ij} 's represent the coefficients of interaction between species. Setting $a_{ii} = -1$, and all $a_{ij} = 0$ (no interspecific interactions) yields the classical discrete logistic equation of population growth for the i^{th} species:

$$N_{i,t+1} = N_{i,t} + r_i N_{i,t} \left(1 - \frac{N_{i,t}}{K_i} \right) \quad (2)$$

The K parameter in LV-type models is phenomenological, and lacking a biological basis to assign differential carrying capacities, we assume that all K_i 's are equal, yielding

$$X_{i,t+1} - X_{i,t} = \Delta X_i = r_i X_{i,t} \left(1 + \sum_{j=1}^n (a_{ij} X_{j,t}) \right) \quad (3)$$

where $X = N/K$. Note that the differential equation corresponding to eqn (3), which is generally used in modeling community and food-web dynamics (May 1974; Roughgarden 1996) is,

$$\frac{dX_i}{dt} = r_i X_i \left(1 + \sum_{j=1}^n (a_{ij} X_j) \right) \quad (4)$$

In this study, we will use eqn(3) instead of (4) in order to be able to model different regimens of environmental stochasticity (see below). The interaction coefficients a introduce the effect of interspecific density dependence relative to intraspecific density dependence (Berlow et al. 2004; MacArthur 1972; Laska and Wootton 1998), and can be represented in an $n \times n$ matrix with the $n(n - 1)$ off-diagonal elements representing interspecific density dependence effects and the n diagonal elements the intraspecific density dependence:

$$A = \begin{pmatrix} a_{11} & \cdots & a_{1n} \\ \vdots & \ddots & \vdots \\ a_{n1} & \cdots & a_{nn} \end{pmatrix} \quad (5)$$

Depending upon the signs and distributions of interaction coefficients, this model allows for predator-prey or parasite-host (+,-), symbiotic (+,+), competitive (-,-), commensalistic (+,0) and amensalistic (-,0) food-web links. This general framework has been used previously by a number of theoretical studies, including the seminal work by MacArthur (MacArthur 1972), May (May 1974) and Roughgarden (Roughgarden 1979).

Model with demographic and environmental stochasticity:

To incorporate demographic stochasticity, eqn(3) can be modified to

$$X_{i,t+1} = X_{i,t} \left[1 + r_{i,t}^D \left(1 + \sum_{j=1}^n (a_{ij} X_{j,t}) \right) \right] \quad (6)$$

Where the maximal growth rate r_i in eqn(3) is now $r_{i,t}^D$, a Gaussian random variable with mean r_i and variance, $V_i = \sigma_d^2 / X_i$. Thus each population experiences random increases and decreases in maximal growth rate that are uncorrelated with those in other populations. These fluctuations in growth rates are also uncorrelated in time (no serial correlation), but because V_i scales inversely with X_i , larger populations experience lower demographic stochasticity, and as X_i in turn changes with time till the population reaches equilibrium, V_i is time-dependent (May 1974; also see Lande et al. 2003).

All natural environments experience a combination of uncorrelated, correlated and periodic fluctuations in variables such as temperature, precipitation and insolation (Vasseur and Yodzis 2004) that can result in density-independent effects on birth and growth rates (May 1974; Lande et al. 2003). To model these situations, we assume that environmental fluctuations affect all individuals of all populations similarly, and modify eqn(6) to

$$X_{i,t+1} = X_{i,t} \left[1 + r_{i,t}^D \left(1 + \sum_{j=1}^n (a_{ij} X_{j,t}) \right) \right] (1 + \varepsilon_t) \quad (7)$$

where ε_t is a random variable with mean = 0 and variance σ_ε^2 . This introduces density-independent environmental stochasticity in population sizes (for alternative models, see Lande et al. 2003; May 1974), that are correlated between populations, but uncorrelated with respect to time (no serial correlation). In other words, all populations experience “good” and “bad” in a perfectly correlated manner, but for any

two time steps t and k , ε_t is independent of ε_k . Temperature is a key factor that sets metabolic limits on growth and death rates in all populations (Brown et al. 2004; Savage et al. 2004), and so our model is appropriate at least for fluctuations in environmental temperature which is a dominant feature in the real world (Vasseur and Yodzis 2004). Later in this paper, we discuss extensions of this model framework that use allometric scaling relationships emulating environmental stochasticity more realistically (see conclusions section below).

The catastrophe model:

Finally, we add another detail to further our understanding of the effects of fluctuating environments. Populations often experience density-independent catastrophic declines due to sudden changes in conditions, such as the advent of droughts or temperature declines. To model this scenario, we retain all the features of eqn (7), and add a probabilistic catastrophe term:

$$X_{i,t+1} = \begin{cases} f(X_{i,t})(1-\delta) & \text{if } \varepsilon < p_\varepsilon, \\ f(X_{i,t}) & \text{otherwise.} \end{cases} \quad (8)$$

Where $f(X_{i,t})$ is given by eqn(7). The parameter p_ε is the per-time step probability of catastrophe. Each catastrophe is assumed to reduce the size of all populations instantaneously by a proportion δ . This extension allows us to model the effects of catastrophes occurring at different characteristic frequencies.

Network stability and stability analyses:

To some extent, the complexity-stability debate has been confounded by inconsistency in the definition of stability, which has been considered variously as robustness to species removal (or “keystoneness”), local stability in the region of deterministic equilibria, or simply as temporal variation in abundance (Grimm and Wissel 1997). Here we only consider local (or neighborhood) stability properties of emergent food-webs (also termed “resilience” by some). Although this provides little or no information about global stability, the advantage of this technique is that it allows us to compare our results with those of previous studies, which have used the same local stability analyses techniques (May 1974; Roughgarden 1996; Jansen and Kokkoris 2003; Haydon 2000; Jonsson and Ebenman 1998). Moreover, for multi-species systems described by eqns (6-8), global stability criteria such as Lyapunov functions are practically impossible to find and/or calculate, except for special forms of interaction matrices (May 1974). Here, we first show the local stability analysis for a n -species system described by eqn (3).

Consider the equilibrium for the i^{th} species, obtained by setting the left hand side of eqn(3) to 0, and solving the resulting equations,

$$\sum_{j=1}^n (a_{ij} \hat{X}_j) = -1 \quad (9)$$

Because we are interested in the persistence of all species', the only non-trivial, interior equilibrium is for all $\hat{X}_i > 0$, i.e., all populations have positive sizes. Then, we calculate the Jacobian matrix J , which is the $n \times n$ matrix of partial derivatives,

$$J = \begin{pmatrix} \frac{\delta F_1(\square)}{\delta X_1} & \dots & \frac{\delta F_1(\square)}{\delta X_n} \\ \vdots & \ddots & \vdots \\ \frac{\delta F_n(\square)}{\delta X_1} & \dots & \frac{\delta F_n(\square)}{\delta X_n} \end{pmatrix} \quad (10)$$

Where $F_i(\square)^{i=1, \dots, n}$ are given by eqn(3). Evaluating J at the equilibrium population sizes obtained from eqn(9) yields the $n \times n$ "community matrix" A^c :

$$A^c = - \begin{pmatrix} r_1 \hat{X}_1 & \dots & r_1 \alpha_{1j} \hat{X}_1 & \dots & r_1 \alpha_{1n} \hat{X}_1 \\ \vdots & \ddots & \vdots & & \vdots \\ r_i \alpha_{i1} \hat{X}_i & \dots & r_i \hat{X}_i & \dots & r_i \alpha_{in} \hat{X}_i \\ \vdots & & \vdots & \ddots & \vdots \\ r_n \alpha_{n1} \hat{X}_n & \dots & r_n \alpha_{nj} \hat{X}_n & \dots & r_n \hat{X}_n \end{pmatrix} \quad (11)$$

The local stability criterion of the system is that the real parts of all the n eigenvalues, $\lambda_{i=1, \dots, n}$ of A^c lie in left half of the plane of complex numbers, i.e., $\max [\lambda_{i=1, \dots, n}] = \lambda_{\max} < 0$. The distance of the this leading eigenvalue from the origin on the complex plane defines the speed at which the system returns to equilibrium following small perturbations, and hence for a locally stable system we can define a useful property, "Return time": $t_r = -1 / \max [\lambda_{i=1, \dots, n}]$. This is also one of the mathematical definitions of the widely used concept of "resilience" in the food-web and community ecology literature; the larger the return time, the smaller the resilience (May 1974; Jonsson and Ebenman 1998). In addition, we also

define the system's "dynamic dimensionality", D as the number of eigenvalues required to account for 95% of the total sum of the eigenvalues. This is a measure of the number of dimensions that determine the system's return time and hence is indicative of the amount of redundancy. We therefore define redundancy, $R = D^{-1}$, i.e., greater the dimensionality, lower its dynamical redundancy. It is also worth noting here is that A^e is the "true" community matrix rather than the "raw" matrix of interaction coefficients A , because its off-diagonal elements embody the magnitude and frequency of inter-specific effects.

Finally, we briefly summarize the results and insights of previous analyses on stochasticity in food-web and community ecology models. As mentioned above, there appears to be a dearth of theoretical as well as empirical work on this topic. To the best of our knowledge, the work done by May (1974) is the most comprehensive and general as it examines the stability conditions for arbitrary numbers of species as well as all possible interactions, both under serially uncorrelated random, and in much less detail, periodic fluctuations. Later authors have examined more specific models for smaller systems, such as competitive exclusion under demographic and environmental stochasticity in phytoplankton (Anderies and Beisner 2000), environmental stochasticity (Chesson and Huntly 1997) and periodicity (Namba 1984). Ives et al (1999), Ives and Hughes (2002) and Ripa and Ives (2003) have primarily examined the effects of correlation in response of community members to environmental fluctuations. We will consider all these studies to the extent that they concern our focus on the effects of differences in fluctuation regimes on entire food-webs. We are not aware of any study that has looked at the effects of catastrophic environments on food-web or community assembly, evolution and dynamics.

For the stochastic systems described by eqns(6-8), the problem of finding stability criteria are considerably more difficult. However if one makes certain assumptions about the distribution, mean and higher moments of the stochastic variables, then it is possible to use eqn(4), and model one or both of the parameters (r_{\max} or X) as Gaussian random variables in essentially the same manner as eqns (6-7) above. This is equivalent to assuming that stochasticity in these systems is continuous-time, serially uncorrelated "white" noise with a small variance, which allows diffusion approximations for individual populations using Ito stochastic calculus (May 1974; Karlin and Taylor 1975). The calculation for food-webs then involves finding the multivariate Gaussian distribution at equilibrium, under the assumption that there is no covariance between the fluctuations in the i^{th} and the j^{th} species (based on the properties of the joint distribution of a number of independent Gaussian variables). Using this approach, May (1974) showed that for an n species food-web to persist in a stochastic environment, assuming a symmetric interaction matrix, and a common variance in environmental stochasticity σ_ε^2 , the stability criterion is $-\lambda_{\max} > \sigma_\varepsilon^2$, thus indicating (somewhat intuitively) that in uncorrelated environments, food-webs need to be more resilient, the level of resilience depending upon the of stochasticity experienced by the system. Our model

differs from the one for which this result is valid on four counts: we include demographic stochasticity, we do not constrain the interaction matrices to be symmetric, we assume that environmental stochasticity is perfectly correlated for all populations, and lastly, we include catastrophes in the “full” model. Thus, although we expect a characteristic distribution of λ_{max} for evolved food-webs, the precise range is unknown. Ripa and Ives (2003) have shown that imperfect between-population correlation in response to environmental stochasticity can have substantial effects on food-web stability characteristics.

Network evolution algorithm and numerical techniques:

The analytical results for stochastic systems described above are typically valid for random variables with small values for mean and higher moments (May 1974pp. 130-133; Karlin and Taylor 1975). This is a serious limitation when two facts are considered. Firstly, noise in the real world can often be catastrophic, have a non-gaussian distribution, and exhibit high variance (for example, catastrophic events are often poisson distributed or power-law distributed). Secondly, environmental variables such as temperature, and precipitation generally show varying degrees of serial autocorrelation (Vasseur and Yodzis 2004; often termed "colored" noise; Halley and Inchausti 2004). These effects are difficult to resolve for multiple interacting species' systems with a purely analytical approach. Thus by using eqn(3) (instead of eqn (4)) and it's stochastic extensions in eqns(6-8) we lose analytical tractability, but gain the ability to explore the effects of wider range, and different kinds of stochasticity. We implement an algorithm for network evolution that allows us to find evolving food-webs that exhibit local stability properties as described above, for deterministic (eqn(3)) as well as stochastic dynamics (eqns(6-8)). The algorithm is as follows:

- (1) Generate a network of n randomly chosen species from a life history set (from a real-valued interval consisting of growth rates);
- (2) Initialize the food-web as a fully connected graph, with pairwise connections drawn with equal probability from the interval $[-1, 1]$.
- (3) Iterate node dynamics forward in time until one or more species go extinct, determined by an extinction threshold X_e .
- (4) Repopulate extinct node(s) with species' drawn at random from the same life history set, at a population size slightly higher than the X_e , and re-establish edges with probability p_{ij} , and interaction strengths drawn from same interval as before.
- (5) Repeat steps 3-4 for a specified time length T_{min}
- (6) After T_{min} time steps, test for two exit criteria at each time step:
 - a. No extinctions have occurred for a length of T_s time steps before current.

- b. If (a) is satisfied, test if all populations have a positive equilibrium (as defined in the previous section).
- (7) Repeat steps 3, 4 and 6 until exit criteria (a) and (b) are satisfied, or abort if a maximum of T_{max} time steps is reached.

The reason for introducing life-history sets is as follows. The stability of the system described above depends not just on the interaction coefficients, but also the magnitudes of the *maximal growth rates* (Strobeck 1973). Therefore we allow networks to evolve under immigration-speciation from a source pool of species' with a range of growth rates, because all food-webs are assembled and evolve with species' having a wide range of life history properties. This allows us to examine whether specific life history attributes are selected for in different environments, and how they affect the stability and evolution of food-webs.

For all runs, p_{ij} was chosen to be 0.1, because this approximate mean of the value reported for a number of real world food-webs (Dunne et al. 2002a; 2004; Vazquez 2005; Stouffer et al. 2005; Montoya and Sole 2002). This implies that we predispose food-web evolution towards a connectance around 0.1, thus allowing us to compare the values of other topological properties. At the end of each successful simulation, the stability characteristics of the emergent network (as described in the previous section) as well as a set of key network characteristics (described below) were calculated. This algorithm was implemented in Matlab. The particular settings for T_{min} , T_{max} and T_s were fine tuned on the basis of test runs to gauge the computational time required a given n . Table 1 lists all the parameters of the models used in this paper.

Network characteristics

We now identify and describe a set of topological and non-topological features of networks that were used to characterize emergent and evolving food-webs. All graph theoretic and network topological terminology is after Newman (2003).

Abundance-frequency distributions: Natural population assemblages have characteristic frequency-abundance distributions, and the mechanisms that generate them are a contentious issue (Hubbell 2001). Recently, Wilson et al. (Wilson and Lundberg 2004; Wilson et al. 2003) have made an attempt to link patterns of species abundance distributions, community size, and species interaction strengths using the GLV framework, showing that a wide range of abundance distribution patterns are possible. This study extends these results by considering the role of fluctuating environments on food-web evolution and emergent patterns of abundance. We use two measures to summarize the frequency-abundance

characteristics of emergent food-webs. The first is “evenness” of abundance-frequency distribution, measured by the Shannon entropy function,

$$Evenness = - \sum_i^n \frac{X_i}{X} \ln \frac{X_i}{X} \quad (12)$$

Evenness is frequently used as a component of species’ diversity measurements, with lower values of the index considered characteristic of communities that are at interspecific interaction equilibrium (Magurran 1988). The second characteristic is the skewness of the abundance-frequency distribution, which can be measured as

$$Skew(X) = \sum_{i=1}^n \frac{(X_i - \bar{X})^3}{(n-1)\sigma_X^3} \quad (13)$$

Positive skew (right skewed) values indicate that the distribution has a heavy tail to the right (i.e., most species are rare), and *vice versa*.

Distribution of r_{\max} values: By introducing life history sets as source pools for immigration-speciation dynamics in network evolution, we allow networks to “find” characteristic growth rate distributions of the component species’ populations. We are interested mainly in the effect of environmental uncertainty on this emergent property, and whether there is a consistent relationship between the two. For example, Fussmann and Heber (2002) suggest that “natural food-webs possess architectural properties that may intrinsically lower the likelihood of chaotic community dynamics”. We calculate two summary statistics about the life history distribution in emergent networks; the mean and the skewness of the r_{\max} distributions (eqn(13)).

Interaction types and strength: We will look at the relative frequencies of all possible interaction types, and also at the mean interaction strength I , which we define as the total strength of interactions relative to the maximum possible interaction strength in the system:

$$I = \frac{\sum_{i,j=1}^n |a_{ij}| + |a_{ji}|}{n^2} \quad (14)$$

Interaction strength is an important feature because stability of random food-webs decreases not just as a function of the number of species and links (connectance), but also strengths of interactions (May 1974). For example, May (1974) concludes that interaction strength should be inversely proportional to $(nC)^{1/2}$ in stable systems. At the same time, a skew towards weak interactions can increase return time and thus resilience (e.g., see Emmerson and Yearsley 2004).

Network energetics: Although the current model is not an explicitly energy in- and out-flow model, we can examine, albeit somewhat phenomenologically, the energetics of emergent food-webs considering two characteristics. The first is storage S , defined as the total amount of energy in the network (Fath et al. 2001), which is simply the sum of all population sizes, and secondly, the mean interaction strength I of the network can also be interpreted as the “power”, or net energy throughput in the network (Fath et al. 2001).

Degree and degree distributions: In graph theory, degree is the number of edges connected to a vertex. The distributions of degrees in networks is a key characteristic that often emerge from specific functional properties of networks (Barabasi and Albert 1999). The degree distribution of real- and model food-webs is a useful measure for assessing universality in topology, and its relationships with stability and robustness deserve further exploration (Dunne et al. 2002a; 2004; Vazquez 2005; Stouffer et al. 2005; Montoya and Sole 2002). A directed graph has both an in-degree and an out-degree for each vertex, which are the numbers of incoming and outgoing edges respectively. Here we measure the degree of the directed, weighted food-webs by converting the corresponding adjacency matrix A to an unweighted, binary (but directed) one A^{UB} with its $n(n-1)$ off-diagonal elements given by,

$$a_{ij}^{UB} = \begin{cases} 1 & \text{if } |a_{ij}| > 0, \\ 0 & \text{otherwise} \end{cases} \quad (15)$$

$$a_{ji}^{UB} = \begin{cases} 1 & \text{if } |a_{ji}| > 0, \\ 0 & \text{otherwise} \end{cases}$$

The degree of each node was then calculated from A^{UB} as a sum of its in- and out-degree. From this, the average degree (k_{av}), the skewness ($Skew(p_k)$; from eqn (13)), and cumulative degree distribution $P(k)$ were calculated, where

$$P(k) = \sum_{i=k}^{\infty} p_i, \quad (16)$$

the probability that the degree is greater than or equal to k .

Connectance: Connectance is the number of edges in a graph relative to the total number that are possible. This characteristic is especially relevant to linking our results to the work of May (1974) and to the recent work focusing on these network features (Dunne et al. 2002a; Stouffer et al. 2005). We measure connectance from A^{UB} as,

$$C = \frac{\sum_{i,j=1}^n a_{ij}^{UB} + a_{ji}^{UB}}{n^2} \quad (17)$$

where a_{ij}^{UB} and a_{ji}^{UB} are directed edges between the i^{th} and the j^{th} nodes.

Geodesic paths and average path length: For unweighted, undirected, graphs a geodesic path (also called “characteristic” or “shortest” path length in the food-web literature) G_{ij} is the shortest path from the i^{th} to the j^{th} vertex (Newman 2003). The average geodesic path length, G_{av} is then simply the average of all the G_{ij} 's. Here because A^{UB} represents a directed graph, we calculated G_{av} as,

$$G_{av} = \frac{\left(\sum_{i,j=1}^n G_{ij} + G_{ji} \right)}{n(n-1)} \quad (18)$$

Distributions of G_{ij} 's and G_{av} provide insights into the characteristic lengths of chains and loops (chains of edges that begin and originate at single nodes without traversing any node twice) in food-webs.

Clustering coefficients: Clustering means the overrepresentation of triangles in a network; sets of three vertices, each connected to each of the others. There are alternative measures of this parameter, but we use the one defined by Watts and Strogatz (1998), because it appears to be the predominant one used in food-web literature (e.g., Dunne et al. 2002a; Dunne et al. 2004; Stouffer et al. 2005; Montoya and Sole 2002). The clustering coefficient for the i^{th} node can be defined as,

$$CC_i = \frac{\text{number of triangles connected to vertex } i}{\text{number of triples centered on vertex } i} \quad (19)$$

where a “triple” means a single vertex with edges running to a pair of others (Newman 2003). For nodes with degree 0 or 1, both numerator and denominator are zero and $CC_i = 0$. The average CC_{av} is then simply the average for all n nodes.

RESULTS AND DISCUSSION:

The results of two sample runs for a deterministic (eqn(3)) and a fully stochastic (eqn(8)) case are shown in Figure 1. In both cases, the stable food-webs emerge between 9000 and 10000 time steps. During evolution, interactions strengths, connectance, and evenness in abundance drop rapidly and then fluctuate until network stabilization. Of the emergent properties, while on one hand many topological parameters appear similar in both cases, there are noticeable differences in the distributions of species’ abundance and r_{max} values. Geodesic paths also appear to be slightly shorter on average for the food-web emerging in a stochastic environment. The overall pattern is clarified by figure 2 and Tables 2 and 3, which summarize the results for 250 evolved food-webs for a range of values for environmental stochasticity. Note that we use the terms “weak” and “strong” in the context of the strength of fluctuations purely as a relative measure.

Dynamical properties

Figure 2 clearly shows that the λ_{max} distributions tend towards more negative values on the real line, thus qualitatively supporting the analytical results of May (1974; for a more restricted model, as discussed above). The effect of frequent catastrophic declines (10% decline in every time step) increases this effect, pushing food-webs towards configurations that impart greater resilience. This result can be understood in more detail by examining table 2, which shows that not only does the average return time t_r decrease substantially with the level of environmental fluctuations (corresponding to increasing λ_{max} ’s), but also that the mean growth rate, \bar{r} increases and right-skewness ($Skew(r)$) decreases for certain types of fluctuations, showing that stability is attained in fluctuating environments by selection for species’ with higher growth rates. The interesting exception to this is the case of strong environmental stochasticity sans catastrophes, where the right skewness increases and \bar{r} decreases. This is not a numerical artifact because the same results are obtained with a range of values for $\sigma_e^2 > 10^{-2}$. This indicates that there is a critical range or (threshold) of environmental fluctuations above which the selection for high \bar{r} is reversed, and selection favors species’ with lower growth rates, as in the deterministic case. This is a very interesting result, which we are yet to explore further.

Another interesting result is that the dynamical redundancy of the system decreases with environmental fluctuations, being the lowest under the regime of frequent catastrophes. Interestingly, for most features, the effects of demographic stochasticity are very different than the cases with environmental stochasticity and catastrophes added. The only previous community or food-web study with which some comparisons can be made in this respect is that of Anderies and Beisner (2000), who modeled a phytoplankton community in a chemostat-like environment. They find significant differences between the effects of demographic and environmental stochasticity. Specifically, a result of theirs that qualitatively matches ours is that they find greater possibility of coexistence for a wider range of life history strategies under demographic and environmental stochasticity (also see Chesson and Warner 1981; Chesson 1994; Chesson and Huntly 1997; Namba 1984).

Despite these differences in dynamical properties, all emergent food-webs attain very similar patterns of species' abundance. A more detailed exploration of this aspect will be pursued with an augmented model that includes variable carrying capacities instead of the fixed parameter used here (see last section).

Structural properties

Table 3 lists the topological feature of evolved food-webs. All emergent food-webs show remarkably consistent values for interaction strength, relative distributions of different kinds of interactions, average degree, clustering coefficient, and geodesic paths. Thus, environmental fluctuations appear to have little effect on food-web topology, despite the effects on dynamical properties. The notable exception is the skewness of the clustering coefficient, which decreases with the level of environmental fluctuations. Here again, the results of the simulations with demographic stochasticity are very different from those with environmental stochasticity. The relative distributions of interactions have been considered crucial in determining the stability of food-webs (Berlow et al. 1999; May 1974). Our results match the qualitative stability analyses (based upon examination of the signs of interactions only) of May (1974) which suggested that while predator-prey interactions, commensalisms and amensalisms stabilize food-webs, mutualisms and symbioses should be destabilizing (Also see Dambacher et al. 2003). Irrespective of environmental stochasticity, the evolved food-webs result in a large proportion of commensalistic and amensalistic interactions compared to predations, mutualisms and competitive interactions. The validity of these results is difficult to determine, because empirical food-web data collection rarely allows the quantifications of unidirectional, weak interactions. Moreover, as pointed out by Williamson (1972) many of the cases of predation parasitism and herbivory in nature are probably in effect commensalistic and amensalistic because of the asymmetries in interactions.

Food-web structure: universality, and relationships with stability

A number of recent studies have focused on the topological properties of food-webs, searching for general features as well as relationships between stability and structure (e.g., Dunne et al. 2002a; Dunne et al. 2004; Stouffer et al. 2005; Montoya and Sole 2002; Neutel et al. 2002). Our results show that certain commonly measured topological features of food-webs might be more universal than thought before, as they emerge even under a wide range of environmental conditions. That these topological parameters show much more variation in empirical data could be accounted for by the fact that while our model food-webs include most of the spectrum of possible interactions, real data on certain kinds of interactions (such as amensalism and parasitism) are extremely difficult to measure. Although we do not quantify the power law or scale-free characteristics of cumulative degree distributions, the mean degree, the clustering coefficients, and average geodesic paths do fall within the range of existing empirical data. The issue of skewness among degree distributions is an interesting one. The values for skewness in our emergent food-webs fall within the range reported by Montoya and Sole (2003). However, in contrast to previous studies, which found that species richness is positively correlated with right-skewness (thus indicating deviation from distribution of degrees in random webs, which is Poisson distributed), we find that for a given number of species, skewness varies with environmental stochasticity. This raises the intriguing possibility that a quantification of environmental stochasticity might explain some of the variation in the observed degree distributions of food-webs. Moreover, this topological feature is clearly linked with stability. Figure 3 shows that there is a positive relationship between the skewness of degree distribution and stability properties of in emergent food-webs: while resilience (t_r) increases with skewness, and dimensionality (redundancy) decreases. These results qualitatively match those of Solé and Montoya (2001), who showed that food-webs with right skewed degree distributions showed resilience to random species removal (but were sensitive to targeted removals).

On the whole then, our results cast doubt on the existence of any general relationships between the more commonly measured topological properties of food-webs and their stability. Moreover, they also indicate the necessity of finding more informative topological parameters, and deeper analyses of the structure of food-webs to pinpoint general characteristics that enhance stability. For example, Neutel et al. (2002) have identified the length and strength of loops as being crucial to stability in real world food-webs. We hope to explore such relationships in future work.

Diversity begets stability, or vice versa?

Previous studies have focused mainly on relationships between species diversity, redundancy, and food-web stability and function; our results suggest a crucial role of environmental stochasticity in modulating this relationship. Moreover, it has been observed that more species rich food-webs (such as

those in the tropics) exhibit greater redundancy, the reasons for which are poorly known. The fact that resilience increases while redundancy (D^{-1}) decreases with environmental stochasticity in our model, has interesting implications for this debate. In this context, it is also worth noting that the number of extinction-colonization-speciation events required for food-web stabilization increases with stochasticity (Table 2). Altogether, these results suggest that food-webs will assemble more slowly in fluctuating environments, and will equilibrate at lower species' numbers unless the rates of immigration-speciation are proportionally higher. This prompts for an extension of Hubbell's (2001) results about the persistence of diverse species' assemblages under a balance of speciation-immigration and extinction from demographic stochasticity.

Because tropical regions have more predictable environments relative to those at higher latitudes, these results suggest that latitudinal gradients in species richness could be partly determined by environmental stochasticity, which shows the opposite geographical trend as species richness (Vasseur and Yodzis 2004). Most theories for geographic gradients on the other hand, focus mainly on niche-partitioning and energy availability, rarely considering the effects of environmental stochasticity (Evans et al. 2005).

CONCLUSIONS AND FUTURE DIRECTIONS

To summarize, our main results are, (1) Demographic stochasticity, environmental stochasticity, and catastrophic fluctuations have very different results on the speed of assembly, evolution, and emergence of food-web properties. (2) Food-webs can attain stability by selection on life history characteristics of component population, depending upon the regimen of environmental stochasticity, (3) Resilience increases and redundancy decreases in food-webs persisting in fluctuating environments, (4) The right-skewness of degree distributions depends on the level of environmental fluctuations under which food-webs assemble and persist, and (5) this skewness is positively related with resilience, and negatively related with dynamical redundancy of evolved food-webs. The potential applications of network models to food-web theory appear endless, especially because of the sophisticated structural analyses techniques that they bring to food-web research. Here, we have shown that modeling evolution of food-webs can provide many interesting insights, not just for biology, but for understanding network dynamics in general. In the near future, we hope to explore the following directions.

Future directions

Including colored noise and periodicity:

We have included a very restricted variety of environmental noise here, compared to the pattern observed in nature. In particular, it will be important to gain a better understanding of the effects of different degrees of serial autocorrelation (“colored noise”), because most of the noise in nature is not just seasonal or stochastic, but also shows different degrees of color (Halley and Inchausti 2004; Vasseur and Yodzis 2004).

Effect of preferential attachment:

Here we have assumed that new populations that enter food-webs establish links at random. However, in real world situations, it is likely that initial interactions and hence link formation is density dependent, i.e., new populations establish connections on the basis of the relative abundances of existing species, either for fitness maximization, as simply due to the higher probability of encounter. This rule is qualitatively similar to the preferential attachment model of Barabasi et al. (1999), and to the best of our knowledge has not been explored in food-web theory.

Abundance-diversity distributions at single trophic levels:

A majority of the estimates of frequency-abundance patterns and corresponding theoretical models are from competing populations from a single trophic level (e.g., Wilson and Lundberg 2004; Etienne and Olf 2004b; Etienne and Olf 2004a; Etienne and Olf 2005; Hubbell 2001). It is not clear whether theoretical predictions about frequency-abundance distributions will hold if competing communities embedded in food-webs are examined. This is important because most empirical data from communities comes from subsets of larger food-webs. Within the framework of the current study, it is possible to extract single trophic levels (of predators, consumers, etc), and examine the frequency-abundance distributions. For example, it will be interesting to see if communities in emergent food-webs follow some of distributions that arise from community ecology theory, such as the zero-sum multinomial, the multivariate Poisson lognormal, and the discrete broken stick (based on MacArthur’s broken stick model) (Etienne and Olf 2005; Hubbell 2001).

Allometric scaling, closed food-web models, and the effects of biological evolution

As mentioned above, our results about the way in which stochastic environments select for specific growth rate distributions in food-webs draw attention to the potential role for evolution in food-web assembly and resilience. One way to incorporate the effects of intra-specific evolutionary dynamics in the above framework is to use allometric scaling relationships. For example, because r_{\max} as well as mutation rate scales according to body mass for a wide range of organisms (Brown et al. 2004; Savage et al. 2004; Gillooly et al. 2005), rates of evolution and species turnover (by immigration and/or speciation)

should increase with r_{\max} because of the combined effects of elevated mutation rate and shorter generation times (for organisms with non-overlapping generations, the generation time is approximately the reciprocal of the r_{\max}). Based on this observation, the effects of differential rates speciation-immigration on food-web evolution can be modeled by assuming a probability density function over a range of growth rates from which species are drawn at random for each repopulation event during network evolution. Such an approach is qualitatively similar to deriving life-history specific parameterizations of the of the colonization-speciation parameter θ of Hubbell (Hubbell 2001). This approach would allow us to address the effect of evolution in stable as well as fluctuating environments on food-web dynamics and topology. The use of allometric scaling theory opens up the possibility of extending (or replacing) the largely phenomenological GLV framework with one that involves explicit resource input and output.

Autocatalytic sets:

Recently, Jain and Krishna (2001) demonstrated that “cooperative” autocatalytic sets can emerge in networks evolving by simple rules. Beginning with a randomly connected network, they showed that extinction-recolonization dynamics result in the evolution of the net towards a stable attractor state dominated by autocatalytic sets (ACS), defined set of nodes such that each node has at least one incoming positive link from a node in its set (Kluge 1982). The ACS phenomenon qualitatively matches the prediction of May (1974) regarding the importance of unidirectional commensalisms, supported by our results about the emergence of strongly commensalistic food-webs. It will be interesting to explore whether the emergence of commensalisms is driven by a mechanism similar to, or the same as that leading to the formation of ACSs.

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Table 1: List of model parameters.

Parameter	Description
N	Number of species in the food-web
X_i	i^{th} species' population size
X_e	Populations size below which a species' goes extinction
X_r	Abundance at which to repopulate nodes
r_i	i^{th} species' maximal growth rate, drawn from the life history set \mathbf{R}
A	The interaction matrix with elements $a_{ij,1\dots n}$
σ_d^2	Variance of the Gaussian demographic stochasticity parameter $r_{i,t}^D$
σ_ε^2	Variance of the Gaussian environmental stochasticity parameter ε_e
δ	$\in (0,1)$, strength of catastrophic population decline.
p_e	$\in (0,1)$, per-time-step probability of catastrophe
J	The Jacobian matrix
A^c	The community matrix
λ_i	The i^{th} eigenvalue of the community matrix; λ_{max} is the maximum value
\mathbf{R}	$\in \mathbf{R}^+$, life history set from which to draw populations for node repopulation
p_{ij}	$\in (0,1)$, probability of node reconnection of the i^{th} reintroduced species with each of the $n - 1$ others
T_{min}	Minimum number of time steps to evolve network
T_{max}	Maximum number of time steps to evolve network
T_s	The number of time steps over which to test for exit criterion (a), as outlined in the methods section

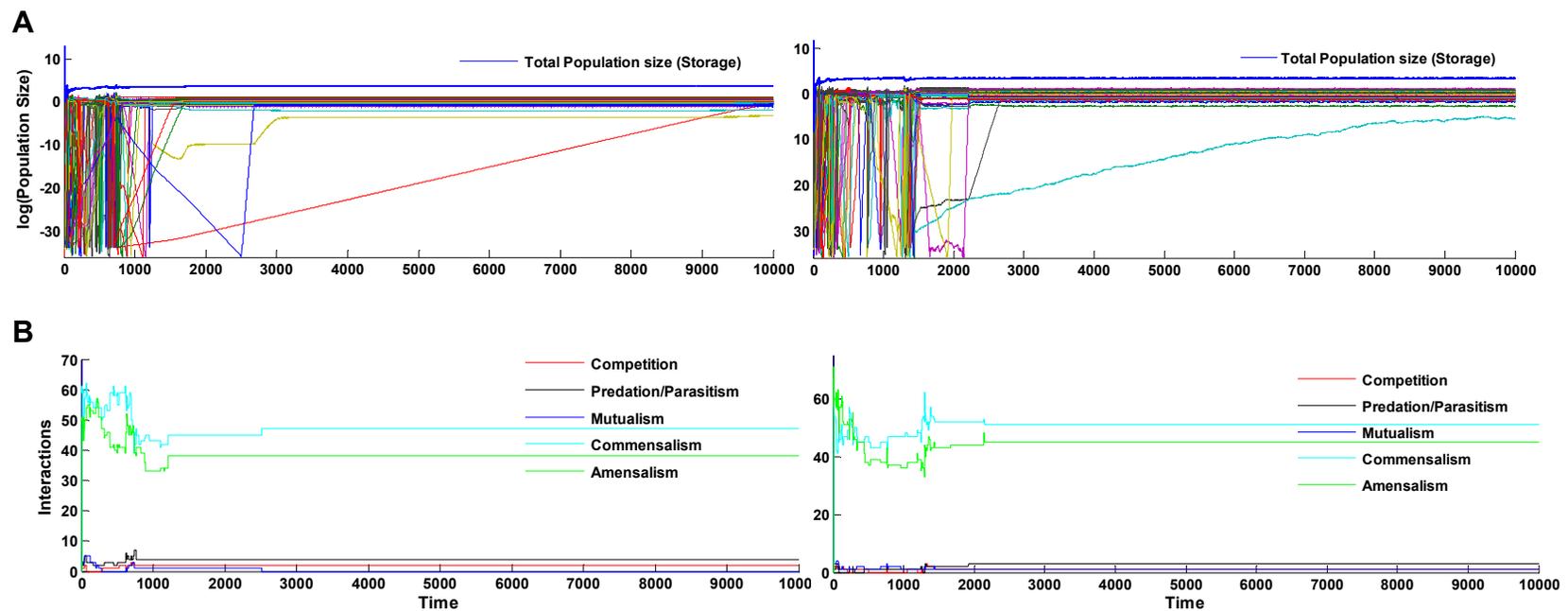
Table 2: Dynamical properties of emergent networks. These results are based on 200 simulations of each of the models in eqns (3, 6-8), for different parameter values, as given below. The deterministic parameter settings for all runs were, $n = 30$, $R = (0, 2)$, $X_e = 10^{-12}$, $X_r = 10^{-11}$, $p_{ij} = 0.1$, $T_{min} = 10^5$, $T_{max} = 3 \times 10^5$, $T_s = 5 \times 10^3$. For runs with demographic stochasticity (DS), $\sigma_d^2 = 10^{-11}$. Parameter settings for environmental stochasticity (ES) and catastrophic fluctuations (CF) are given in the table. t_r : Return time; D : dynamic dimensionality; X_{tot} : total population size; \bar{X} : mean population size; $Skew(X)$: skewness of frequency-abundance distribution; \bar{r} : mean growth rate; $Skew(r)$: skewness of frequency distribution of growth rates; $Extinctions$: number of extinctions before network stabilization.

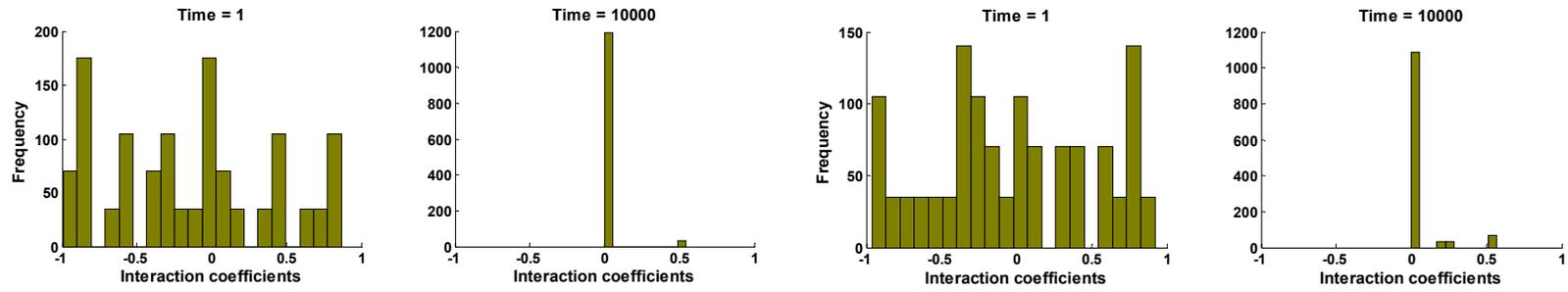
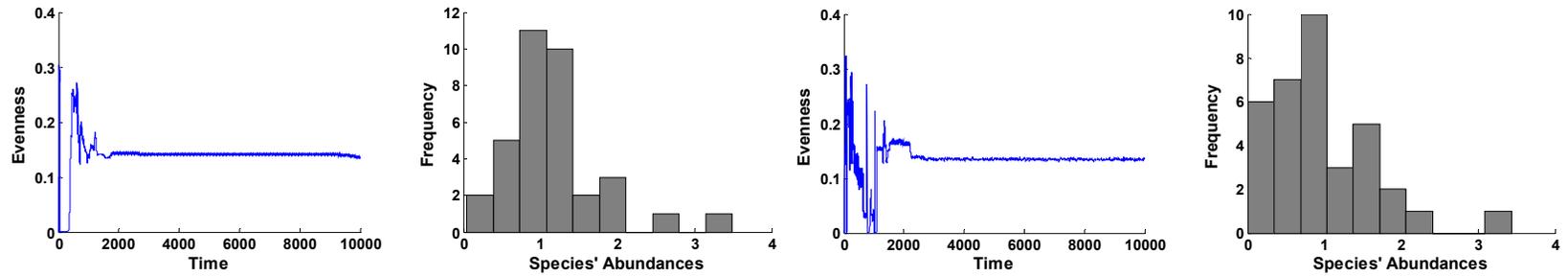
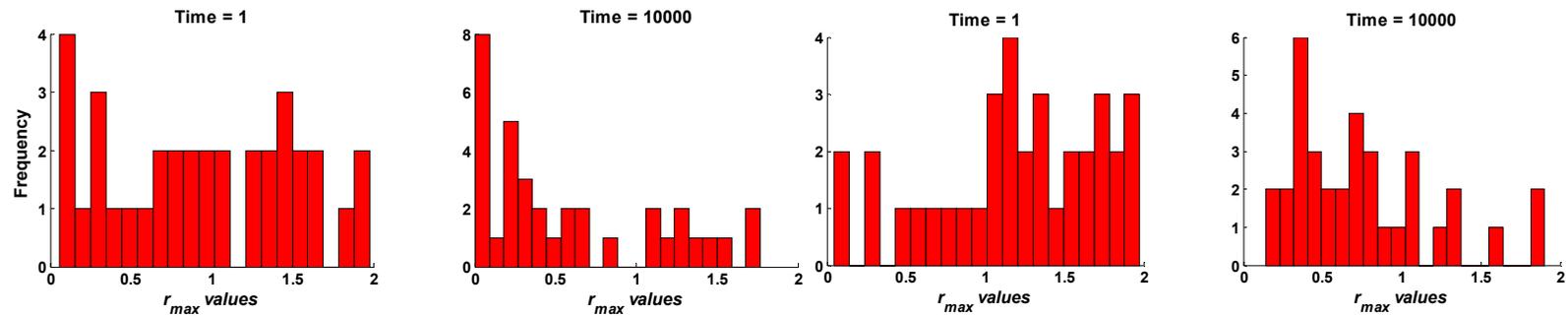
Property	Deterministic	DS	DS + Weak ES ($\sigma_e^2 = 10^{-4}$)	DS + strong ES ($\sigma_e^2 = 10^{-2}$)	DS + Weak ES ($\sigma_e^2 = 10^{-4}$) + CF ($\delta = 0.1, p_e = .02$)	DS + Weak ES ($\sigma_e^2 = 10^{-4}$) + CF ($\delta = 0.1, p_e = 1$)
t_r	595.462 (+/-2150)	6436.193 (+/-85338)	530.19 (+/-5184)	199.699 (+/-851)	79.072 (+/-302)	48.37 (+/-156)
D	20.968 (+/-1.458)	21.911 (+/-1.312)	22.047 (+/-1.056)	22.237 (+/-1.187)	22.54 (+/-1.21)	23.611 (+/-0.946)
X_{tot}	38.258 (+/-6.557)	36.946 (+/-6.899)	36.764 (+/-6.159)	35.524 (+/-7.881)	33.89 (+/-6.361)	30.641 (+/-4.487)
\bar{X}	1.275 (+/-0.219)	1.232 (+/-0.23)	1.225 (+/-0.205)	1.184 (+/-0.263)	1.13 (+/-0.212)	1.021 (+/-0.15)
$Skew(X)$	0.981 (+/-0.567)	0.961 (+/-0.548)	1.016 (+/-0.548)	0.958 (+/-0.614)	1.026 (+/-0.589)	0.916 (+/-0.597)
\bar{r}	0.618 (+/-0.109)	0.672 (+/-0.112)	0.673 (+/-0.11)	0.575 (+/-0.111)	0.718 (+/-0.111)	0.864 (+/-0.097)
$Skew(r)$	0.785 (+/-0.329)	0.756 (+/-0.325)	0.723 (+/-0.308)	0.986 (+/-0.416)	0.705 (+/-0.353)	0.493 (+/-0.291)
$Extinctions$	144.347 (+/-57)	157.495 (+/-70)	165.884 (+/-71)	232.147 (+/-116)	169.69 (+/-77)	151.558 (+/-74)

Table 3: Structural properties of emergent networks, from the same simulations as Table 2; all parameter settings and abbreviations are the same. *I (or Power)*: Average interaction strength; *C*: Connectance; k_{av} : Average degree distribution; *Skew(k)*: Skewness of degree distribution; CC_{av} : Average clustering coefficient; G_{av} : Average geodesic path; Predations (and parasitism), Mutualisms, Competitions, Commensalisms and Amensalisms: relative frequency of the five interaction types

Property	Deterministic	DS	DS + Weak ES	DS + strong ES	DS + Weak ES + CF	DS + Weak ES + CF
<i>C</i>	0.086 (+/-0.009)	0.084 (+/-0.009)	0.085 (+/-0.008)	0.083 (+/-0.01)	0.082 (+/-0.01)	0.084 (+/-0.009)
<i>I (Power)</i>	0.039 (+/-0.005)	0.038 (+/-0.005)	0.039 (+/-0.005)	0.037 (+/-0.005)	0.038 (+/-0.005)	0.038 (+/-0.005)
<i>Predations</i>	0.025 (+/-0.017)	0.028 (+/-0.019)	0.024 (+/-0.018)	0.027 (+/-0.019)	0.027 (+/-0.019)	0.023 (+/-0.018)
<i>Mutualisms</i>	0.01 (+/-0.012)	0.01 (+/-0.012)	0.009 (+/-0.011)	0.008 (+/-0.01)	0.01 (+/-0.015)	0.011 (+/-0.013)
<i>Competitions</i>	0.008 (+/-0.01)	0.009 (+/-0.012)	0.01 (+/-0.011)	0.008 (+/-0.01)	0.011 (+/-0.013)	0.007 (+/-0.01)
<i>Commensalisms</i>	0.523 (+/-0.051)	0.524 (+/-0.057)	0.524 (+/-0.058)	0.527 (+/-0.054)	0.523 (+/-0.067)	0.54 (+/-0.058)
<i>Amensalisms</i>	0.434 (+/- 0.053)	0.429 (+/- 0.06)	0.433 (+/- 0.058)	0.43 (+/- 0.056)	0.43 (+/- 0.068)	0.419 (+/- 0.052)
k_{av}	4.964 (+/-0.52)	4.876 (+/-0.54)	4.912 (+/-0.475)	4.829 (+/-0.558)	4.771 (+/-0.575)	4.898 (+/-0.512)
<i>Skew(p_k)</i>	0.437 (+/-0.431)	0.143 (+/-0.252)	0.409 (+/-0.325)	0.314 (+/-0.263)	0.272 (+/-0.43)	0.182 (+/-0.411)
CC_{av}	0.075 (+/-0.022)	0.077 (+/-0.024)	0.081 (+/-0.025)	0.077 (+/-0.021)	0.075 (+/-0.023)	0.077 (+/-0.022)
G_{av}	2.3345 (+/-0.69)	2.2935 (+/-0.682)	2.319 (+/-0.7405)	2.2895 (+/-0.675)	2.492 (+/-0.606)	2.391 (+/-0.709)

Figure 1: Two sample runs of network evolution, showing, (A) Changes in population abundances over time (B) Relative frequencies of types of interactions (C) Initial and final distributions of interactions strengths (D) Evenness (over time) and distribution of abundances (after network satibilization) (E) Initial and final distributions of growth rates (r_{max}) and (F) Final cumulative degree distributions $P(k)$ and geodesic paths. The panel on the left is the purely deterministic model (eqn(3)), and one on the right the fully stochastic model (eqn (8)). For both runs, the parameter settings were: $n = 35$, $\mathbf{R} = (0, 2)$, $X_e = 10^{-12}$, $X_r = 10^{-11}$, $p_{ij} = 0.1$, $T_{min} = 10^5$, $T_{max} = 3 \times 10^5$, $T_s = 5 \times 10^3$. In addition, the parameters eqn (8) were, $\sigma_d^2 = 10^{-11}$, $\sigma_e^2 = 10^{-2}$, $\delta = 0.1$, and $p_e = 1$ (i.e, catastrophes occur at every time step).



C**D****E**

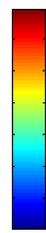
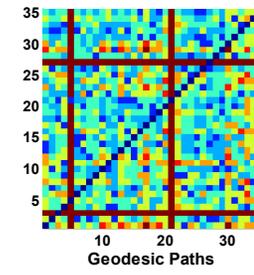
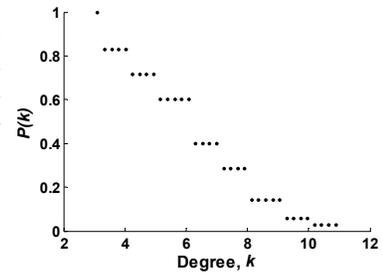
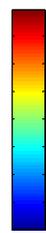
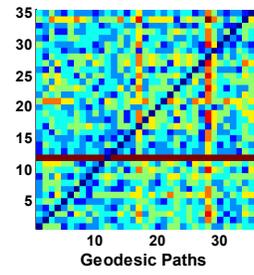
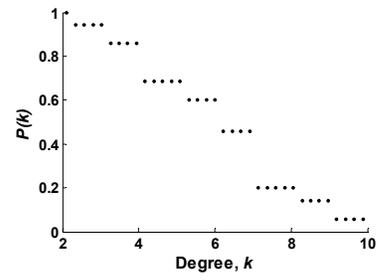
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Figure 2: The distribution of λ_{max} for of 250 evolved food-webs each, under different levels of stochasticity: (A) For the deterministic model, (B) with demographic stochasticity ($\sigma_d^2 = 10^{-11}$), (C) with demographic ($\sigma_d^2 = 10^{-11}$) and environmental $\sigma_e^2 = 10^{-3}$ stochasticity (D) in a catastrophic environment ($\delta = 0.1$, and $p_e = 1$) with demographic ($\sigma_d^2 = 10^{-11}$) and weak environmental stochasticity $\sigma_e^2 = 10^{-3}$.

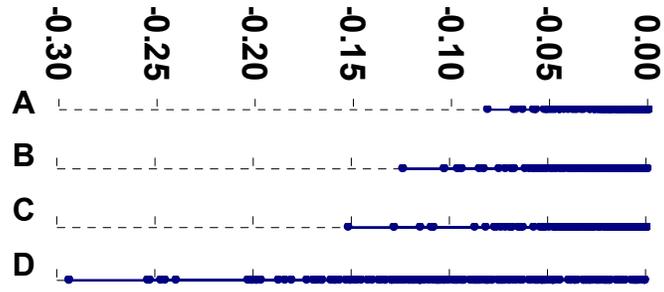


Figure 3: The relationship between the topological parameter $Skew(p_k)$, and two stability properties, return time and dimensionality of food-webs. While resilience (t_r) increases with skewness of degree distribution, dimensionality decreases. The skewness of degree distribution in turn decreases with increasing environmental stochasticity.

