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**Increasing community size and connectance can increase stability in competitive communities.**

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ABSTRACT: The relationship between community complexity and stability has been the  
10 subject of an enduring debate in ecology over the last 50 years. Results from early model  
communities showed that increased complexity is associated with decreased local stability. I  
demonstrate that increasing both the number of species in a community, and the connectance  
between these species results in an increased probability of local stability in discrete-time  
competitive communities, when some species would show unstable dynamics in the absence  
15 of competition. This is shown analytically for a simple case and across a wider range of  
community sizes using simulations, where individual species have dynamics that can range  
from stable point equilibria to periodic or more complex. Increasing the number of  
competitive links in the community reduces per-capita growth rates through an increase in  
competitive feedback, stabilising oscillating dynamics. This result was robust to the  
20 introduction of a trade-off between competitive ability and intrinsic growth rate and changes  
in species interaction strengths. This throws new light on the discrepancy between the

theoretical view that increased complexity reduces stability and the empirical view that more complex systems are more likely to be stable, giving one explanation for the relative lack of complex dynamics found in natural systems. I examine how these results relate to diversity-biomass stability relationships and show that an analytical solution derived in the region of stable equilibrium dynamics captures many features of the change in biomass fluctuations with community size in communities including species with oscillating dynamics.

Keywords: Stability, Complexity, Community, Competition, Connectance, Intrinsic growth rate, Periodic dynamics

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## INTRODUCTION

The debate surrounding complexity and stability in community dynamics remains an enduring ecological discussion, with both theoretical and empirical evidence for qualitatively different stability-diversity relationships (Ives and Carpenter, 2007; McCann, 2000). Many of the discrepancies can be put down to the huge variety of definitions used to describe what different authors mean by complexity, diversity and stability (Grimm and Wissel, 1997; Ives and Carpenter, 2007). Of the results from model communities, the most convincing mathematical argument for decreased dynamical (local asymptotic) stability with increasing complexity (in terms of community size) was put forward by May (1972; 1973). He showed that increasing the number of links between species in randomly assembled communities and/or the strength of interactions between these species led to a decrease in the tendency for such communities to be locally stable, i.e., for species densities to return to their equilibrium level following a small perturbation. Empirical tests of simple randomly assembled microcosm systems have supported May's general theoretical findings (e.g., Fox and McGrady-Steed, 2002; Weatherby et al., 1998).

The community framework has generated a large body of theoretical work (reviewed in Berlow et al., 2004; Ives and Carpenter, 2007). For example, some work attempts to corroborate the universality of May's result (Chen and Cohen, 2001; Sinha and Sinha, 2005) while others suggest that the relationship is not as general as suggested (Cohen and Newman, 1985) or that increased complexity can both decrease and enhance stability (Rozdilsky and Stone, 2001). Other research has demonstrated the various results through analysis of the mean and variance of interaction coefficients (Jansen and Kokkoris, 2003), community assembly methods (Wilmers et al., 2002), or examined what conditions are required to

produce maximally stable communities (Haydon, 2000). Ives and Carpenter (2007) have recently shown that of 13 potential diversity-stability relationships tested in competitive communities, only four indicated a positive relationship: two were related to biomass stability (characteristic return rate and size of biomass fluctuations); one to increased compensation (increased abundance of surviving species) following species removal; and the last to an increase in the number of attempts required for an invader to successfully enter a community.

Increased stability with increasing complexity has been noted under various conditions in multitrophic foodwebs (Brose et al., 2006; De Angelis, 1975; Fussman and Heber, 2002; McCann and Hastings, 1997; McCann et al., 1998; Neutel et al., 2007; Otto et al., 2007; Williams and Martinez, 2004). While these foodweb studies include systems with non-equilibrium dynamics, little work has so far been carried out on non-equilibrium systems focusing on direct competition. Most trophically structured foodwebs assume logistic growth at the basal level, often with direct competition between basal species for shared resources, therefore understanding processes occurring at this level is of crucial importance. Recent evidence from a study of bacterial diversity has highlighted high levels of ecotype diversity within the same bacterial clades (Koeppel et al., 2008), further emphasizing the need to understand functional relationships within a trophic level (Berlow et al., 2004). Previous theoretical work has shown that variation in species intrinsic growth rate in the community may (Ruokolainen et al., 2007) or may not (Fowler and Lindström, 2002) lead to qualitative differences in community responses following different disturbances in simulated competitive communities. These two studies only examined under- and/or damped overcompensatory dynamics in the stable equilibrium range. While consumer-resource studies have traditionally been interested in investigating cycling systems, it is surprising how little work has investigated non-equilibrium dynamics in competitive systems.

Here, I investigate how the probability of finding deterministic, locally (asymptotically) stable communities varies with the number of species present, or the connectance among species in the community. I examined the limits to the classical result that increasing the complexity of competitive communities through changes in the number of links or interaction strength leads to a reduction in (local) stability; and results from more recent studies that show that while increased connectance can both reduce and enhance stability, larger communities are less stable than smaller (Chen and Cohen, 2001; Fussman and Heber, 2002; Ives and Carpenter, 2007; Rozdilsky and Stone, 2001). I relaxed the commonly applied assumption that species share a common intrinsic growth rate, and for the first time, to my knowledge, explicitly allowed growth rates to vary over a range of qualitatively different species-specific population dynamics within the community (although this has been done in a continuous time predator-prey context elsewhere, e.g., Drake, 1990; Kondoh, 2003); from under- and overcompensatory stable point equilibrium, to periodic and more complex oscillations. For the first time, I highlight that increasing species numbers and/or connectance can actually increase the probability of local stability in competitive communities. These results were examined under a range of conditions and the general result was found to be robust to variations in the model framework. I also examined how biomass fluctuations are affected under a stochastic version of this model framework, and show that a solution derived under the assumption of stable equilibrium dynamics (Ives and Hughes, 2002) captures many of the relationships between the variability in biomass fluctuations and community size under different correlation structures of environmental variation.

## METHODS

To model community dynamics, I assumed a discrete-time Ricker model incorporating Lotka-Volterra type interspecific interactions between species. The population density  $N$  for each species  $i$  in an  $m$ -species community can be calculated over consecutive time-steps  $t$  as

$$N_{i,t+1} = N_{i,t} \exp \left( r_i \left[ 1 - \frac{\sum_{j=1}^m \alpha_{ij} N_{j,t}}{K_i} \right] + \varepsilon_{i,t} \right), \quad (1)$$

5 where  $r_i$  represents species specific intrinsic growth rates,  $K_i$  is species specific carrying capacity in the absence of competitors and  $\alpha_{ij}$  is the species interaction coefficient. For simplicity, all  $K_i = 1$ , scaling all population sizes to their equilibrium density in the absence of interspecific interactions. The environmental fluctuations experienced by different species are represented by  $\varepsilon_{i,t}$  and were only set to non-zero values for the study of variability in

10 biomass fluctuations described below. All intraspecific interaction terms  $\alpha_{ii}$  were set to unity. Values for  $\alpha_{ij}$  ( $i \neq j$ ) were drawn at random from a beta distribution with parameters  $p$  and  $q$  selected to generate distributions where weak interactions dominate, which is thought to be the case in natural communities (Berlow et al., 2004; McCann, 2000; McCann et al., 1998). Specifically, parameter values used here were  $p = 1$  and  $q = 9$  giving an expected value  $\mu =$

15  $0.1$  and variance  $\sigma^2 = 9/1100$ . Other values were chosen to examine the effect of changing the mean and variance of the distribution independently (see Supporting Material). The beta distribution was chosen as it provides this flexibility and produces values in the range  $0 < \alpha_{ij} < 1$  without having to curtail the distribution.

The vector of equilibrium population densities of these communities can be found as  $\mathbf{N}^* = \mathbf{A}^{-1} \mathbf{K}$ , where  $\mathbf{A}$  is the  $m$  by  $m$  interaction matrix of  $\alpha$ -values, and  $\mathbf{K}$  is the  $m$  element column vector of carrying capacities (May, 1973). Communities with all  $N_i^* \geq 0$  are termed feasible,

and local stability can be found from the absolute value of the dominant eigenvalue,  $|\lambda_1|$ , of the Jacobian matrix ( $\mathbf{J}$ ) of this system of linked equations (eqn. 1), evaluated at equilibrium (e.g. Ranta et al., 2006), where

$$\mathbf{J} = \begin{bmatrix} 1 - r_1 N_1^* & -\alpha_{12} r_1 N_1^* & \cdots & -\alpha_{1m} r_1 N_1^* \\ -\alpha_{21} r_2 N_2^* & 1 - r_2 N_2^* & \cdots & -\alpha_{2m} r_2 N_2^* \\ \vdots & \cdots & \ddots & \vdots \\ -\alpha_{m1} r_m N_m^* & -\alpha_{m2} r_m N_m^* & \cdots & 1 - r_m N_m^* \end{bmatrix}. \quad (2)$$

5 Each element in the Jacobian matrix,  $J_{ij}$ , represents the effect of a small perturbation of the density of species  $j$  on the population growth rate of species  $i$ . When the absolute value of the dominant eigenvalue  $|\lambda_1| < 1$ , the community is said to be locally stable in a discrete time system (May, 1973). Any small perturbation to the species density will therefore result in the density returning to equilibrium. Conversely, if  $|\lambda_1| > 1$ , the system is said to be locally

10 unstable and any small perturbation from equilibrium will grow over time until the system arrives at a new attractor state. In some cases, this will lead to species loss from the system, as at least one species will settle to a new equilibrium density at the extinction boundary,  $N_i^* = 0$ . Alternatively, all species persist, yet some may oscillate with positive densities. These communities are locally unstable but persistent, with a stable periodic or more complex

15 attractor. As real species cannot have negative densities, they cannot ever reach the equilibrium point at which local stability would be evaluated for an unfeasible community, therefore I focus only on the local stability of feasible communities here. Different methods exist to test for permanence in ecological communities (see, e.g., Ebenman et al., 2004; Law and Morton, 1993).

In the first section of the results, *Analytic Results*, I present an analysis of simplified two species communities that vary in connectance and  $r_i$  values, deriving conditions for stability when one community member would have unstable (fluctuating) dynamics in the absence of the other member, giving a locally unstable community. I start with symmetric competition ( $\alpha_{ij} = \alpha, i \neq j$ ) and extend this analysis to examine the biologically more plausible case of asymmetric competition ( $\alpha_{ij} \neq \alpha_{ji}$ ). To ensure that only considering 2 unconnected species as a community and comparing that to a partially or fully connected 2 species community did not represent a special case, I examined the generality of this result by studying the effects of increasing species number and connectance when  $m > 2$  in the *Simulation Results* section.

Here, I tested the effect of drawing species' intrinsic growth rates ( $r_i$ ) from different ranges on the probability of randomly assembled communities being feasible and locally stable, across communities of different sizes. Maximum community size used in all cases was  $m = 16$  species. I selected  $r_i$  values for all  $m$  species in the different sized communities either randomly from a uniform distribution with limits  $[r_{\text{MIN}}, r_{\text{MAX}}]$ , or equally spaced across the same range.  $r_{\text{MIN}} = 0.1$  in all cases examined here, while  $r_m = r_{\text{MAX}}$  for the second case and  $r_{\text{MAX}}$  was varied between 1 and 3.5. The remaining community members were assigned  $r_i$  values on intervals of  $(r_{\text{MAX}} - r_{\text{MIN}})/(m - 1)$ . Thus individual species dynamics were drawn from the entire region of under- to overcompensatory to periodic and more complex dynamics allowable within the range of  $r_{\text{MAX}}$ . Increasing community size therefore reduced the variance in  $r_i$  values in the community. However, all such communities had the same mean value of  $r$ , independently of community size. I then determined the feasibility and local stability of each community for a given number of species. I also examined the effect of varying the connectance ( $c$ ) within the interaction matrix, defined as the proportion of non-

zero  $\alpha_{ij}$  elements in the interaction matrix, excluding intraspecific feedback terms ( $i \neq j$ ). A high connectance indicates a rich web of links between species (Rozdilsky and Stone, 2001). When  $c < 1$ ,  $\alpha_{ij} = 0$  with probability  $(1 - c)$ . Specifically, for a given community size, I varied  $c$  by finding the number of elements that corresponded to the minimum non-zero

5 connectance,  $1/(m^2 - m)$ , and assigned an interaction value to a randomly selected off-diagonal element. This process was repeated by consecutively increasing the number of off-diagonal elements in the interaction matrix that were to be non-zero for increasing connectance values.

I tested the effect of a simple  $r_i$  vs.  $N_i^*$  trade-off, where the community member with the

10 lowest equilibrium density (i.e., the poorest competitor) was assigned the highest  $r_i$  value from the distribution, with increasing equilibrium densities being assigned decreasing  $r_i$  values. This type of trade-off can arise when individuals within a species are selected for a trait that either maximises intrinsic growth rate (density independent factors) or competitive ability (density dependent factors) but cannot simultaneously maximise both, similar to the

15 concept of  $r$  and  $K$  strategists. Ranking community members by equilibrium density has also been shown to be useful in predicting community response to other disturbances (Fowler, 2005). As community size increased, new  $r_i$  values were randomly selected before being assigned, as introducing new species to the system changed the equilibrium densities of existing community members. I also tested the effect of varying the mean and variance of the

20 distribution of  $\alpha_{ij}$ -values, but this did not qualitatively change the results (see Supplementary material).

For each scenario, 10,000 replicate communities were generated for each community size, connectance value and/or value of  $r_{MAX}$ . Feasibility and local stability was recorded for each community.

#### *Variability in Biomass Fluctuations*

- 5 The magnitude of variability in biomass fluctuations is another measure of community stability that is of considerable interest to ecologists. Here, community biomass at any time is defined as  $x_t = \sum N_{i,t}$ , and a common measure of its variability over time is given as the coefficient of variation (CV),

$$CV(x) = \frac{\sigma(x_T)}{\mu(x_T)}, T = 1 \dots 200, \quad (3)$$

- 10 where  $\sigma$  is the standard deviation and  $\mu$  is the mean of the time series. Ives and Hughes (2002) derived the following solution for a broad class of community models to describe the variation in biomass fluctuations when species were not perfectly correlated in their response to environmental variation (their eqn. 7),

$$CV(x') = \sigma_p \left\{ \frac{1 + (m-1)\rho}{m[1 - (1-r)^2]} \right\}^{1/2}, \quad (4)$$

- 15 where  $x'(t) = \sum N_{i,t} - N_i^*$  and  $\sigma_p = \sigma_\varepsilon / N^*$  scales the standard deviation of the environmentally driven variation in the population growth rate by the average number of individuals in the population (Ives and Hughes, 2002). Environmental variation  $\varepsilon_{i,t}$  was generated here as normally distributed white noise (autocorrelation = 0), with mean 0,  $\sigma_\varepsilon = 0.135$  and a

correlation structure of  $\rho = 0, 0.5$  or  $1$ . This was incorporated into eqn. (1), communities were assembled following the same rules as above, checked for persistence, then initiated at equilibrium and simulated over 200 time-steps for different community sizes and values of  $r_{\text{MAX}}$  and  $\rho$ . The  $\text{CV}(x)$  from these simulated time-series was calculated and the mean taken from 10000 replicated communities for each value of  $m$  and  $r_{\text{MAX}}$  and compared with predictions based on equation (4), where the mean value of  $\alpha_{ij}$  (0.1) was used to determine  $\sigma_p$ , while  $r$  was taken as the mean value of  $r_i$  values across the community, i.e.,  $(r_{\text{MIN}} + r_{\text{MAX}})/2$ .

## 10 RESULTS

### *Analytic Results*

Initial insight can be gained by examining the eigenvalues of simple two species communities. Here I assumed that one species has an  $r_i$  value that produces stable point equilibrium dynamics in the absence of competition ( $0 < r_i < 2$ ), while the second species shows sustained periodic (or more complex) oscillations ( $r_j > 2$ ). When there is no interaction between species ( $\alpha_{ij} = \alpha_{ji} = 0$ ), the eigenvalues are  $[1 - r_i, 1 - r_j]$  and the system will be unstable, as the stability determining (dominant) eigenvalue will always have absolute value  $|1 - r_j| > 1$ . Here, species  $j$  will oscillate while  $i$  has stable point equilibrium dynamics.

When amensal competition is introduced, such that the species with the higher intrinsic growth rate suffers competition from the other, but not vice-versa ( $\alpha_{ij} = 0, \alpha_{ji} > 0; c = 0.5$ ), the eigenvalues are  $[1 - r_i, r_j \alpha_{ji} + 1 - r_j]$ . The eigenvalue associated with species  $i$  will always

have absolute value  $|1 - r_i| < 1$  and stability will depend on the other eigenvalue. Here, if  $|r_j\alpha_{ji} + 1 - r_j| < 1$  the community will be stable. By solving  $\lambda_j = r_j\alpha_{ji} + 1 - r_j = \pm 1$ , we can find inequalities for  $r_j$  that satisfy stability at both limits. Thus, when  $0 < r_j\alpha_{ji} < 2$ , the oscillations that would arise from species  $j$  having a high intrinsic growth rate are damped by competition from species  $i$ . The upper limit of 2 is required here to prevent a competitive exclusion instability (fold bifurcation) occurring when  $\lambda_j > 1$ . This shows that there is an increase in the parameter space associated with stable dynamics with increasing connectance (or number of species) in a competitive community.

This can be further illustrated by examining two species competition in a fully connected community with diffuse competition ( $\alpha_{ij} = \alpha_{ji} = \alpha$ ,  $0 < \alpha < 1$ , Fig. 1a & b). Here the eigenvalues are

$$\lambda_{i,j} = \frac{1}{2} \frac{2\alpha + 2 - r_i - r_j \pm \sqrt{r_i^2 + r_j^2 - 2r_i r_j + 4r_i \alpha^2 r_j}}{\alpha + 1}, \quad (5)$$

therefore, assuming that  $r_i < 2$ , conditions for local stability can again be found by solving  $\lambda_{i,j} = \pm 1$ , leading to the following inequality for locally stable systems

$$r_j < 2 \frac{2\alpha - r_i + 2}{r_i \alpha - r_i + 2}. \quad (6)$$

Thus, when  $r_i < 2$  and  $0 < \alpha < 1$ , it is possible for local stability to arise when  $r_j > 2$  as the dominant eigenvalue shifts from being less than to greater than -1 (Fig. 1a), which would lead to unstable, oscillating dynamics in the absence of competition. Decreasing  $r_i$  increases the parameter space of  $r_j$  associated with local stability (Fig. 1b).

The result for local stability with asymmetric competition between two species ( $\alpha_{ij} \neq \alpha_{ji}$ ), otherwise under the same conditions, is

$$r_j < 2 \frac{2\alpha_{ij}\alpha_{ji} + r_i - r_i\alpha_{ij} - 2}{r_i\alpha_{ij}\alpha_{ji} + 2\alpha_{ji} + r_i - r_i\alpha_{ij} - r_i\alpha_{ji} - 2}, \quad (7)$$

as illustrated in Fig. 1c, which shows the maximum  $r_j$  value associated with stability ( $-1 < \lambda_1 < 1$ ) given particular interspecific interaction strengths ( $\alpha_{ij}, \alpha_{ji}$ ). In a simple 2 species case, positive equilibrium densities (feasible communities) are found for all  $\alpha_{ij} < 1$ . Increasing the strength of competition from species  $i$  on  $j$  ( $\alpha_{ji}$ ) leads to an increase in the value of  $r_j$  that is associated with locally stable dynamics. Increasing competition from species  $j$  on  $i$  ( $\alpha_{ij}$ ) reduces the parameter space of  $r_j$  associated with local stability.

These results highlight the importance of considering the actual, rather than the absolute value of the dominant eigenvalue of the system (e.g., eqn. 5, Fig. 1a). A dominant eigenvalue ( $\lambda_1$ ) that shifts from being greater than to less than -1 indicates a loss of stability through a period-doubling (flip) bifurcation, leading to unstable population dynamics with a periodic or more complex attractor. This can arise here with  $r_j$  values  $> 2$ . An eigenvalue of  $\lambda_1 > +1$  indicates an instability associated with the competitive exclusion of at least one species via strong competition (high  $\alpha_{ij}$  values), which is known as a fold bifurcation. Therefore, knowing whether the absolute value of  $\lambda_1$  corresponds to +1 or -1 gives us important dynamical information about how the unstable system will respond to perturbation from the equilibrium, either leading to persistent fluctuations ( $\lambda_1 < -1$ ) or species loss ( $\lambda_1 > 1$ ). Other types of bifurcations exist, but are not relevant for this simple case ( $\alpha_{ij} = \alpha$ ), e.g., complex eigenvalues (associated with a Hopf bifurcation) cannot arise in the parameter ranges

considered here as the term inside the square root in eqn. (5) is always positive given the assumptions about parameter values used here:  $0 < r_i < 2$ ,  $r_j > 2$  and  $0 \leq \alpha < 1$ . Thus, as long as  $r_i^2 + r_j^2 + 4r_i\alpha r_j > 2r_i r_j$ , the square root term in eqn. (5) will be positive and the eigenvalue will not be complex, a condition which always holds given the limits defined here.

5 These analyses may also be applied to more general interpretations of eqn. (1), which can include exploitation and interference (e.g., Case and Casten, 1979; De Angelis, 1975; Drake, 1990; Kondoh, 2003), but that requires a variety of further assumptions to be made about trophic structure and is beyond the scope of the current work.

## 10 *Simulation Results*

In all scenarios studied in deterministic communities where  $r_{\text{MAX}} \leq 2$ , increasing the number of species in the community always eventually led to a reduction in the probability of communities being feasible and locally stable (Figure 2). None of the communities were feasible but locally unstable in this range ( $r_{\text{MAX}} \leq 2$ ), thus those large communities that were  
 15 not locally stable were unfeasible. This result was tested further and found to hold in communities with up to  $m = 50$  species. When  $r_{\text{MAX}} > 2$ , increasing community size was associated with an increase in the probability of finding locally stable communities, a result that arose across all different methods of community formation. This result was more pronounced when  $r_i$  values were distributed evenly across community members (Fig. 2b)  
 20 compared to randomly selected  $r_i$  values (Figs. 2a). While some communities with  $r_{\text{MAX}} > 2$  were found to be feasible and locally unstable (Fig. 3a), this instability was always generated

by crossing a period doubling (flip) bifurcation ( $\lambda_1 < -1$ ) and never lead to species loss ( $\lambda_1 > 1$ ). This was tested and also found to be true even in very large communities ( $m = 50$ ).

Introducing a trade off between competitive ability (equilibrium density) and intrinsic growth rates between species did not qualitatively affect the results (Fig. S2). Increasing the mean while keeping the variance constant led to an increase in stability across much of the parameter space, whilst increasing the variance in  $\alpha_{ij}$  while keeping a constant mean reduced the probability of stable communities (Fig. S2).

Increasing the connectance was also found to increase stability across all community sizes (Fig. 2c), which is accompanied by a decrease in the probability of being feasible but locally unstable (Fig. 2d). Increasing connectance also led to an increase in the probability that communities were unfeasible with high  $m$ , explaining the levelling off of feasibility and local stability in a 16 species community (Fig. 2c). Increasing  $m$  also lowers the minimum possible (non-zero) connectance in a community [ $1/(m^2 - m)$ ]. The probability of being F-LS decreases with increasing  $m$  in low (and zero) connectance communities, related to the increased probability that at least one species has  $r_i > 2$  (giving an unstable community) when sampled randomly from a uniform distribution. There are many other ways in which species could differ and a more complete invasion analysis would provide an interesting extension to this work.

An increase in the number of competitive links in the community, either through increasing  $c$  or  $m$ , leads to an asymptotic increase in the total biomass ( $\Sigma N_i^*$ , Fig. 3b). As community size increases, the total competitive feedback increases at a decreasing rate. This allows a reduction in the per-capita growth rate which stabilises any deterministically fluctuating

(unstable) dynamics and can be seen as an increase in the locally stable parameter space. This is illustrated in Fig. 4a, with locally stable parameter combinations above and to the left of the lines for different sized communities. Eventually, competition becomes so severe it causes the community to become unfeasible, i.e.,  $\mathbf{N}^*$  contains negative equilibrium densities for at least one species (Fig. 4b). Variation in the maximum intrinsic growth rate ( $r_{\text{MAX}}$ ) has no effect on the feasibility results (recall,  $\mathbf{N}^* = \mathbf{A}^{-1}\mathbf{K}$ ). However, variation in  $r_{\text{MAX}}$  does change the probability that communities are locally unstable (eqns. 3 - 5). When  $r_{\text{MAX}} > 2$ , small communities have a non-zero probability of being locally unstable. Increasing the number of species always leads to a reduction in the probability of being locally unstable, faster than the increase in unfeasibility occurs.

The effect of increasing community size on the dominant eigenvalue,  $|\lambda_1|$ , is illustrated numerically for increasing community size in Fig. 4b. In communities with diffuse competition ( $\alpha_{ij} = \alpha, i \neq j$ ), increasing community size leads to an increase in the parameter space associated with stable dynamics ( $|\lambda_1| < 1$ , Fig. 4a). An example from a randomly assembled community highlights the initial effect of introducing new species into an initially unstable two species community (Fig. 4b). In low diversity communities, any species with a high  $r_i$  can dominate the population dynamics, producing fluctuating, persistent, locally unstable communities ( $\lambda_1 < -1$ ). The addition of further species leads to a reduction in  $|\lambda_1|$ , eventually dropping below the critical threshold,  $|\lambda_1| = 1$  (Fig. 4b). Adding extra species or links will tend to reduce the absolute value of any element in  $\mathbf{J}$  (eqn. 2), as  $N_i^*$  is generally reduced through increasing  $m$ . This indicates that a change in density of species  $j$  will have a smaller effect on the response of the population density of species  $i$  than before, however, the

increase in the number of species feeding back more than compensates for this reduction, stabilising dynamics.

The change from locally unstable to locally stable communities is illustrated in terms of the resultant dynamics of locally unstable communities, which may respond to small

5 perturbations from the internal equilibrium ( $\mathbf{N}^*$ ) in different ways, in Figs. 4c & d.

Communities may fluctuate with some characteristic period around the equilibrium following a disturbance (Fig. 4c). Adding species to these communities leads to an increase in the strength of density dependent feedback ( $\sum N_i$ ), which dampens oscillations through a

10 reduction in per-capita growth rates, changing communities from being locally unstable with oscillating population densities to locally stable with damped oscillations following disturbance (Fig. 4d). This can occur even though new species entering the community have relatively high  $r_i$  values.

In terms of the variability of biomass fluctuations, larger  $CV(x)$  values represent lower biomass stability (i.e., greater values of  $1/CV$  show greater biomass stability), simulations of

15 eqn. (1) show that  $CV(x)$  varied with  $m$ ,  $r_{MAX}$  and the environmental correlation ( $\rho$ ) (Figs. 5a - c). Substituting the single  $r$ -value used to derive the  $CV(x')$  in Ives & Hughes (2000), with

mean( $r_i$ ) (eqn. 4) allows us to generate reasonable predictions of how community biomass will fluctuate under environmental variation when  $\rho < 1$  (Figs. 5d - e). Increasing  $m$  always

leads to an increase in biomass stability for the simulated system ( $1/CV$ , Fig. 5a - c). For any

20 given community size, the maximum biomass stability is seen with a mean  $r$  value of 1 ( $r_{MAX} \approx 1.9$ ). When  $\rho < 1$ , eqn. (4) tends to overestimate the simulated values of  $1/CV$ . When all

species experience the same environment ( $\rho = 1$ ), eqn. (4) captures the general relationship

between variation in  $r_{MAX}$  and  $1/CV$ , but does not predict the increase in biomass stability

seen with increasing community size, particularly noticeable in communities with high  $r_{\text{MAX}}$  (Fig. 5c). Thus eqn. (4) underestimates biomass stability in larger communities. Potential mechanisms leading to this result are discussed below (see also Fig. S3).

## 5 DISCUSSION

In the debate over how species diversity affects community stability, results from model randomly assembled competitive communities have previously shown that increased species number and/or connectance always leads to reduced probability of finding locally (asymptotically) stable communities (May, 1972; May, 1973). For the first time, to my  
 10 knowledge, I have shown that independently increasing species number and/or connectance in competitive communities can increase stability across a range of community sizes. This result arises when the assumption that all species in the community share the same intrinsic growth rate which results in locally stable dynamics in the absence of competition is relaxed. Earlier results are confirmed here under a certain parameter range ( $r_{\text{MAX}} \leq 2$ ), yet stability  
 15 increases with complexity when  $r_{\text{MAX}} > 2$  over a wide range of different scenarios, connectance and community sizes (Figs. 1 – 3, S2). Results were most pronounced when species'  $r_i$  values were distributed evenly across the whole community, although this method was associated with an increase in variation across all  $r_i$ 's with increasing community size. Introducing a trade-off between competitive ability ( $N_i^*$ ) and  $r_i$  reduced the effect in  
 20 communities with random  $r_i$  values, but it remained clear when  $r_i$  was equally distributed across the community (Fig. S1). Increasing the expected value of  $\alpha_{ij}$  or the variance of the distribution of  $\alpha_{ij}$  values had a quantitative but not qualitative effect on the relationship, with

increased mean  $\alpha_j$  leading to an increase in stability, while an increase in variance decreased stability over most of the parameter space (Fig. S2).

Relaxing the assumption that all species have stable equilibrium dynamics in the absence of competition leads to results that oppose earlier findings that were based upon this assumption  
5 (Chen and Cohen, 2001; May, 1972; May, 1973; Rozdilsky and Stone, 2001). While  
Rozdilsky and Stone (2001) clearly showed an initial decrease followed by an increase in the  
probability of feasibility and stability with increasing connectance, communities with more  
species were always less likely to be stable than those with fewer species under their  
conditions, whenever differences occurred. The main difference between the results I show  
10 here and those in Rozdilsky and Stone (2001) is that I show an increase in stability with  
complexity through a switch from feasible, locally unstable communities to those that are  
feasible and locally stable, through period halving across a flip bifurcation ( $\lambda_1 = -1$ ).  
Rozdilsky and Stone's (2001) results rely on a switch in feasibility – from feasible (and  
locally stable) to unfeasible communities or vice-versa with increasing complexity. Chen &  
15 Cohen (2001) examined different measures of stability in model food webs; local and global  
stability, and permanence, finding that all three measures predicted the same qualitative  
relationship of decreasing stability with increasing complexity in the Lotka-Volterra cascade  
model.

All communities that were not locally stable here were either unstable or unfeasible. All  
20 unstable communities produced under the conditions used in this study were persistent,  
oscillating around their equilibrium densities, confirmed through long-term simulation of  
these randomly assembled communities (e.g. Figs. 4c & d) - all unstable communities had a  
dominant eigenvalue  $\lambda_1 < -1$ . In other words, while period halving (reverse flip) bifurcations

occurred here, fold bifurcations ( $\lambda_1 > 1$ , associated with species loss) never occurred. Flip bifurcations are a feature of the discrete-time formulation of this model, that do not occur in continuous time versions. Increasing the number of species in the community does not have any effect on the persistence of those communities that were feasible, as species loss would only occur in unfeasible communities. Considering the effect of adding species to the community on the eigenvalues of the Jacobian matrix (Figs. 1, 4), it can also be seen that adding additional species to small communities reduced the absolute value of the dominant eigenvalue (increased the value associated with  $\lambda_1 < -1$ ) and increased the parameter space within which stable dynamics were possible. The additional density dependent feedback terms ( $\sum \alpha_{ij} N_j$ ) are more important to system stability than the additional  $r_i$  values associated with new species.

Increasing community size generally leads to a reduction in biomass variability (Fig. 5), often termed increased community biomass stability (Ives and Hughes, 2002). This result relies upon the assumption that species do not respond to environmental variation in a perfectly correlated way, a phenomenon known as the “portfolio effect” (Ives et al., 1999; Stearns, 2000). The result derived by Ives & Hughes (2002) was shown to apply more generally than first thought (Fig. 5), i.e., to communities where species differ in their intrinsic growth rates ( $r_i$ ) and when some species show unstable dynamics in the absence of competition. Even when species respond to the environment in the same way, increasing community size leads to an increase in biomass stability (Fig. 5c). There are two mechanisms associated with this increase in biomass stability with  $m$  in simulated communities (Fig. S3). (i) Differences in  $r_i$  values mean that species with very low or high  $r_i$  will exhibit differences in their per-capita response to the environment, even though they experience the same exogenous forcing. This

leads to a reduction in synchrony across species, which is translated into an increase in biomass stability. (ii) Increasing  $m$  can change the underlying local stability of the community. Initially unstable, persistent communities can become stable with increasing  $m$ , which would be associated with an increase in biomass stability. The basic model framework used here is used to examine biomass variability in autocorrelated stochastic environments more carefully elsewhere (Ranta et al., 2008a; Ranta et al., 2008b, in revision).

The presence of complex population dynamics in natural systems remains an interesting ecological discussion. There are examples of field and laboratory populations with cyclic or more complex dynamics, similar to those generated by the Ricker function, among plants (Crone and Taylor, 1996; Tilman and Wedin, 1991), insects (Dey and Joshi, 2006; Dixon, 1990; Hassell et al., 1976; Mueller and Joshi, 2000; Turchin, 2003) and other taxa (Zeng et al., 1998). The Ricker function represents a simple unstructured population model, however, the results presented here indicate that when individual species may have the potential to show stable periodic or more complex dynamics, these may not always be seen in real ecosystems due to interspecific feedback. Many insect species have the capacity to reproduce at very high rates, corresponding to high  $r_i$  values, and are likely to compete over resources to some degree with closely related species. If competition occurs with other species that show very different growth rates, then the current modelling framework should be able to capture these differences. There is no *a priori* reason to assume that all species in natural systems will have intrinsic growth rates  $< 2$  (i.e. in the stable region), although most of the theory that deals with population and/or biomass stability rests upon that assumption. In the absence of simple, general analytical tools to relate complexity to different stability measures (e.g., Hughes and Roughgarden, 2000; Ives and Hughes, 2002; May, 1972; May, 1973), simulations become a useful tool to explore these relationships. Other methods have been

proposed to predict, e.g., Variance-Covariance relationships in structured population models (Greenman and Benton, 2005) which can be used to evaluate the biomass variability, but these methods are limited to conditions close to the equilibrium, i.e., with very weak environmental forcing (Ruokolainen and Fowler, 2008).

5 Cohen & Newman (1985) suggested some counter-examples to question the generality of the negative diversity-(local) stability relationship. They utilised a simple, general approach to studying the problem that did not include any information about specific dynamical properties of the different community members. The examples they introduce relied upon decreased connectance with increasing number of species in the community. This feature was  
10 assumed as it was thought that “increasingly severe constraints must be imposed on the distribution of the interspecific interaction coefficients to assure the stability of the community.” (Cohen and Newman, 1985, p. 153). My approach differs in at least one crucial way. Decreased connectance with increasing community size effectively means that species in a large community interact (on average) with the same number of species as those in a  
15 smaller community. Therefore, increasing community size does not have a great effect on diversity, as it does not lead to any change in the average number of interactions within the community. This modelling framework is similar to that used to model limiting similarity mentioned above. I vary community size and connectance independently, showing that the probability of communities being stable can be increased through increases in either measure  
20 of complexity. I also include specific details about species dynamics in the absence of competitors. Cohen & Newman (1985) dealt only with random matrices that would be equivalent to matrix  $\mathbf{J}$  in my work, in a similar manner to Haydon (2000); the mean value of elements of  $\mathbf{J}$  is not assumed to be zero here. All matrix elements are expected to become smaller (more negative) with any increase in  $r_{\text{MAX}}$ , with the main diagonal decreasing faster

than off-diagonal elements, due to the relatively stronger within-species competition ( $\alpha_{ii} = 1$ ). The main diagonal elements may be positive for large communities, but off-diagonal elements are always negative. Increases in community size tend to increase the value of both the main- and off-diagonal elements of  $\mathbf{J}$  (approaching one or zero, respectively) through a  
5 reduction in  $N_i^*$ , with main diagonal elements increasing faster than off diagonals.

Natural food-webs are made up of species that show a great variety of life-history strategies.

While some species within a large community or food web may have discrete or non-overlapping generations, others will almost certainly have overlapping generations.

Modelling these large systems with a single mathematical method, e.g., discrete- or

10 continuous-time growth functions, represents a necessary simplification in the approach used.

Relating the complexities of scaling different birth and death rates among different species to different modelling methodologies represents an intriguing future challenge for community ecology. Case & Casten (1979) demonstrated how the multispecies (Lotka-Voterra) Logistic function can be generalised to incorporate trophic structure without any change to its

15 formulation. Examination of a trophically structured version of the model presented here through selection of appropriate parameter values would represent an interesting avenue for further exploration, extending the generality of the results presented here. While trophically structured models have previously shown positive diversity-stability relationships (e.g., De Angelis, 1975), these generally come at the expense of an increase in the number of model

20 parameters and potential functional forms, which can become increasingly difficult to estimate from natural systems (Abrams, 2001). This generates an interesting conflict in terms of model parsimony – when a simple model that lacks components of some natural systems

and more complex models can both generate the same qualitative predictions of population dynamics, we must decide which provides the most useful insight?

Various features of randomly drawn communities have been shown to differ to communities drawn using sequential assembly rules (Virgo et al., 2006), while Haydon (2000) has  
5 demonstrated the conditions required to produce maximally stable communities. However, randomly assembled communities have proven a popular starting point when asking questions of community stability (Chen and Cohen, 2001; Cohen and Newman, 1985; Ives and Hughes, 2002; Ives and Carpenter, 2007; Ives et al., 1999; Ives et al., 2000; Jansen and Kokkoris, 2003; Rozdilsky and Stone, 2001) and can serve as a useful null hypothesis for  
10 comparison with communities assembled under different ecological and evolutionary rules. Investigating different assembly rules in communities whose component species differ in their intrinsic dynamics also represents an interesting avenue for further research.

The results presented here show for the first time that increasing the number of species and/or the connectance between species in the community can increase local stability in randomly  
15 assembled communities, when some members have the potential to show oscillatory dynamics. The main finding is robust to changes in the mean and variance in the community interaction strengths, variation in the connectance of the interaction matrix and a trade-off between competitive ability ( $N^*$ ) and intrinsic growth rate. These results help to extend and clarify important elements of the complexity – stability discussion.

20

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## FIGURE CAPTIONS:

**Figure 1:** Stability regions for simple, deterministic, two species communities, where one species shows stable equilibrium dynamics in the absence of competition ( $r_i < 2$ ) and the other has oscillatory dynamics ( $r_j > 2$ ). (a) The two eigenvalues ( $\lambda_{1,2}$ ) of a community with symmetric competition ( $\alpha_{ij} = \alpha_{ji} = \alpha$ ) vary with both  $\alpha$  and  $r_j$ . Instability of the whole system is driven by high  $r_j$  values ( $\lambda_1 \leq -1$ ), seen with combinations of high  $r_j$  and low  $\alpha$ -values. (b) The regions of stability (below the line) for the same system ( $r_i = 1$ , dashed line) and with lower ( $r_i = 0.1$ , solid line) and higher ( $r_i = 1.9$ , dotted line) growth rates. (c) Asymmetric competition, with the surface showing the parameter combinations that lead to the bifurcation point between the stable (below the surface) and unstable (above) regions. Increasing the competitive pressure of the species with stable dynamics ( $r_i = 1$ ) on the species with unstable dynamics ( $\alpha_{ji} > \alpha_{ij}$ ) increases the value of  $r_j$  associated with community stability. In all cases, the unstable region is associated with persistent, oscillating dynamics across the community.

**Figure 2:** The probability of finding feasible, locally stable communities increases with community size and/or connectance, when some community members show oscillatory dynamics in the absence of competition ( $r_{\text{MAX}} > 2$ ). Species' intrinsic growth rates ( $r_i$ ) were drawn at random from a uniform distribution with limits  $[0.1, r_{\text{MAX}}]$  (panels a, c & d) or equally distributed across the same range (b). A value of  $r_{\text{MAX}} = 2.5$  was used in panels (c – d) and all communities were formed with  $\alpha_{ij}$  values drawn from a beta distribution with mean 0.1, variance  $^9/_{1100}$ , with results shown for 3 (solid line), 6 (dashed), 9 (dotted) and 16 (dash-dot) species communities.

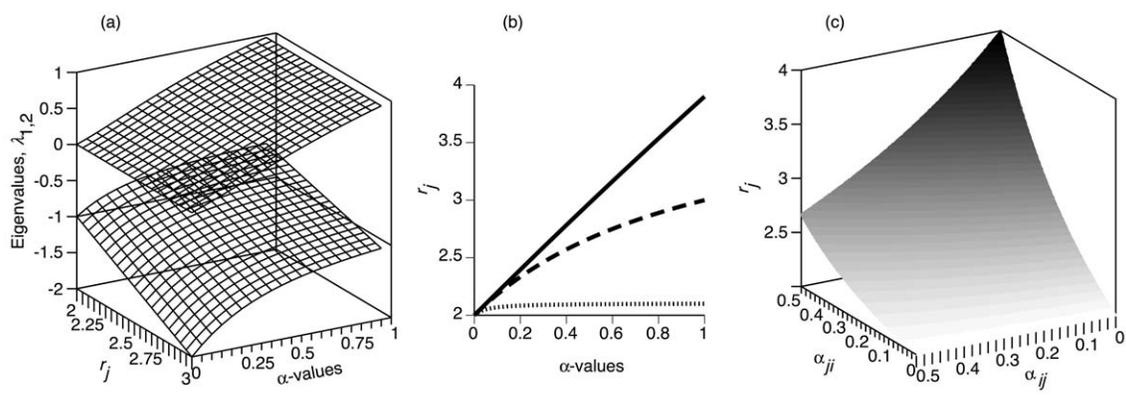
**Figure 3:** Community characteristics are affected differently by community size,  $r_{\text{MAX}}$  or connectance. (a) The probability of communities being unfeasible increases with community size, but is unaffected by  $r_{\text{MAX}}$ , however, both  $m$  and  $r_{\text{MAX}}$  affect the probability of being feasible and locally unstable (F-LU). (b) The total equilibrium density increases asymptotically with community size (individual equilibrium densities therefore decrease with increasing  $m$ ) and decreases with connectance, with results shown for 3 (solid line), 6 (dashed), 9 (dotted) and 16 (dash-dot) species communities. All communities were assembled as in Fig. 2. N.B. The axes in panel (a) have been rotated to make viewing easier.

**Figure 4:** The dominant eigenvalues ( $|\lambda_1|$ ) and population dynamics change with increasing community sizes. (a) Parameter space above and to the left of the lines shows stable point equilibrium dynamics in communities with diffuse competition ( $\alpha_{ij} = \alpha, i \neq j$ ), below and to the right are unstable (periodic or more complex) dynamics, therefore increasing community size from 2 to 11 species increases the size of the stable region. Panels (b – d) use the same example community to illustrate these effects with asymmetric competition, with  $r_{\text{MAX}} = 2.75$  and all other parameter values drawn as in Fig. 2a. (b) Increasing the number of species leads to an initial reduction in  $|\lambda_1|$  from being greater than, to less than one, the critical threshold for local stability. The solid line shows the randomly assembled community. Adding more species eventually leads to an unfeasible community ( $m = 16$ , marked \*). Dotted line shows a diffuse competition community where  $\alpha = 0.1$ ,  $r_i$  values linearly spaced linearly between 0.1 and 2.75. (c) If at least one species in a small community has high  $r_i$  values, populations may oscillate and the community is locally unstable. Here,  $r_1 = 2.45$ ;  $r_2 = 1.16$ ;  $r_3 = 2.05$ . (d) A new species added to the community increases the strength of density dependent feedback,

which dampens population oscillations. In this case a further species was added to the same community shown in panel (c) ( $m = 4$ ,  $r_4 = 0.98$ ), the new community is locally stable.

**Figure 5:** The variability of fluctuations in community biomass (presented as  $1/CV$ ) changes with community size,  $r_{MAX}$  and the correlation ( $\rho$ ) in the environmental signals ( $\epsilon_{i,t}$ ) experienced by different species. Larger values of  $1/CV$  relate to lower variability, i.e., greater stability in community biomass over time. Panels (a – c) show results from simulated communities (results show mean  $1/CV$  from 10000 different communities for each data point), with  $\alpha_{ij}$ -values drawn randomly as described in the methods. Panels (d – f) show predictions from the analytical solution (eqn. 4) assuming  $\alpha = 0.1$ ,  $r = (0.1 + r_{MAX})/2$ . The correlation structure increases from left to right panels with (a, d:  $\rho = 0$ ), (b, e:  $\rho = 0.5$ ) and (c, f:  $\rho = 1$ ). The analytical solution captures many important features of the simulated results.

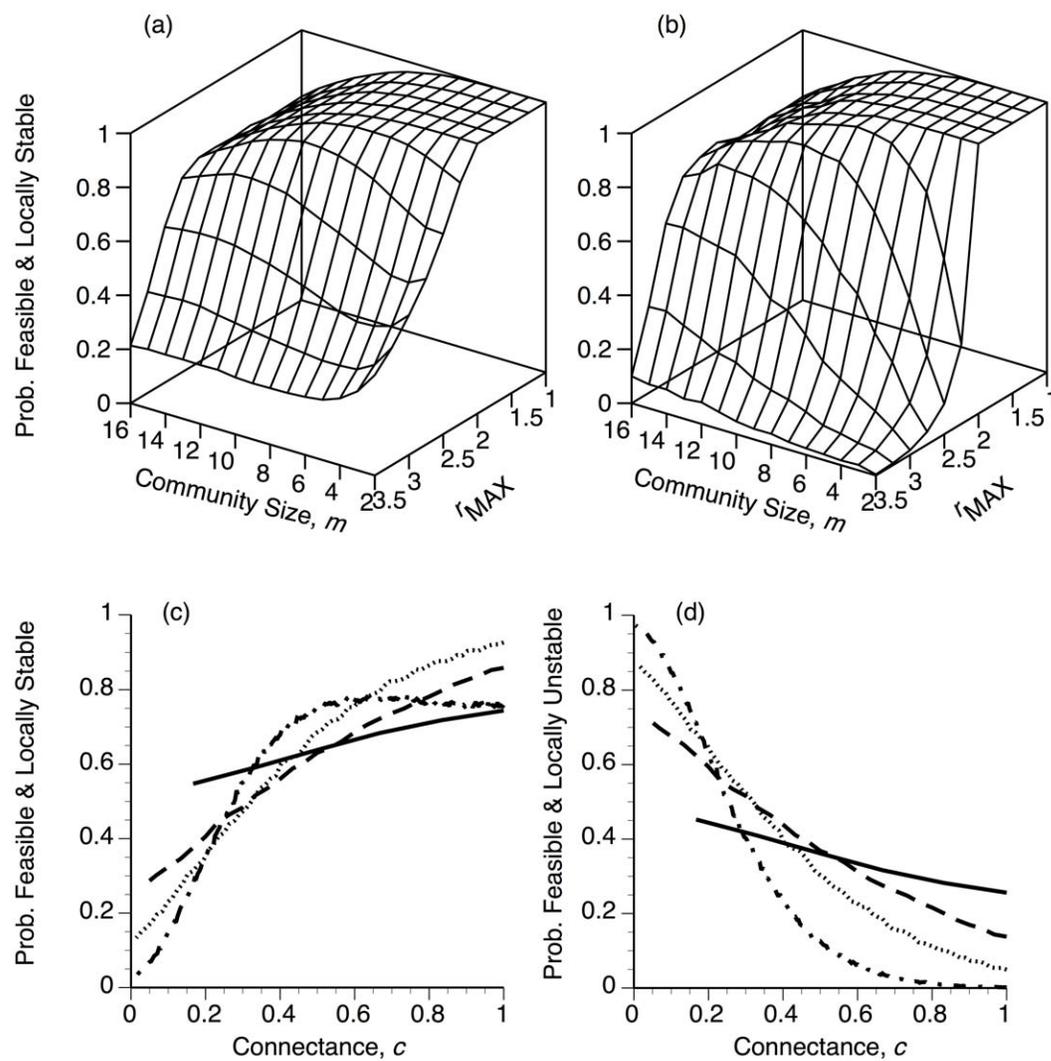
Fig. 1



FOWLER, FIGURE 1

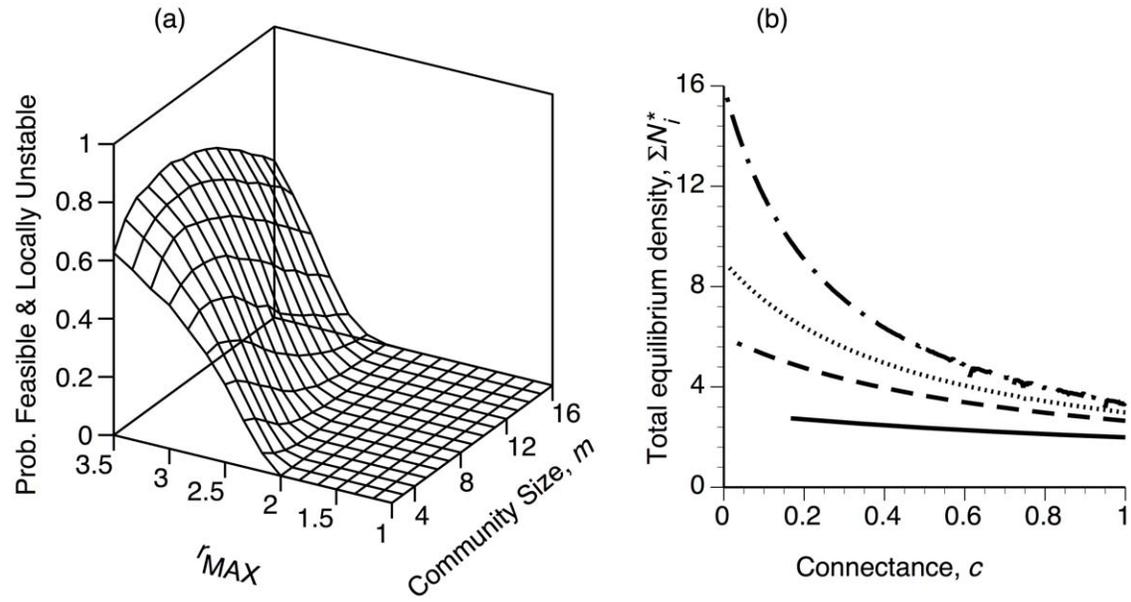
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Fig. 2



FOWLER, FIGURE 2

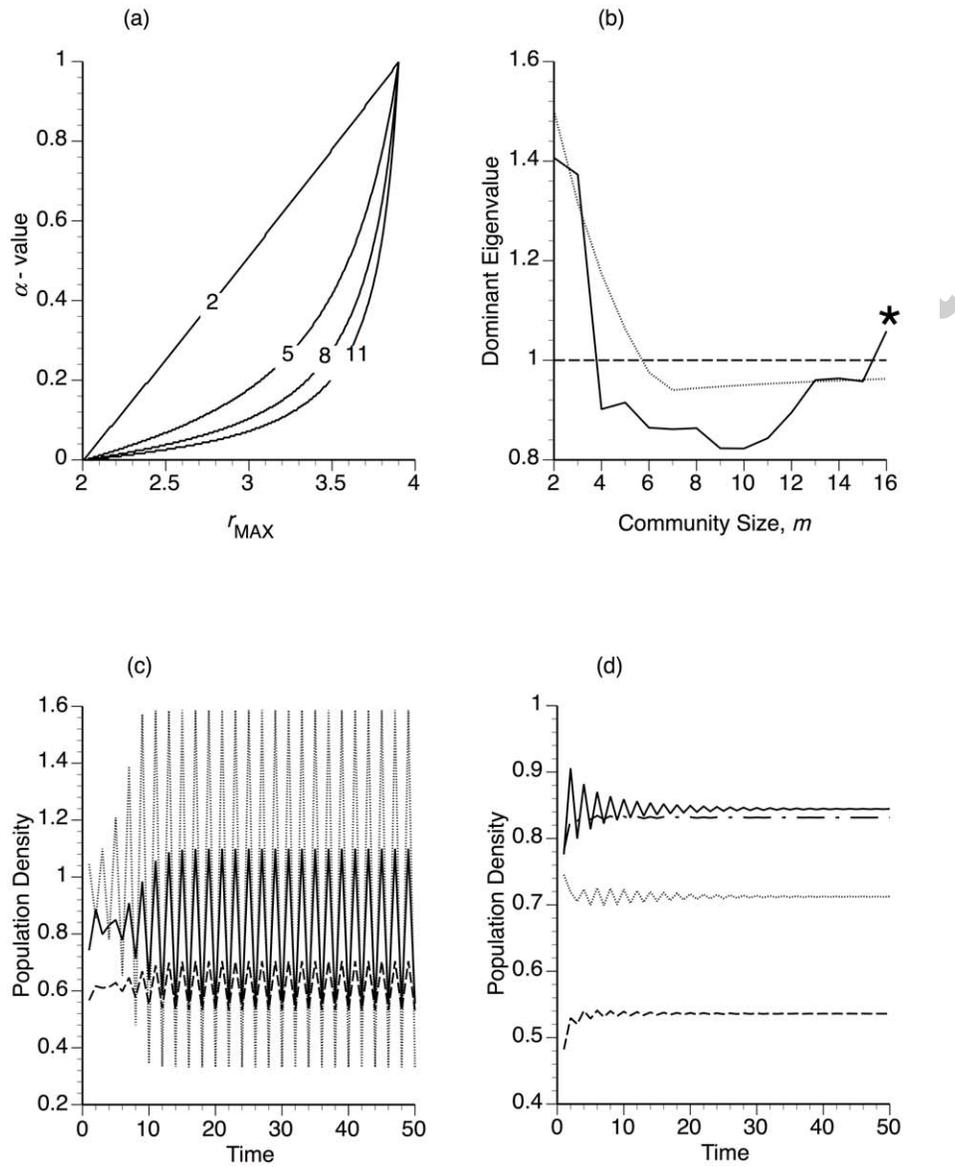
Fig. 3



FOWLER, FIGURE 3

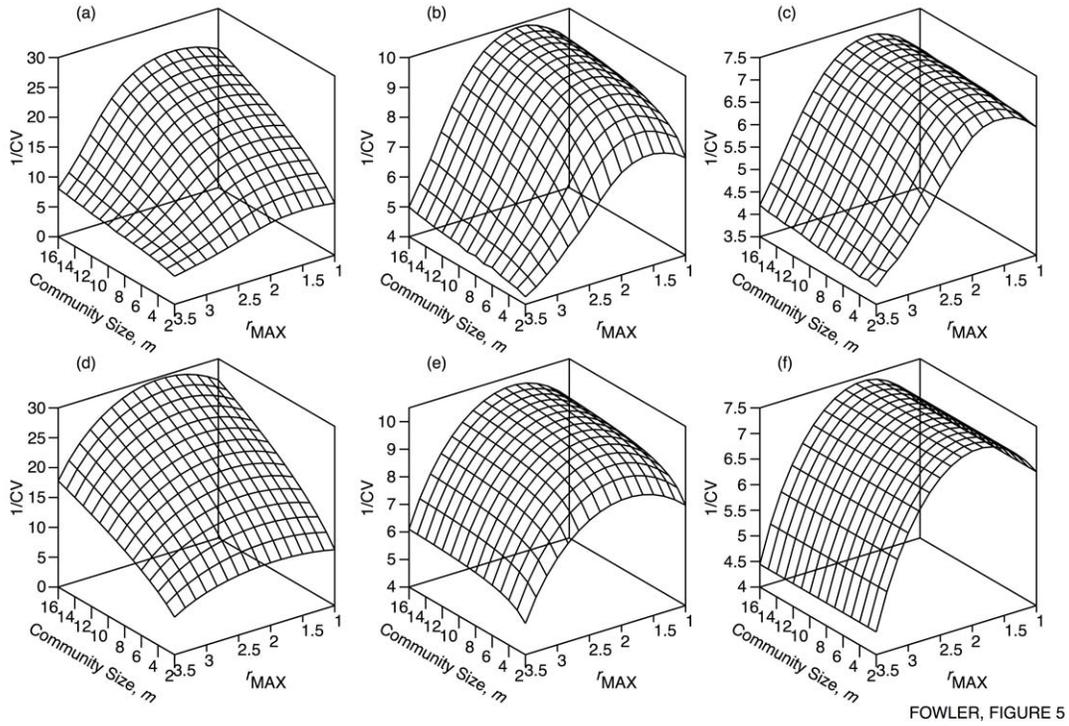
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Fig. 4



FOWLER, FIGURE 4

Fig. 5



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