

Complexity can enhance stability in competitive systems

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Abstract

Empirical observations often indicate that complexity enhances stability, while most theoretical studies, such as May's (1972) classic paper, point to the opposite. Despite the wide generality of these latter theoretical analyses, our examination of the well-known competitive Lotka–Volterra system reveals that increasing complexity (measured in terms of connectance) can enhance species coexistence and persistence in model communities (measured in terms of their feasibility and stability). The high feasibility and stability found for tightly interconnected competitive subsystems might provide an explanation for the clumped structure in food webs.

Keywords

Compartmentalization, competition, complexity vs. stability, connectance, Lotka–Volterra systems.

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One of the most controversial issues in ecology concerns whether community “complexity” begets “stability”. In the 1950s, MacArthur (1955) and Elton (1958) maintained that ecosystem stability is a function of the number of links or energy pathways in a food web. Richly connected food webs should cope far better with the loss of a single link or a perturbation than poorly connected webs that have only a few links to begin with. Thus the rich diversity of tropical ecosystems endows them with high stability. However, May (1972), in his study of randomly assembled model food webs, found exactly the opposite: “too rich a web connectance ... leads to instability”. May's results became extremely influential, changing the paradigm set by Elton and MacArthur (although see Haydon 2000). We intend to provide a counter example to May's result by showing that, for the classical diffuse competition model, increasing web connectance can increase usual measures of stability.

We examine an M -species Lotka–Volterra competition model in a form that has a long history in the ecological literature (May 1972, 1974; Maynard Smith 1974; Stone & Roberts 1991; Hughes & Roughgarden 2000):

$$\frac{dN_i}{dt} = r_i N_i \left[1 - \alpha_{ii} N_i - \sum_{\substack{j=1 \\ j \neq i}}^M \alpha_{ij} N_j \right] \quad i = 1, 2, \dots, M. \quad (1)$$

where N_i is the population density of species i at time t and the growth rate and self-interaction terms are scaled to the constants $r_i = r$, $\alpha_{ii} = 1$, respectively (as in May 1972; Stone & Roberts 1991; Hughes & Roughgarden 2000). The species interactions α_{ij} ($i \neq j$) specify the effect of species j on species i and, for competition-based systems, all $\alpha_{ij} > 0$.

The connectance C ($0 \leq C \leq 1$) of a system is defined as the proportion of non-zero interactions of the total possible $M(M-1)$ species interactions α_{ij} . The higher the connectance C , the richer is the web of links between species. In the usual diffuse competition system, connectance is maximal ($C = 1$), and each species competes with every other at the same strength $\alpha_{ij} = \gamma$ where $0 < \gamma < 1$ (see Hughes & Roughgarden 2000). Communities for which $C < 1$ may be constructed by setting:

$$\alpha_{ij} = \gamma \text{ with probability } C \quad (2a)$$

$$\alpha_{ij} = 0 \text{ with probability } (1 - C) \quad (2b)$$

The Lotka–Volterra model (eqn 1) is said to be feasible if all species have positive equilibrium populations (Roberts 1974), and locally stable if it returns to equilibrium after a small perturbation. Local stability may be determined by examining the community matrix

$$\mathbf{A} = -\text{Diag}(N_i^*) \boldsymbol{\alpha} \quad (3)$$

where $\boldsymbol{\alpha} = (\alpha_{ij})$ is the interaction matrix. If all M eigenvalues (λ_i) of the community matrix \mathbf{A} have negative real parts, the system is locally stable (May 1974). Alternatively, if the

eigenvalue having the largest real part is defined as $\lambda = \text{Re}(\lambda_{i,\text{max}})$, the system is locally stable if $\lambda < 0$.

Stone (1988) has shown that, for ensembles of competitive systems in which the interactions vary about some fixed mean strength, feasibility, as opposed to local stability, is often the bottleneck which limits the ability of all M species to persist. We will pursue this line of thought when examining the effects of connectance.

The feasibility properties of eqn 1 were determined as a function of the connectance C . For each value of C , 1000 interaction matrices were constructed according to eqn 2a. The equilibrium populations N_i^* of each interaction matrix were found by solving:

$$1 - \alpha_{ii}N_i^* - \sum_{\substack{j=1 \\ j \neq i}}^M \alpha_{ij}N_j^* = 0 \quad \text{for } i = 1, 2, \dots, M \quad (4)$$

and the feasibility was checked. The local stability was determined by numerically calculating $\lambda = \text{Re}(\lambda_{i,\text{max}})$ of the community matrix \mathbf{A} . In keeping with Stone (1988), all feasible systems examined were found to be stable. The fraction of feasible systems was then tallied and plotted as a function of connectance C , as in Fig. 1(A) for the case in which the competition strength $\gamma = 0.2$ and $M = 7, 8, 12$.

It is clear from Fig. 1(A) that, for large enough M , as the connectance C is increased from zero, the fraction of feasible and stable (FS) systems rapidly decreases from FS = 1 to FS \approx 0, only to increase again when $C \approx 0.6$. As C is further increased, the proportion of feasible and stable systems returns to its initial high value of FS \approx 1. The graph thus has a characteristic ‘‘U-shape’’. The same qualitative result was found over a wide range of competition strengths γ and community sizes. May (1972) argued that increasing the connectance of a system should lead to instability (but see DeAngelis 1975 for a counter example in a purely linear system). In contrast, for this model, there is a significant regime in which increasing connectance leads to a higher probability of finding a feasible and stable system.

In the above example, all competitive interactions were unrealistically assumed to be of the same constant strength. Hence, we also examined eqn 1 after allowing the competition strengths to vary in a realistic fashion as in Cohen & Newman’s (1988) ‘‘changing community matrix’’ approach (see also Stone 1988; Stone & Roberts 1991). Stochastic terms (ϵ_{ij}) were added to the interaction matrix by setting:

$$\alpha_{ij} = \gamma + \epsilon_{ij} \quad \text{with probability } C \quad (5a)$$

$$\alpha_{ij} = 0 \quad \text{with probability } (1 - C) \quad (5b)$$

The characteristic ‘‘U-shape’’ for the fraction of FS systems as a function of the connectance C was found to be relatively insensitive to added noise. The thin dotted line in

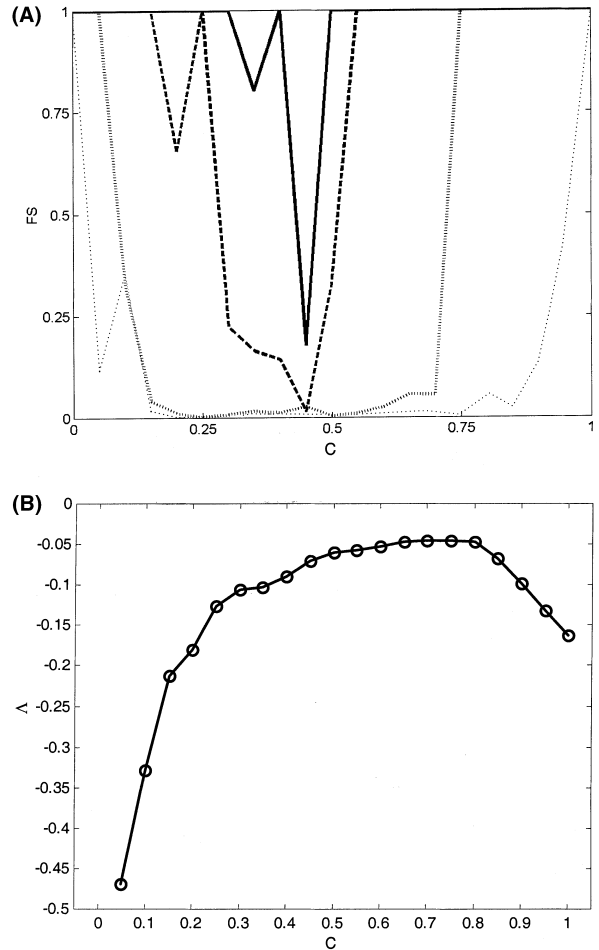


Figure 1 (A) The proportion of feasible and stable (FS) systems (of a total of 1000) plotted against the connectance C , for $M = 7$ species (dark full line), $M = 8$ (dark broken line) and $M = 12$ (light dotted line). The interaction strength $\gamma = 0.2$ in all the cases listed above. In addition, for the very light dotted line, $M = 12$ and $\gamma = 0.2 + \epsilon_{ij}$ where ϵ_{ij} is evenly distributed over the interval $[-0.1, +0.1]$. (B) The mean value of λ (i.e. largest real part of the eigenvalues of each system) averaged over 1000 systems, and plotted against the connectance C . Parameters: $M = 12$, $\gamma = 0.3$.

Fig. 1(A) shows the fraction of FS systems for $\gamma = 0.2$ where ϵ_{ij} is uniformly distributed over the interval $[-0.1, +0.1]$. Here the noise level reaches 50% of the average interaction strength, yet the characteristic ‘‘U-shape’’ is still observed.

The ‘‘U-shape’’ seen in Fig. 1(A) may be understood via the following intuitive argument. The feasibility criterion can be shown to depend on the central limit theorem (Stone 1988). When the connectance C is large (approaching unity), each species experiences many competitive interactions which it ‘‘averages over’’. Assuming a fixed number of species M , for large C , extreme values of competition coefficients will tend to cancel out, and dominant compet-

itors are less likely to exert strong influences on any single species. Feasibility is thus relatively high. On the other hand, at intermediate levels of connectance, each species experiences fewer interactions and the averaging effect is less pronounced. This tends to increase the impact of a dominant competitor reducing system feasibility. When connectance is very small, however, the intrinsic self-regulation of any given species is large enough to survive in the face of one or a few strong competitors. Feasibility is again relatively high. By putting this all together, one gains an insight into why the feasibility vs. connectance curve of Fig. 1(A) has a characteristic “U-shape”.

Figure 1(A) shows that, when there is maximal connectance ($C = 1$), all systems examined are feasible and stable, which might at first seem unusual. To further test the robustness of this result, we increased the noise level of these maximally connected systems to the point where stability and feasibility were sharply reduced, thereby destroying the characteristic “U-shape”. Figure 2 shows that, for small systems ($M \approx 5$ species), a sharp reduction in the fraction of feasible and stable systems occurs for 90–100% noise levels approximately equal to the competition coefficients (i.e. $\gamma = 0.2 + \varepsilon_{ij}$, where ε_{ij} is uniformly distributed over the interval $[-0.2, +0.2]$). As the system grows larger, sensitivity to noise increases. For $M \approx 15$ species, the sharp reduction in feasibility and stability occurs for noise levels of approximately half the magnitude of the competition coefficients.

Lastly, we examined the distribution of $A = \text{Re}(\lambda_i)_{\text{max}}$ in feasible systems (Fig. 1B). The parameter A should be a reasonable measure of overall resilience (DeAngelis 1992) as it is an indicator of the time for a system to return to equilibrium after a small perturbation. The more negative A is, the faster is the return time and the greater is the system resilience. The relationship found between A and C was not dissimilar to that already found for feasibility (Fig. 1A), namely increasing C first decreases resilience (increasing $\langle A \rangle$), but at higher levels of connectance the trend reverses and resilience then increases with C (Fig. 1B).

Given the unusual generality of May’s (1972) result, it is quite surprising to find that increasing “complexity”, as measured by the connectance C , can enhance the stability and feasibility of a simple competition system (although see Haydon 2000). These results could have implications regarding the structure of competitive systems. If highly connected systems are likely to be feasible, this might give even more credence to the possibility that compartmentalized food webs are easily able to assemble themselves into feasible configurations with pockets of highly connected competing species. This may provide support for the result of Solow & Beet (1998), who showed that food webs in nature tend to have “clumped” interactions. Indeed, despite recent reports to the contrary (Solow *et al.* 1999), our preliminary findings indicate that compartmentalization of this type is advantageous in competitive systems (Rozdilsky *et al.* in preparation).

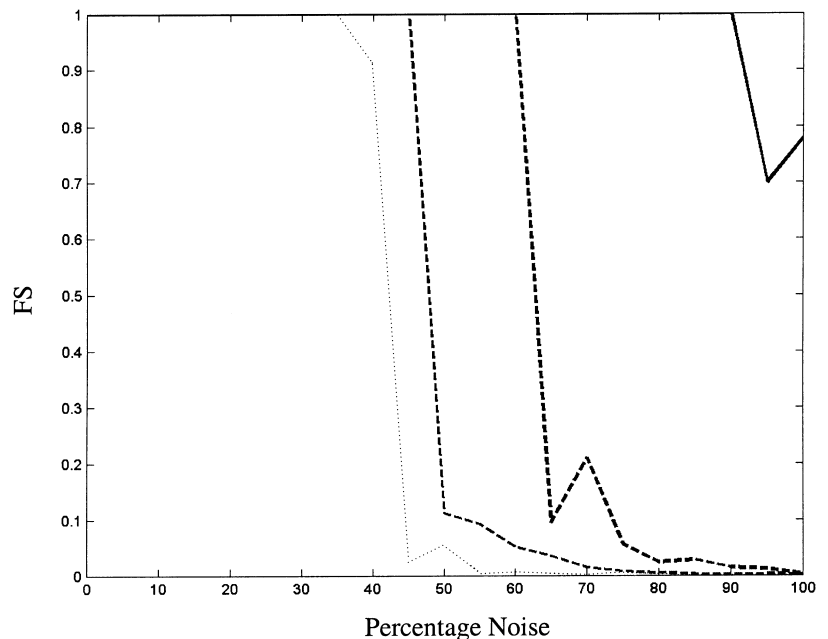


Figure 2 The proportion of feasible and stable (FS) systems (of a total of 1000) plotted against the “percentage noise” level inserted into the interaction strengths (see text). All systems have maximal connectedness ($C = 1$) with $M = 5$ species (full line), $M = 10$ (dark broken line), $M = 15$ (light dotted line) and $M = 20$ (very light dotted line).

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BIOSKETCH

Ian Rozdilsky has broad interests in the applications of theoretical ecology to conservation policy. He is currently exploring how habitat destruction affects the structure of ecosystems and strategies for biodiversity conservation on continental scales.

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