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Are large complex ecosystems more unstable? A theoretical reassessment with predator switching

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Abstract

Multi-species Lotka–Volterra models exhibit greater instability with an increase in diversity and/or connectance. These model systems, however, lack the likely behavior that a predator will prey more heavily on some species if other prey species decline in relative abundance. We find that stability does not depend on diversity and/or connectance in multi-species Lotka–Volterra models with this ‘predator switching’. This conclusion is more consistent with several empirical observations than the classic conclusion, suggesting that large complex ecosystems in nature may be more stable than previously supposed. © 2000 Elsevier Science Inc. All rights reserved.

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1. Introduction

Almost 30 years ago, May [1] overturned the conventional wisdom that large complex ecosystems are more stable than small simple ecosystems by analyzing the stability of multi-species Lotka–Volterra models. He showed that more complex models (i.e. those with a greater number of species and/or more links between species) were never more stable and generally much less stable than smaller and/or less strongly connected model ecosystems. Stability is defined as the condition that a system will return to equilibrium when perturbed from its equilibrium state. Recently, McCann et al. [2] cast doubt on the correlation between complexity and instability studying a model that includes a number of realistic assumptions that differ from May’s classic model. In this paper we reconsider the multi-species Lotka–Volterra model and let the interaction strengths between predator and prey be a function of the relative abundance of prey, consistent

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with predator switching. We conclude that models with predator switching have a high probability of having a stable fixed point, independent of diversity or connectance. This is consistent with the theoretical analyses of Matsuda et al. [3] and Khan et al. [4] in addition to McCann et al. [2] and the empirical results of Abrams and Matsuda [5] on the stabilizing effects of predator switching. The advantage of our formulation over other recent food web models which include many new components is that our model differs from May's classic model only in its more realistic dynamic interaction strengths. As such, it provides a simple counterexample to the theoretically derived correlation between complexity and instability.

2. Methods

We first consider the classic multi-species Lotka–Volterra model without predator switching. The model consists of two trophic levels consisting of n predators and n prey with the abundance of each given by P_i and H_i , $i = 1..n$, respectively. Each predator species interacts with a fraction C of all prey species and no predator species. Similarly, prey species interact only with the predator species that prey on them and do not interact with any prey species. The equations governing the model are

$$\begin{aligned} \frac{dH_i}{dt} &= H_i \left(a_i - \sum_{j=1}^n b_{ij} P_j \right), \\ \frac{dP_i}{dt} &= P_i \left(\sum_{j=1}^n c_{ij} H_j - d_i \right), \quad i = 1..n. \end{aligned} \quad (1)$$

The birth rate of the prey species i , a_i , the death rate of the predator species i , d_i , the number of prey species i killed by predator species j per unit time per capita of predator species j , b_{ij} , and the number of predators of species i born per unit time per capita of prey species j , c_{ij} , are each lognormal random variables with a mean and a coefficient of variation of 1 and are constant in time. However, to model variable connectance, $b_{ij} = c_{ji} = 0$ with probability $1 - C$ where C is a number between 0 and 1. To determine the stability of (1), the fixed point is determined by obtaining the root, H_i^* and P_i^* , of the following matrix equations by Gauss–Jordan elimination [6]:

$$\sum_{j=1}^n c_{ij} H_j^* = d_i, \quad \sum_{j=1}^n b_{ij} P_j^* = a_i. \quad (2)$$

A single, unique solution with finite roots is obtained from (2). If any of the H_i^* or P_i^* are negative, new choices are made for a_i , b_{ij} , c_{ij} , and d_i until choices which result in positive values for H_i^* and P_i^* are obtained. To investigate the stability of the fixed point, we can integrate (1) forward in time with initial values corresponding to the fixed point plus a small perturbation. If any of the abundances drift off to zero or ever-increasing values, the fixed point is unstable. The initial conditions of predators and prey are chosen to be $H_i^*(1 + 0.1\eta_i)$ and $P_i^*(1 + 0.1\nu_i)$, respectively, where η_i and ν_i are Gaussian random variables with a mean of zero and a coefficient of variation of 1. Gardner and Ashby [7] and May [8,9] found, using a random matrix model similar to (1), that the probability of a stable fixed point decreases rapidly with an increase in n and/or C . The

stability of the fixed points of (1) can also be obtained without integration by solving for the eigenvalues of (1). However, we prefer to integrate the equations in our analysis to facilitate comparison with the results of the model with predator switching where integration of the model is necessary to determine the stability of the fixed points. Although the model we consider has only two trophic levels, May argued that the stability of a system of two trophic levels and a similar model with more than two trophic levels will generally be the same [1].

When a prey species decreases in abundance in (1) the predators decrease in abundance by an amount proportional to the interaction strength c_{ij} . However, it is likely that in many cases a predator will consume more individuals of other species when one of its prey becomes relatively less abundant. This behavior is termed predator switching. With predator switching the interaction strengths are variable in time and depend on the relative abundance of the prey species. Thus, the revised model we consider with predator switching multiplies the interaction terms by the relative interaction with each prey species, $c_{ji}H_i/((\sum_{k=1}^n c_{jk}H_k)/n)$ in the equation for dH_i/dt and $c_{ij}H_j/((\sum_{k=1}^n c_{ik}H_k)/n)$ in the equation for dP_i/dt to yield the following equations:

$$\frac{dH_i}{dt} = H_i \left(a_i - \sum_{j=1}^n b_{ij} \left(\frac{c_{ji}H_i}{(\sum_{k=1}^n c_{jk}H_k)/n} \right) P_j \right), \tag{3}$$

$$\frac{dP_i}{dt} = P_i \left(\sum_{j=1}^n c_{ij} \left(\frac{c_{ij}H_j}{(\sum_{k=1}^n c_{ik}H_k)/n} \right) H_j - d_i \right), \quad i = 1..n.$$

The relative interaction terms must appear in both equations since when a predator preys more heavily on a prey species both the population growth rate of the predator and the death rate of the prey will be modified by the same factor. The justification offered for applying May’s conclusion of a negative correlation between stability and complexity to real ecosystems has been that even if the precise form of the models is incorrect, the Lotka–Volterra model represents a linear approximation to the true behavior which is accurate for small deviations from equilibrium [8]. This argument is invalid, however, if the linear term is zero and the leading order term is approximately quadratic as in (3). For the well-studied case of one predator and one prey, (3) reduces to (1).

The equilibrium values H_i^* and P_i^* for (3) must be found using a different procedure than the Gauss–Jordan elimination procedure used to solve (2) since (3) is non-linear. The equations defining the equilibrium values H_i^* and P_i^* for (3) are

$$\sum_{j=1}^n c_{ij} \left(\frac{c_{ij}H_j^*}{(\sum_{k=1}^n c_{jk}H_k^*)/n} \right) H_j^* = d_i, \tag{4}$$

$$\sum_{j=1}^n b_{ij} \left(\frac{c_{ij}H_j^*}{(\sum_{k=1}^n c_{ik}H_k^*)/n} \right) P_j^* = a_i. \tag{5}$$

We solve for the root of (4) using the globally convergent Newton’s method [6] with the root of (2) as an initial guess. The root of the linear equation (5) is then obtained by using the equilibrium values H_i^* in (5) and performing Gauss–Jordan elimination [6]. The stability of the root is then determined by integrating (3) forward in time with initial conditions perturbed from the fixed point in the same manner as the simulation of (1).

3. Results

Prey switching has a strongly stabilizing influence (Fig. 1). In Fig. 1(a) we plot the evolution of (1) with $n = 4$ integrated with the Burlisch–Stoer method (3). All of the abundances have been scaled to their equilibrium values. The evolution graphed in Fig. 1(a) is an example of the general result that for $n > 1$ and for many sets of parameters a_i , b_{ij} , c_{ij} , and d_i the fixed point is unstable such that eventually one or more of the species becomes extinct or drifts off to ever-increasing abundance [1]. In Fig. 1(b) we plot the evolution of (3) with the same coefficients a_i , b_{ij} , c_{ij} , d_i , and initial values as in Fig. 1(a). The initial perturbations damp out indicating that the model with predator switching has a stable fixed point for these parameter values. Note the different scales of Fig. 1(a) and (b). Fig. 1(a) is plotted only up to $t = 7$ when one of the species becomes extinct. Fig. 1(b) is plotted for a longer period of time to indicate that the

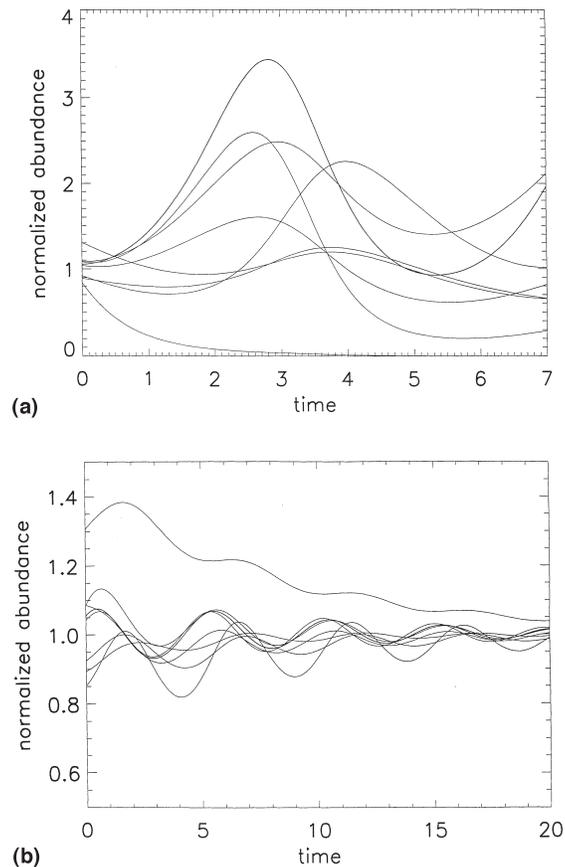


Fig. 1. Plot of normalized abundance of the predator and prey populations of the multi-species Lotka–Volterra model as a function of time for $n = 4$ (a) without predator switching (1) and (b) with predator switching (3). The model plotted in (b) has the same coefficients and initial conditions as (a). The evolution of (a) indicates an unstable fixed point while the evolution of (b) indicates a stable fixed point.

model is stable out to times much longer than the time at which species in Fig. 1(a) become extinct. Also the vertical scale of Fig. 1(a) is larger than Fig. 1(b) indicating its greater variability.

Gardner and Ashby [7] and May [8,9] recognized that it is unlikely for any one set of parameter values to be applicable to all ecosystems or even to a single ecosystem for all time. Thus, these authors considered the stability of many realizations of a random matrix model similar to (1) by computing the probability that a given realization of the random matrix model will have a stable fixed point. We have performed the same analysis for (1) and (3). The probability that a single model from the ensemble of random matrix models (1) and (3) has a stable fixed point is plotted in Fig. 2 for constant connectance ($C = 1$). Similar results were obtained by keeping n constant and varying the connectance. Results for both the classic multi-species Lotka–Volterra model (filled circles) and the revised model with predator switching (unfilled circles) are plotted. Each point was obtained by integrating 1000 realizations of (1) or (3) with different randomly chosen coefficients. A fixed point was considered to be stable if none of the species were extinct (had normalized abundances below an arbitrary threshold value of 0.0001) at the end of a long integration (chosen to be $t = 100$, much longer than the mean characteristic growth and decay time of the species, a_i and d_i , of 1 time unit). We were only able to study models up to $n = 4$ since for $n > 4$ it becomes computationally unfeasible to find models that yield all positive values for H_i^* and P_i^* by random trial-and-error searching. The results for the model without predator switching are consistent with the results of Gardner and Ashby [7] and May [8,9] who found, using a similar random matrix model, that the probability of a stable fixed point decreased rapidly with increasing diversity and/or connectance. The results for the fixed points of (3) indicate a high probability of a stable fixed point (0.90 ± 0.01) independent of diversity n . The probability of a stable fixed point was independent of connectance when diversity was held constant.

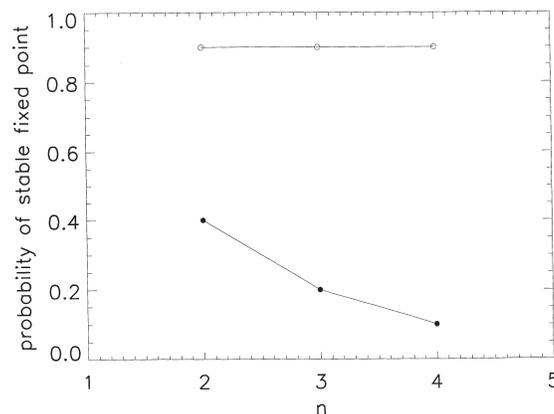


Fig. 2. Probability of a stable fixed point of (1) (filled circles) and (3) (unfilled circles) for fixed connectance ($C = 1$) as a function of model diversity, n . Increased diversity leads to a lower probability of stable fixed points in the classic model without predator switching and a greater probability of stable fixed points in the revised model with predator switching.

4. Discussion

Several empirical results suggest that species-rich communities are as stable or more stable than species-poor communities. Although comparing field evidence with theoretical predictions is complicated by the multiple facets of stability [10] (including resilience, persistence, resistance, and variability) two studies suggest a direct positive correlation between complexity and stability. Redfearn and Pimm [11] observed a negative correlation between population variability and degree of polyphagy for Canadian moths when corrected for abundance. Their study supports MacArthur's [12] suggestion, based on the idea of predator switching, that monophagous species should be more variable than polyphagous species. Pimentel [13] found that insect herbivores reach levels that endanger their food supply in species-poor but not species-rich ecosystems. These empirical observations are more consistent with our results than with the conclusions drawn by May [1,8,9] with the classic Lotka–Volterra model. It is not possible to make a more quantitative connection between our model results and the empirical studies of Redfearn and Pimm [11] and Pimentel [13] because of the different definitions of stability employed and our analyses of an ensemble of random matrix models rather than a single community. Our results have shown that of all possible communities, a higher fraction will be stable when predator switching is included in the model. This is generally consistent with, but not the same as, the empirical studies of Redfearn and Pimm [11] and Pimentel [13] which have shown that population variability is reduced in a single ecosystem when predator switching is encouraged by increased ecosystem complexity.

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