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LETTER

Complexity and stability revisited

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Abstract

Since Robert May's work on random community matrices it has been known that stability tends to decrease with complexity. Recently, it was shown that this is not necessarily true in competitive ecosystems. We investigated the stability of random ecosystems and found that it can largely be predicted by simple matrix statistics such as the mean and the variance of the interaction coefficients. We use this to explain why stability can increase as well as decrease with complexity in ecological communities. We argue that the variance, and to a lesser extent the mean, of the interaction coefficients go a long way in explaining patterns in the stability of ecosystems.

Keywords

Assembly, community ecology, community matrix, complexity, ecosystems, interaction matrix, Lotka–Volterra model, random matrix.

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INTRODUCTION

Does complexity beget stability after all? Rozdilsky & Stone (2001) claim it does. Since May's (1972, 1974 seminal work many theoretical ecologists have studied ecological communities using random community matrices (see Pimm 1982, 1984; Hall & Raffaelli 1993; McCann 2000 for reviews). Most of this work supports the conclusion drawn by May that an increase in the number of links in a food web decreases the ecosystem's stability. In May's model all types of interaction are possible and species can be engaged in mutualistic (+, +), antagonistic (+, −) and competitive interactions (−, −). However, in strictly competitive systems increased complexity can lead to increased stability (Rozdilsky & Stone 2001). Also in food webs this might be the case (Fussmann & Heber 2002).

In this paper we will reconcile these results and show that in random ecosystems the local stability and feasibility of the equilibrium depends on simple statistical properties of the interaction matrix, such as the mean and the variance of the interaction coefficients. This provides a more parsimonious explanation for stability than the complexity. We also discuss the importance of weak links in communities and argue that, rather than to look at the presence of weak interactions per se, the effect of weak interactions depends on their effect on the mean and the variance of the interaction matrix. To understand the effect of weak interactions they need to be compared with the distribution of the interaction coefficients in the rest of the community.

METHODS

We used a generalized Lotka–Volterra interaction model to describe the population dynamics of a community of n interacting species. The density of species i is given by x_i and changes according to

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = r_i x_i \left(1 + \sum_{j=1}^{n} \alpha_{ij} x_j\right) \tag{1}$$

The interaction coefficients, α_{ij}, represent the per capita effect of interaction of an individual of species j on species i. The interaction matrix has the interaction coefficients as elements. The intraspecific interaction coefficients α_{ii} are set to −1 and the basic growth rates, r_i, are set to unity. The interspecific interaction coefficients are chosen randomly according to the following scheme: $\alpha_{ij} = 0$ with probability $1 - C$ and with probability C the interaction coefficient is drawn randomly from a uniform distribution on the interval $[a, b]$. The connectance, C, determines the fraction of links in the community. For competitive communities $a, b \leq 0$, for food webs $a \leq 0 \leq b$. For simplicity we will refer to the interspecific interaction coefficients as interaction coefficients.

The equilibrium densities $\hat{x}_i$ of this model can be found by solving the n equations:

$$\sum_{j=1}^{n} \alpha_{ij} \hat{x}_j = -1$$

The equilibrium is feasible if all equilibrium densities are positive, i.e. $\hat{x}_i > 0$ for all i. The stability properties of the equilibrium follow from the eigenvalues of the Jacobian matrix, $J = \{\hat{x}_i \alpha_{ij}\}$. The equilibrium is locally stable if all eigenvalues of J are negative if real or have negative real parts if complex. The diagonal elements of the Jacobian matrix are given by $-\hat{x}_i$. In what follows we will refer to locally stable equilibria as stable. This is not necessarily the best measure of stability (see e.g Jansen & Sigmund 1998) but it allows comparison with earlier work.

Model (1) always has one eigenvalue equal to -1 (see Appendix 1). We are not aware of any other analytical results with regard to the distribution of the remaining eigenvalues [but see Stone 1988 for sufficient conditions on global stability in large systems]. The stability of the equilibrium strongly depends on the statistical properties, like the mean and the variance, of the interaction coefficients (Kokkoris *et al.* 2002). We numerically investigated how the probability of model (1) to have a stable and feasible equilibrium depends on the mean and variance of the interaction coefficients for varying levels of connectance.

RESULTS

We studied the dependence of the probability of a stable and feasible equilibrium by varying the model parameters whilst keeping either the variance or the mean of the interaction coefficients constant. We did this in two different ways: either by changing the connectance, C, while choosing all non-zero interaction coefficients the same, i.e. $a = b$, or by keeping the connectance constant but by varying the midpoint and the width of the interval $[a,b]$. The mean of the interaction coefficients is given by $\mu = (C/2)(b + a)$ and the variance by $\sigma^2 = \left(\frac{4}{3C} - 1\right)\mu^2 - \frac{Cab}{3}$ and from these expressions the inverse relationships by which the model parameters can be changed but for which either mean or variance remain constant can be found.

In Fig. 1 the probability for the equilibrium of model (1) to be stable and feasible is plotted against the variance of the interaction coefficients. The mean interaction coefficient is constant in these graphs. The probability of the equilibrium to be feasible and stable decreases with increasing variance. On the left of the graph the interaction coefficients are always negative and we are dealing with competitive communities. On the right the interaction coefficients can be negative as well as positive and food webs can exist. The probability of a stable and feasible equilibrium changes in a continuous fashion between these regimes and is approximately the same for the simulations in which the connectance was kept constant as for those in which the connectance differed. The larger the number of species, the smaller the difference between the two curves. Note the saw tooth in the curves for which $a = b$. At the point of discontinuity $a = b = -0.5$ and a 'team' of two species compete with another team for, what can be interpreted as, a single resource (see Appendix 2). In the vicinity of a saw tooth feasible but unstable equilibria tend to occur. By changing the interaction strength from below -0.5 to above interaction changes abruptly from competitive exclusion to competitive coexistence.

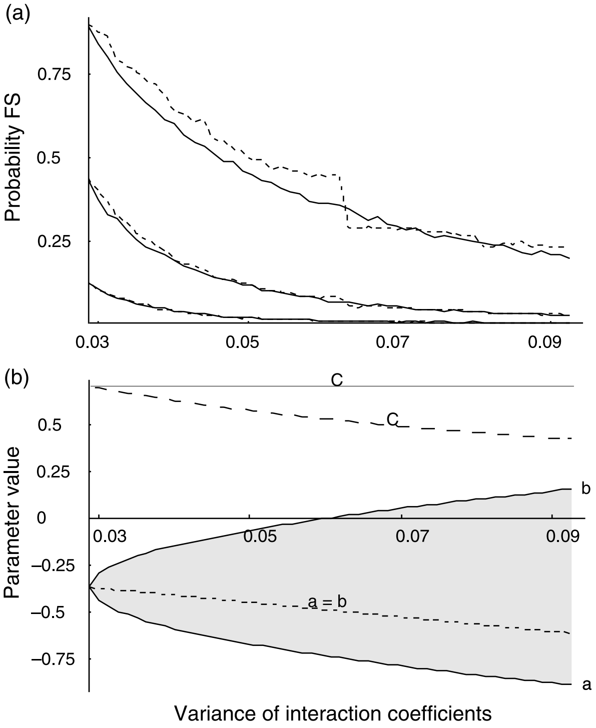

Figure 1 (a) The probability that model (1) has a stable and feasible equilibrium (FS) as a function of the variance of the interaction coefficients. The variance was changed in two ways: for the drawn curves the connectance was constant and the interval from which the non-zero interspecific interaction coefficients were chosen was varied. The interaction coefficients were chosen from the grey area in Fig. 1b while the connectance was $C = 0.7$. For the dashed curves all non-zero interaction coefficients were chosen identical ($a = b$) but the value and the connectance varied as shown by the dashed lines in Fig. 1b. The mean value of the interaction coefficients was kept constant in both cases. The different lines depict the results for communities of six (top curves), nine (middle curve) and 12 (bottom curve) species. Per curve 50 equally spaced data points were used, for each data point 10 000 matrices were generated.

In Fig. 2 the mean of the interaction coefficients was varied while the variance was kept constant. For one set of curves the connectance was kept constant while it varied for the other set. With an increase in the mean value the probability to be feasible and stable can increase as well as decrease, however, for a large range the stability increases with the mean, and, hence, for the dashed curves more

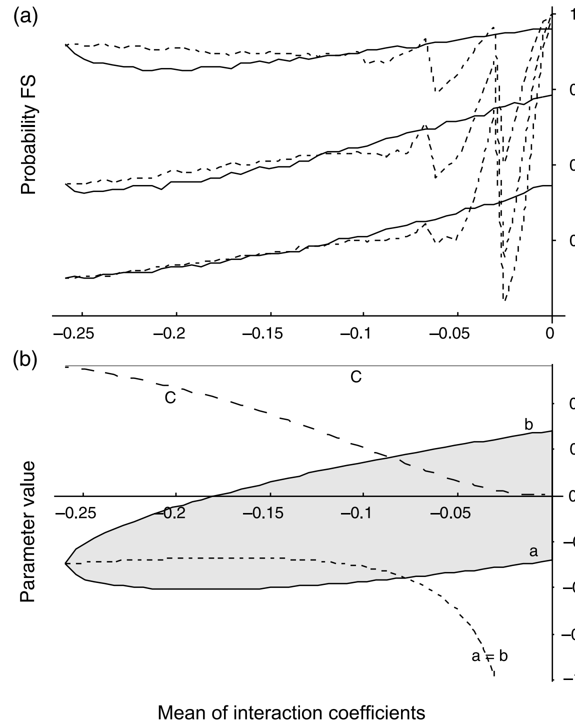

Figure 2 The probability that model (1) has a stable and feasible equilibrium (FS) as a function of the mean of the interaction coefficients. For the drawn curves the connectance was kept constant at $C = 0.7$ while the interval from which the non-zero interaction coefficients were drawn varied as shown in Fig. 2b. For the dashed lines all non-zero interaction coefficients were chosen identical but their value and that of the connectance varied (Fig. 2b). The different lines depict the results for communities of six (top curves), nine (middle curve) and 12 (bottom curve) species. Per curve 50 equally spaced data points were used, for each data point 10 000 matrices were generated.

connected systems tend to be more stable. Two saw teeth can be seen in the dashed curves for $a = b = -0.5$ and $a = b = -1$. Generally, the variance has a stronger impact on the probability to be feasible and stable than the mean.

Rozdilsky & Stone (2001) demonstrated that in model (1) the probability of the equilibrium to be feasible and stable takes a U-shaped form if the connectance is changed from 0 to 1. To illustrate how their result can largely be explained by the variance of the interaction coefficients we choose $a = b$ and reconstructed their U-shaped graph (Fig. 3a). For this choice of parameters the mean $\mu = Ca$ is an increasing function of connectance. The variance, $\sigma^2 = C(1 - C)a^2$, increases for small C, takes its maximum value at $C = 0.5$ and then decreases in the same manner (Fig. 3b). We constructed a similar U-shaped curve by keeping the connectance constant at unity and by changing the interval from which the interaction coefficients were chosen in such a way that the interaction coefficients had the same mean and variance as in the dashed curve. The two curves are very similar. This demonstrates that the mean and the variance, rather than the connectance, determine the probability of the equilibrium to be feasible and stable.

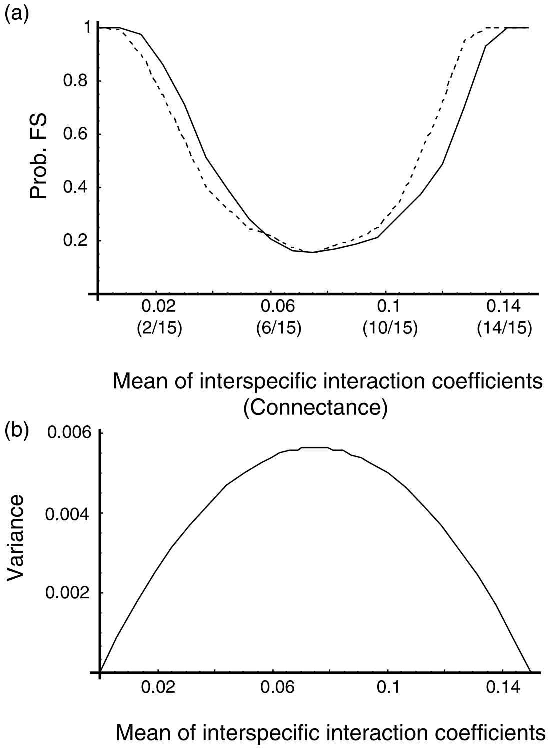

Figure 3 (a) The probability of a stable and feasible equilibrium (FS) as a function of the mean of the interaction coefficients for communities with 40 species. For the dashed curve the connectance was varied while the non-zero interaction coefficients were all set at the same value $a = b = 0.15$: the mean therefore changes linearly with the connectance. The corresponding values for the connectance are given in brackets. For the drawn curve the connectance was set at $C = 1$ (no non-zero entries) while values of a and b were chosen such that the mean and variance of the interaction coefficients matched the mean and the variance of the dashed curve; 1000 matrices were generated per data point. (b) Variance of the interaction coefficients as a function of the mean of the interaction coefficients for the curves in Fig. 3a.

In Rozdilsky & Stone's (2001) study all feasible equilibria were found to be stable. Although this may often be the case in competitive systems, it is by no means the rule. For instance, if we choose $a = -0.8$, $b = -1.25$ and $C = 0.15$ we found that out of 10 000 randomly constructed six species systems 12.33% were feasible and stable, 2.27% unfeasible and stable, 1.53% were feasible and unstable and the remainder unfeasible and unstable (see also Kokkoris *et al.* 2002). This illustrates the merit of using a Lotka-Volterra model over a Jacobian matrix model, as in the latter it is not possible to discern between stable and feasible equilibria and stable and unfeasible equilibria.

DISCUSSION

The stability of ecosystems strongly depends on statistical properties of the interaction matrix, such as the mean and the variance of the interaction coefficients. This indicates that in our model the distributions of the equilibrium densities and the eigenvalues converge in a fashion that is relatively independent of the way in which the interaction matrices are generated. This in itself is hardly surprising. What is surprising is that even for the relatively small ecosystems used here the specific details of the way in which the species interact hardly matter beyond the mean and the variance of the interaction coefficients (see also Stone 1988).

This is not to say that there are no factors beyond the mean and the variance of the interaction coefficients. Haydon (2000) showed that the statistical properties of stable matrices can differ from the properties of the set of all matrices. This indicates that stable matrices have a special internal structure. Such structures can, but need not, manifest itself in the mean and the variance of the interaction coefficients. Kokkoris *et al.* (2002) show how correlations between different interaction coefficients can have a large impact on the feasibility and stability of a system.

We argue that the mean and variance of the interaction coefficients provide a more parsimonious explanation for the change in stability than the complexity. This seems to contradict May's (1974) conclusion. However, in May's (1974) model, a perfect balance between positive and negative interactions is assumed. Therefore, the mean of the interaction coefficients is zero, variance always increases with the number of connections and stability always decreases with complexity. In competitive communities the mean value of the interaction coefficients is not zero. If the mean value is small, increased complexity leads to reduced stability. However, if the mean is large a U-shaped relationship between complexity and stability is found.

A change in connectance can decrease as well as increase the variance. This explains why the probability of a community to have a stable and feasible equilibrium can increase with increasing connectance. Obviously, if none of the species interact all interaction coefficients are zero, hence there is no variance and this ensures stability. Also if all species interact the variance in the interaction coefficients is small, which again leads to stability. For intermediate cases the interaction coefficients have considerable variance because they are either zero or come from a range not containing zero. This leads to the U-shape of the probability of finding a stable equilibrium when plotted against complexity as found by Rozdilsky & Stone (2001). However, this U-shape can also result from other effects and we managed to recreate this result by keeping the connectance constant but changing the variance of the interaction coefficients in a different way.

The mean and variance of interaction coefficients can explain the effects of weak interactions on stability. Weak interactions have been found in abundance in natural communities (Paine 1992; Raffaelli & Hall 1992; Fagan & Hurd 1994; Berlow 1999) and assembled theoretical communities (Kokkoris *et al.* 1999). It has been shown that in specific systems weak interactions can lead to stability (Ives & Jansen 1998; McCann *et al.* 1998). Rather than look at the presence of weak interactions per se, our results suggest that the effect of weak interactions depends on how interactions are distributed in the rest of the community. If most interactions are strong, a few weak interactions will increase the variance and decrease the probability of stability. If most interactions are weak, the effect of a few more weak interactions will make little difference. If all interactions are weak the mean interaction strength and the variance is low which correlates with increased stability (Kokkoris *et al.* 2002). This shows how the variance and mean of the interaction coefficients can be used to understand the stability of ecosystems.

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APPENDIX

1 The stability of the non-zero equilibrium of model (1) can be derived from eigenvalues of the Jacobian matrix J. One of these eigenvalues for model (1) is always -1. This can be shown as follows: the vector which contains the equilibrium densities $\hat{x} = (\hat{x}_1, \ldots, \hat{x}_n)^T$ is an eigenvector of matrix J. Let the $A = \{\alpha_{ij}\}$ and note that $\hat{x} = -A^{-1} \cdot (1, \ldots, 1)^T$ and $J = Diag(\hat{x}) \cdot A$. It follows that $J.\hat{x} = -Diag(\hat{x}) \cdot A \cdot A^{-1} \cdot (1, \ldots, 1)^T = -\hat{x}$ hence $\hat{x}$ is an eigenvector of J and the eigenvalue associated with this eigenvector is -1.

2 If $a = b$ teams of two competing species can exist. This happens if the interaction matrix is similar to

$$A = -\begin{bmatrix} 1 & 0 & a & a \\ 0 & 1 & a & a \\ a & a & 1 & 0 \\ a & a & 0 & 1 \end{bmatrix}.$$

An interaction governed by this matrix eventually converges to a state in which $x_1 = x_2$ and $x_3 = x_4$ (this can be shown by means of the Lyapunov functions $((x_1 - x_2)/(x_1 + x_2))^2$ and $((x_3 - x_4)/\ (x_3 + x_4))^2$). In this state the system can be described as $\mathrm{d}v_1/\mathrm{d}t = v_1(1 - v_1 - 2av_2)$, $\mathrm{d}v_2/\mathrm{d}t = v_2(1 - 2av_1 - v_2)$, where $v_1 = x_1 + x_2$ and $v_2 = x_3 + x_4$. This system has a feasible and stable equilibrium if $a < 1/2$, and a feasible and unstable equilibrium if $a > 1/2$. If $a = 1/2$ determinant of the interaction matrix is zero. This situation can be interpreted as competition for a single resource. For teams of n species a similar analysis is possible. The critical point is at $a = -1/n$.