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STABILITY VS. COMPEXITY IN MODEL COMPETITION COMMUNITIES

Pavel KINDLMANN

Czechoslovak Academy of Sciences
Institute of Entomology
Na sadkach 702
370 05 Ceske Budejovice
Czechoslovakia

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Pavel Kindlmann

INTRODUCTION

The question of the so-called stability vs. complexity relationship, i.e. the question whether a complex ecosystem tends to be more or less stable than a simple one, was broadly discussed in last years. In the 'fifties, ecologists put forward the hypothesis that complex biological communities would be more stable than simple ones (MacArthur, 1955; Elton, 1958; Hutchinson, 1959), but recent theoretical investigations have demonstrated that stability is not a simple mathematical consequence of complexity. The contrary frequently seems to be true (Gardner and Ashby, 1970; May, 1972).

The mathematical analysis of the stability vs. complexity relationship is based on the assumption that the population dynamics of a system of m interacting species can be described by a system of m (-in general nonlinear) first order differential equations of the following form:

$$dn_i(t)/dt = F_i(n_1(t), n_2(t), \ldots, n_m(t));\quad i = 1,2,\ldots,m, \qquad (1)$$

where $n_i(t)$ represents the population of i-th species at time t. This system is said to be stable if the corresponding linearized system

$$dx/dt = Ax \qquad (2)$$

is locally asymptotically stable, i.e., if all the eigenvalues of the so-called interaction or community matrix in (2) have negative real parts (or lie within a unit circle if, instead of (1), the corresponding discrete model is analysed).

The first step to the clarification of the stability vs. complexity relationship was done by Gardner and Ashby (1970) and by May (1972). May assumed

that the interaction matrix A of a great ecosystem may be considered as being a random matrix consisting of the elements

$$a_{ij}\begin{cases} = 0 \text{ with probability } 1-C, \\ \neq 0 \text{ with probability } C, \text{ where } a_{ij}\text{'s are chosen} \\ \quad \text{from random number distribution with mean} \\ \quad =0, \text{ standard deviation } = s, \end{cases} \text{for } i \neq j \qquad (3)$$
$$a_{ij} = -1 \text{ for } i=j.$$

He has shown that for large m, $m \to \infty$, the probability of stability of such system, P_{stab}, tends to 0 if $s\sqrt{mC} > 1$ and P_{stab} approaches 1 if $s\sqrt{mC} < 1$, where, in the ecological sense, s (defined above) represents the average interaction strength near the equilibrium, m is the number of species in the community, and C is connectance (i.e., the fraction of non-zero off-diagonal elements in the matrix A).

May's criterion reflects the asymptotic relationship of the largest real part, $R(\lambda)_{max}$, of the eigenvalues of the random matrix A to m, s and C, for $m \to \infty$:

$$R(\lambda)_{max} \simeq s\sqrt{mC} + \overline{a_{ii}}, \qquad (4)$$

where $\overline{a_{ii}}$ denotes the mean of the a_{ii}'s. In May's case, $\overline{a_{ii}} = -1$.

This relationship has been confirmed, by means of numerical simulation, by McMurtrie (1975). His simulations indicate that for $m \gg 1$ the complex eigenvalues of a matrix of rank m, the elements of which are chosen from some distribution with the mean = 0 and the mean square value = σ^2, are uniformly distributed in a disc in the complex plane with the centre 0 and radius $\sigma\sqrt{m}$. Specially, the complex eigenvalues of May's matrix A are, for $m \gg 1$, uniformly distributed in a disc in the complex plane with the centre -1 (due to the choice of the diagonal elements) and radius $s\sqrt{mC}$.

We have verified this conclusion for various matrices and distributions of

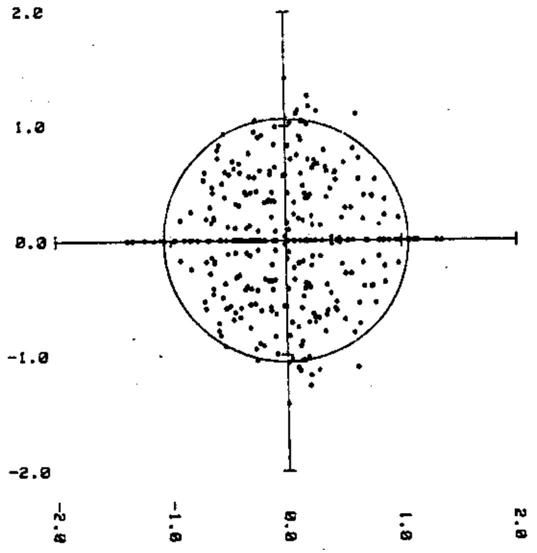


Fig. 1. The eigenvalue distribution of 50 matrices generated randomly with the elements chosen as in (3). Here, m = 10, s = 0.4, C = 0.7 and the diagonal is equal to 0.

their elements and the results supported those of McMurtrie (see Fig. 1 for example). As it was shown by McMurtrie, the fraction of real eigenvalues in the eigenvalue spectrum is scaling like $1/\sqrt{m}$. Therefore, if $m \gg 1$, this fraction becomes negligible.

A broad discussion arose with the aim to clarify the discrepancy between May's and empirical results. One of the arguments in this discussion was that matrices generated entirely randomly do not present ecologically plausible systems in most cases. The length of trophic chains is not limited and such phenomena as "plant eating a carnivore" are not excluded in a random construction. It is rather difficult to construct a random matrix representing a biological plausible system with more than one trophic levels. Furthermore, the analysis of such systems would have to take into account, e.g., the ratios between numbers of species at different trophic levels etc. But construction and analysis of behaviour of a randomly generated system with only one trophic level is quite easy (Rejmánek, Kindlmann and Lepš, 1983).

COMPETITIVE COMMUNITIES

We have constructed random matrices the elements of which were set equal to:

$$b_{ij} = \begin{cases} -\,\mathrm{RAND} & \text{for } i \neq j, \\ -1 & \text{for } i = j \end{cases} \tag{5}$$

where the values of RAND were chosen from a normal distribution with the mean = 0 and standard deviation = s. The connectance C (≤ 1) had been introduced by zeroing a certain number of randomly chosen off-diagonal b_{ij}-b_{ji} pairs. Such "competitive matrices" represent models of quite general multispecies competitive communities.

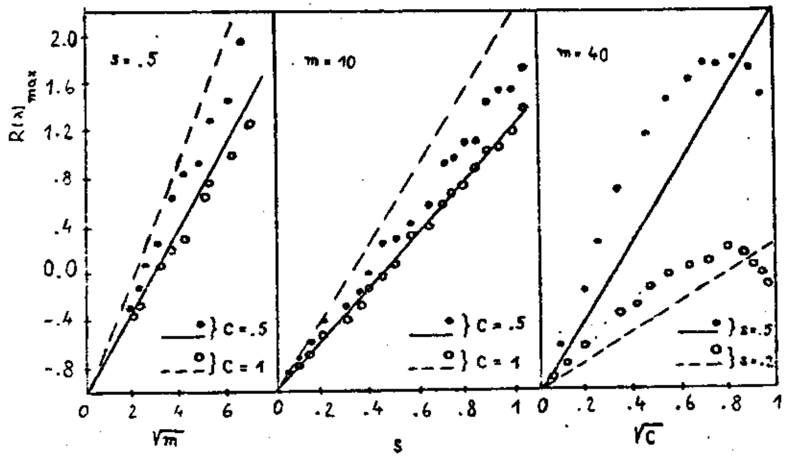


Fig. 2. The mean largest real parts, $R(\lambda)_{max}$, of eigenvalues of competitive matrices (see (5) for construction) against $\sqrt{m}$, s and $\sqrt{C}$. The circles are results of our simulations, the lines are May's prediction.

We have determined the largest real parts, $R(\lambda)_{max}$, of eigenvalues of interaction matrices B consisting of the elements defined in (5). Samples of

200 matrices were generated for each selected combination of m, s and C values. Results of this analysis are presented in Fig. 2. The dependence of mean $R(\lambda)_{max}$ on $\sqrt{m}$ and on s is positive and linear, differing more or less from May's prediction, depending on connectance. On the contrary, the relationship between mean $R(\lambda)_{max}$ and $\sqrt{C}$ is conspicuously non-linear and partly in direct contradiction to May's rule. Not only does it indicate decrease of stability until connectance $\sqrt{C} \doteq 0.8$ is achieved, but it also indicates an increase in stability (decrease of mean $R(\lambda)_{max}$ with the subsequent increase in C.

In the same way as Gardner and Ashby (1970), we have expressed the proportion of stable systems A and B (estimate of P_{stab} of A and B) against C for three different m values (see Fig. 3). The extent of the interval of C within which P_{stab} increases with C depends on m, s and b_{ii}. In Fig. 3, s = 0.4 and b_{ii} = -1.

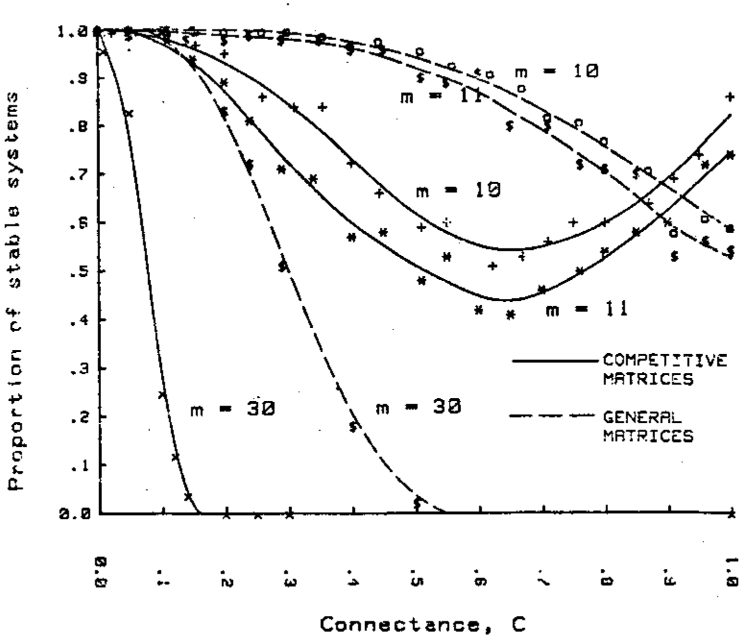


Fig. 3. Proportion of stable systems against connectance for general and competitive matrices (see (3) and ([illegible]) for construction). Each point represents the proportion of stable matrices in a sample of 200 matrices.

For m = 10 and for m = 11 the increase of stability with increasing connectance for higher values of connectance is obvious. For m = 30 and higher values of connectance, the probability of stability is zero. There also occurs decrease of $R(\lambda)_{max}$ in higher values of connectance, but $R(\lambda)_{max}$ remains positive. But if suitable s or b_{ii} were chosen, the same phenomenon could be observed for m = 30 or for any other m. Furthermore, from Fig. 3. it is evident that a more complex competitive system, i.e., a more connected system having more species (m = 11 and C = 1 in our case) may be more stable than a simpler one (i.e. the system with m = 10 and C being about 0.6).

By contrast to the trophic webs, the values of C under discussion (within the interval $\langle 0.6;1\rangle$) are not rare in real competition communities.

Many natural systems are organized in such a way that the zeros are not distributed symmetrically along the main diagonal of the interaction matrix, i.e., that not only competitive but also amensalistic interactions occur in the system. In this case, our computer simulations resulted in a similar qualitative behaviour as that shown in Figs. 2 and 3: increase of stability with complexity in some cases. Moreover, such systems are a better subject for analytical investigation than pure competitive ones.

I shall restrict my analysis only to the critical case of the transition from stable to unstable systems. As I shall show, this transition occurs for the values Cms^2 not being very large in the competitive/amensalistic systems, too. Moreover, it is clearly seen that if for given C, m and s the corresponding matrix is almost certain to be unstable, then a random matrix with the same rank and connectance and standard deviation $s' > s$ is almost certain to be unstable, too. Therefore, I shall assume that there exists such a constant K, $\infty > K > 1$, that for each matrix under question $Cms^2 < K$. The matrices excluded are almost certain to be unstable.

Let the elements b'_{ij} of the "competitive/amensalistic" matrix B' be chosen in the same way as the elements of B with the exception that the zeros are distributed entirely randomly and asymmetrically along the main diagonal:

$$b'_{ij} \begin{cases} = 0 \text{ with the probability } 1 - C, \\ \neq 0 \text{ with the probability } C, \text{ then} \\ \quad b'_{ij} = -|X|,\ X \sim N(0, s^2), \\ = -1 \text{ for } i=j. \end{cases} \Bigg\} \text{ for } i \neq j \qquad (6)$$

The mean of the elements b'_{ij} is $\mu = Cs\sqrt{2/\pi}$ for $i \neq j$ and -1 for $i=j$. The variance of the elements b'_{ij} is $\sigma^2 = Cs^2(1 - 2C^2/\pi)$ for $i \neq j$ and 0 for $i=j$. We shall denote the eigenvalues of B' as $\lambda'_1, \lambda'_2, \ldots, \lambda'_m$. Let $A' = B' + \mu I_m$, where μ is the mean of non-diagonal elements of B' and I_m is a matrix of rank m, all elements of which are equal to 1. The mean of the elements a'_{ij} of the matrix A' is 0 for $i \neq j$ and $\mu - 1$ for $i=j$. The variance of the elements a'_{ij} is the same as that of the elements b'_{ij}. I shall denote the eigenvalues of A' as $\lambda_1, \lambda_2, \ldots, \lambda_m$. On the basis of McMurtrie's and our simulations we may assume that the eigenvalues of A' lie, for $m \gg 1$, in a uniform-density disc with the centre $\mu - 1$ and radius $\sigma\sqrt{m} = s\sqrt{mC(1 - 2C^2/\pi)}$.

In order to elucidate the relationship between eigenvalue distributions of A' and B' I shall introduce auxiliary matrices D_1, D_2, D_3 (see Table 1 for definitions). Evidently, the eigenvalues of D_1 are $\lambda'_1 + 1 - \mu$, $\lambda'_2 + 1 - \mu$, ..., $\lambda'_m + 1 - \mu$, 0 and those of D_3 are $\lambda_1 + 1 - \mu$, $\lambda_2 + 1 - \mu$, ..., $\lambda_m + 1 - \mu$, $-\mu m$. The characteristic matrix of D_1, $D_1 - \lambda E_m$, where E_m is the unit matrix of rank m, is equivalent to the characteristic matrix of D_2, $D_2 - \lambda E_m$, which may be obtained from $D_1 - \lambda E_m$ by the addition of μ-multiple of the last column to each of the remaining columns and subsequent subtraction of μ-multiple of all the rows except the last one from the last row. It might be easily shown that the mean of each of the random variables

$$\mu \left(\sum_{i=1}^{m} a'_{ij} + 1 - \mu \right) \qquad (6)$$

in the last row of $D_2 - \lambda E_m$ is zero and the variance of each of them is $2mC^3s^4(1 - 2C^2/\pi)/\pi$. If Cms^2 is bounded by a constant K, $0 < C \leq 1$, and

Matrix	Elements	
D_1	$_1d_{ij}$	$= b'_{ij} = a'_{ij} - \mu$, for $i,j = 1,2,\ldots,m$, $i \neq j$
	$_1d_{ii}$	$= b'_{ii} + 1 - \mu = a'_{ii} + 1 - 2\mu$, for $i = 1,2,\ldots,m$
	$_1d_{m+1,j}$	$= 0$, for $j = 1,2,\ldots,m+1$
	$_1d_{i,m+1}$	$= 1$, for $i = 1,2,\ldots,m$
D_2	$_2d_{ij}$	$= a'_{ij}$, for $i,j = 1,2,\ldots,m$
	$_2d_{ii}$	$= a'_{ii} + 1 - \mu$, for $i = 1,2,\ldots,m$
	$_2d_{m+1,j}$	= defined by (6), for $j = 1,2,\ldots,m$
	$_2d_{i,m+1}$	$= 1$, for $i = 1,2,\ldots,m$
	$_2d_{m+1,m+1}$	$= -\mu m$
D_3	$_3d_{ij}$	$= a'_{ij}$, for $i,j = 1,2,\ldots,m$
	$_3d_{ii}$	$= a'_{ii} + 1 - \mu$, for $i = 1,2,\ldots,m$
	$_3d_{m+1,j}$	$= 0$, for $j = 1,2,\ldots,m$
	$_3d_{i,m+1}$	$= 1$, for $i = 1,2,\ldots,m$
	$_3d_{m+1,m+1}$	$= -\mu m$

Table 1. Definitions of auxiliary matrices D_1, D_2 and D_3.

$m \to \infty$, this variance tends to zero. (The term $2C(1 - 2C^2/\pi)/\pi$ is bounded by a constant $2/\pi$, $(Cms^2)^2 < K^2$). The matrices D_2 and D_3 differ only in the elements $_2d_{m+1,j}$, $_3d_{m+1,j}$ for $j = 1,2,\ldots,m$. The mean of each of these elements is zero and the variance approaches zero if $m \to \infty$. It follows from the continuous dependence of the eigenvalues of a matrix on its elements that, for $m \gg 1$, the eigenvalues of D_2 differ only little from those of the matrix D_3. The eigenvalues $\lambda_i + 1 - \mu$ of D_3 lie in a uniform-density disc with the centre 0 and radius $\sigma\sqrt{m}$; the eigenvalue $-\mu m$ is real and lies outside the disc for $C > 0.5(-m + \sqrt{m^2 + 2\pi})$, i.e. for nearly all possible connectances, which may be derived from the expressions for μ and $\sigma\sqrt{m}$. The eigenvalues of D_1 differ only little from those of D_3 for $m \gg 1$; therefore we may assume that the asymptotic eigenvalue distribution of D_1 is, for $m \gg 1$, the same as that of D_3. Finally, it follows from these considerations that the asymptotic eigenvalue distribution of B' is, for $m \gg 1$, a uniform-density disc in the complex plane with the centre $\mu - 1$ and radius $\sigma\sqrt{m}$. For $C > \frac{1}{2}(-m + \sqrt{m^2 + 2\pi})$ there appears one isolated eigenvalue outside this disc of the magnitude about $-\mu m + \mu - 1$.

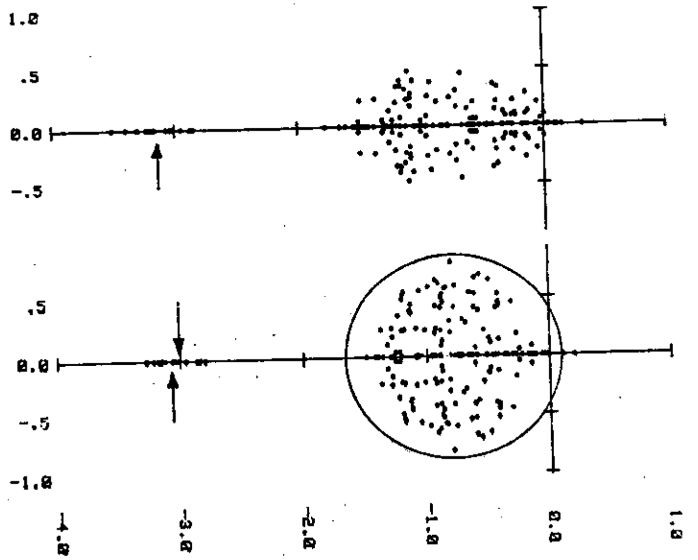


Fig. 4. The eigenvalue distribution of 20 competitive (upper graph) and 20 competitive/amensalistic (lower graph) matrices. In both samples, the rank, standard deviation and connectance were chosen m = 10, s = 0.4 and C = 0.7. The diagonal elements were equal to -1. The circle indicates our estimate of the eigenvalue distribution; ↓ is our estimate of the position of the isolated eigenvalue, ↑ are the actual means of the isolated eigenvalue.

The estimate of the eigenvalue distribution of the competitive/amensalistic matrix B' was in quite a good agreement with the results of our simulations even for m being quite small (see Fig. 4). The flattening of the eigenvalue distribution of competitive matrices is not an artefact which has occured in Fig. 4, but a general phenomenon. It may be attributed to a certain symmetry of competitive matrices - to the symmetrical distribution of their zero elements - which "pushes" the eigenvalues in the direction to the real axis.

By using the expression for μ we obtain an expression for λ_m in the original terms C, m, s:

$$\lambda_m \doteq -\mu m + \mu - 1 = (1 - m)\sqrt{2/\pi}\, sC - 1. \tag{7}$$

Further, all the complex numbers lying inside the disc with the centre $\mu - 1$ and radius $\sigma\sqrt{m}$, as well as the number $-\mu m$, have their real parts less than $\mu - 1 + \sigma\sqrt{m}$. Therefore, we may write an inequality for the greatest real part of the eigenvalues of the competitive/amensalistic matrix B', for $R(\lambda)_{max}$:

$$R(\lambda)_{max} < \mu - 1 + \sigma\sqrt{m} \tag{8}$$

By using the expressions for μ and σ we obtain that

$$R(\lambda)_{max} < s\left(C\sqrt{2/\pi} + \sqrt{Cm(1 - 2C^2/\pi)} \right) - 1 \tag{9}$$

For a given m, the actual expectation of $R(\lambda)_{max}$ is somewhat less than the just mentioned upper bound for $R(\lambda)_{max}$, due to the finite number - m - of the eigenvalues. By using the uniformity of the eigenvalues distribution in the above-mentioned disc a rather formidable relation for the expectation of $R(\lambda)_{max}$ may be derived:

$$E(\,R(\lambda)_{\max}(B')\,) = \int_{-R}^{R} x \frac{d}{dx}\left[\frac{2}{\pi R^2}\int_{-R}^{x}\sqrt{R^2 - y^2}\,dy\right]^{m-1} dx - 1, \qquad (10)$$

where $R = s\sqrt{mC(1 - 2C^2/\pi)}$.

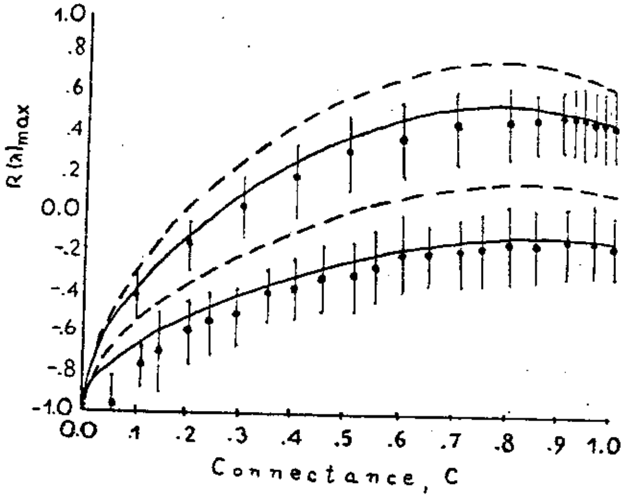


Fig. 5. Maximum real part of eigenvalues, $R(\lambda)_{max}$, against connectance, C, for competitive/amensalistic matrices; $s = 0.4$, $m = 11$ and $m = 30$. Expectation of $R(\lambda)_{max}$ (eq. (10)) is represented by solid curves, upper bound for $R(\lambda)_{max}$ (eq. (9)) by broken curves, points indicate mean values and vertical bars standard deviations of $R(\lambda)_{max}$ obtained by simulations. Each point corresponds to 200 randomly filled matrices.

In Fig. 5 it is shown the comparison of the expectation of $R(\lambda)_{max}$ and of the upper bound for $R(\lambda)_{max}$ with the result of our numerical simulations. The decrease of $R(\lambda)_{max}$ for higher values of connectance is obvious. The same phenomenon as in May's and McMurtrie's figures of the dependence of $R(\lambda)_{max}$ on C occurs in this figure: the eigenvalues obtained by the simulations are slightly less than those predicted by the expression for $R(\lambda)_{max}$. It is a consequence of the fact that the expectation of $R(\lambda)_{max}$ is only an asymptotical estimate valid for $m \gg 1$.

Another interesting fact follows from this analysis: the existence of a real negative isolated eigenvalue with a great magnitude of about $(1 - m)\sqrt{2/\pi}\ sC - 1$. The existence of a real negative eigenvalue with its absolute value equal to the spectral radius of a matrix with negative off-diagonal elements and zeros on its diagonal is predicted also by the Perron-Frobenius theorem. Our findings are in accordance with this theorem, but in our case the absolute value of this eigenvalue is much greater than the absolute values of the remaining $m - 1$ eigenvalues in most cases. This phenomenon demonstrates that between discrete competitive or competitive/amensalistic systems and their continuous counterparts there is a much greater difference in stability than between discrete and continuous systems generated entirely randomly (as by McMurtrie and May). In such competitive or competitive/amensalistic discrete systems an increase of stability within the interval of higher values of connectance does not occur because of the existence of the above mentioned eigenvalue (see Figs. 6 and 7). For example, the shape of the curve for discrete model and $m = 15$ in Fig. 6 is nearly the same as the shape of the curve for discrete model and $m = 10$ in Fig. 7, i.e. for smaller number of species, though the value of s is smaller, too. On the contrary, the shapes of the corresponding curves for continuous models are quite different, especially for higher values of connectance.

The equilibria of our systems were not checked for positivity. But following the way of Goh and Jennings (1977) step by step, it may be easily shown that also the subset of competitive or competitive/amensalistic Lotka-Volterra systems, each of which has a feasible equilibrium, has the

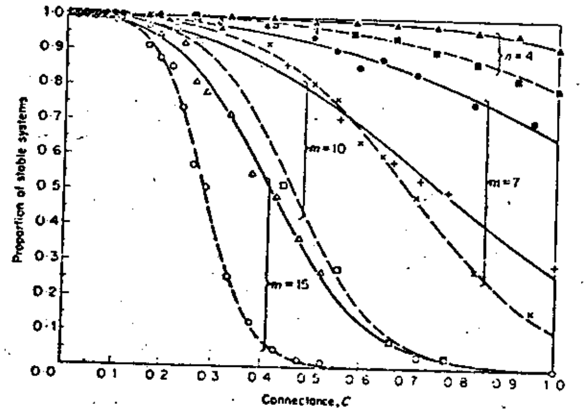
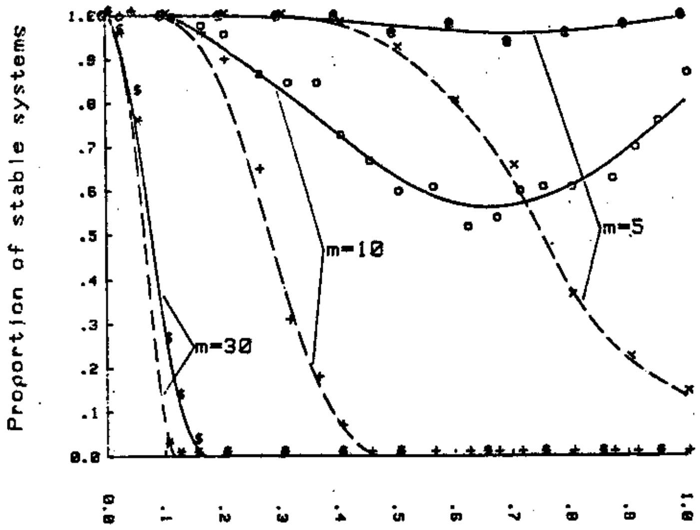


Fig. 6. Proportion of stable systems against connectance for continuous (solid curves) and discrete (broken curves) general systems (see (3) for construction). Each point corresponds to 200 randomly filled matrices. The value of s was chosen s = 0.5.

same stability property as a set of linear competitive or competitive/amensalistic systems which is assembled randomly in the same manner.

Moreover, these findings provide a new insight into the results of stability analysis of 40 real food webs presented recently by Yodzis (1981). He concluded that simulative increase of the proportion of interspecific competitive interactions "usually exerts a destabilizing influence". Five exceptions from this trend (webs nos. 2, 12, 13, 14 and 15 in his table 3) may result from the stabilizing influence of increasing competitive connectance. Only the species richness and structure of these five webs lie within the interval in which the stabilizing influence of increasing



Connectance, C

Fig. 7. Proportion of stable systems against connectance for continuous (solid curves) and discrete (broken curves) general systems (see (5) for construction). Each point corresponds to 200 randomly filled matrices. The value of s was chosen s = 0.4.

competitive connectance can manifest itself.

COMPARISON OF THE KNOWN STABILITY CRITERIA

For randomly generated systems, the following stability criteria are known:

1. For general continuous systems there holds the well known May's criterion $Cms^2 < 1$. May's simulations indicate that it is a rather conservative estimate.

2. For general discrete systems, May's criterion is rather optimistic.

Kindlmann and Rejmánek (1982) have developped another, very conservative criterion for discrete general systems: $Cm(m-1)^3s^2 < 1$.

3. In this paper there were derived rather conservative stability criteria for discrete and continuous competitive/amensalistic systems (see also Rejmánek, Kindlmann and Lepš, 1983). Our simulations have exhibited that the competitive systems are less stable than the competitive/amensalistic ones, but the difference between them is very small. Therefore, the criteria for competitive/amensalistic systems may approximatively be applied to the competitive systems, too.

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