The Stability of Ecosystems*

Tad Hogg, Bernardo A. Huberman and Jacqueline M. McGlade

Abstract

Stability criteria and phase boundaries for complex ecosystems are obtained and contrasted with previously studied scenarios. The stability of such systems is determined by the behavior of the largest eigenvalue of matrices governing the response of the system to small perturbations. As a result we show that ecologies with unstructured cooperative interactions between arbitrary species can be less stable than had been previously determined. We also investigate hierarchical ecologies, and demonstrate their increased stability under certain conditions.

1 Introduction

The stability of complex ecosystems is central to the study of communities of interacting components in fields such as ecology, sociology and distributed computation. Generally, the components investigated in such ecologies consist of species [19, 23, 15], human groups [14, 36] and computational processes [16], respectively, linked through various kinds of interactions. Existing results, such as those of Gardner and Ashby [12], May [22, 23], McMurtrie [27], Pimm [35], and Ulanowicz [37], have established criteria for the stability of ecosystems under certain restrictive conditions, such as zero-sum games. In particular, they have shown that an ecosystem can become unstable against weak perturbations when its complexity increases beyond a certain value, although the transition is not always sharp [5].

However, it was recognized that many of these theoretical results contradicted observations of real ecosystems; this, plus the fact that weak links in a food web were often removed in the construction of a community web, using arbitrary decisions [24], led may ecologists to focus on more mechanical bases for stability, such as predator-prey interactions and competition for resources [31, 4, 7, 8, 9, 6].

In this paper we return to the original problem set out by May and others, and derive a condition of stability for more general systems, as a function of species diversity and the strength of interactions. In the case of non-hierarchical organizations, we show how the removal of a zero-sum game condition can in fact lead to a further reduction of stability and compute the stability boundaries in a number of cases. We then look at the issue of stability in the context of ecosystems with pyramidal organization, and demonstrate that they are intrinsically more stable than unstructured ones.

2 Ecosystems as Food Webs

Ecosystems are often portrayed as food webs or graphs in which all the trophic relations between component species are given [32, 35]. Species can also be grouped into a hierarchy or tree of trophic levels or size spectra [10, 21, 33], a useful abstraction because it facilitates an understanding of the flow of matter and energy through a community and underscores those biological differences in interactions within and between levels, such as the difference between competition for resources and predation. Because of the impacts of pollution and environmental change on the living world, the concept of stability (i.e., the resilience of food webs to perturbations that are either internal or external to the system), has been germane to the argument of how best to depict ecosystems. A common assumption is that the webs observed in nature are the stable forms: the unstable ones having disappeared with time [20]. Similar stability concerns arise in large networks of interacting computers.

*appeared in *Proc. of the Royal Society of London* **B237**, 43–51 (1989)

2.1 Symmetric Matrices

Continuing on from the work of Gardner and Ashby [12], May [23] suggested that the stability of a community plus other attributes, such as rates of energy fixation and flow, turnover efficiencies, diversity and succession, could be examined through an analysis of the type and strength of interaction between species (i.e., their connectance), as given by a random graph or matrix. The values within the interaction matrix could thus be made to reflect competition within and between different levels or size spectra. By resorting to rigorous results concerning the eigenvalues of a particular type of random matrices, i.e., those that have zero-mean in their distributions, he established a criterion for their stability. For an ecosystem whose interactions near equilibrium are such that on the average the benefit accrued by one species is equal to the loss of the other (i.e., zero-sum game), instability sets in when its complexity–measured by the number of species–exceeds a certain bound. Subsequent work [27, 38, 34, 7] extended these results into Monte Carlo studies of stability, and into food webs and chains, while keeping the simplifying assumptions of May [23]. In all these instances, as the complexity increases the ecosystem becomes unstable.

Ecosystems however, are seldom organized along the lines of zero-sum games, as May and others have pointed out; for example there is much evidence to suggest that organisms can learn from experience, which on the whole would generate a much more complicated and hierarchical structure [26]. Thus it is imperative to determine the stability of ecosystems under such general conditions, non-zero sum games, asymmetry of interactions, hierarchical organization, and complexity.

To do this, we consider a community of n species whose interactions are described by weighted links connecting n nodes representing the different species. Furthermore, we assume that any external constraints change slowly over characteristic times of the system. In this case, the evolution of the system is characterized by an autonomous dynamical equation that can be generically written as

$$\frac{d\mathbf{u}}{dt} = \mathbf{f}(\mathbf{u}) \tag{1}$$

where $\mathbf{u}$ is an n-dimensional vector describing the number of each species in the system, and $\mathbf{f}$ is a function that specifies their interrelated growth or decay. This equation produces a number of fixed points whose stability we now investigate. In particular we assume that there exists such a fixed point, which is a solution of $\mathbf{f}(\mathbf{u}) = 0$ and which we denote by $\mathbf{u}_0$. To investigate its stability we write $\mathbf{u} = \mathbf{u}_0 + \mathbf{x}$ and study how the perturbation $\mathbf{x}$ grows or decays in time. Expanding Eq. (1) in a Taylor series expansion around $\mathbf{u}_0$, and remembering that $d\mathbf{u}_0/dt = 0$, gives the linearized matrix equation

$$\frac{d\mathbf{x}}{dt} = M\mathbf{x} \tag{2}$$

where M is the Jacobian $\partial\mathbf{f}/\partial\mathbf{u}$ evaluated at $\mathbf{u}_0$. From the formal solution of this equation it follows that the stability of the fixed point is solely determined by the eigenvalue of M with the largest real part, which we denote by E. This means that the long-time behavior of the perturbation $\mathbf{x}$ is given by $|\mathbf{x}| \propto \exp(Et)$. Therefore, the probability that the fixed point is stable is just the probability that this eigenvalue is less than zero. If each species independently is stable around this fixed point, the diagonal elements of M must be negative, which we can choose to be -1 by appropriate choice of scale. Thus $M = A - I$ where I is the identity matrix and the diagonal terms of A are all zero. Note that $E = R - 1$, where R is the largest real part of the eigenvalues of A.

Because the value of R will depend on the specific choice of the interaction matrix A, we consider instead typical values obtained for various kinds of interacting systems rather than for individual ones. A particular kind of interaction defines a class of possible matrices. The probability that such interactions lead to stable behavior is then defined as the fraction of matrices in the class for which R is less than one. In this paper we will consider interactions corresponding to unstructured ecologies as well as hierarchically structured situations.

Previous studies of such systems have considered the case in which the interactions have zero mean [12, 23, 35, 37, 5]. That is, each nondiagonal term of A is chosen from a random distribution which has zero mean and variance σ^2. Hence, on average, the species interact as in a zero-sum game, i.e., the benefit accrued by one is equal to the loss of the other. For this case, it was shown that R is given in terms of the number of nodes n by the Wigner's semicircle law [39, 28], i.e., $R = 2\sigma\sqrt{n}$ for large n. This implies that typical systems become unstable as their sizes exceed a value of n given by

$$n > \frac{1}{4}\sigma^2 \tag{3}$$

Although in some cases this transition will be sharp (i.e., almost all systems will go unstable at this point), more generally the loss of stability will take place for different systems at a range of values of n around this bound [5].

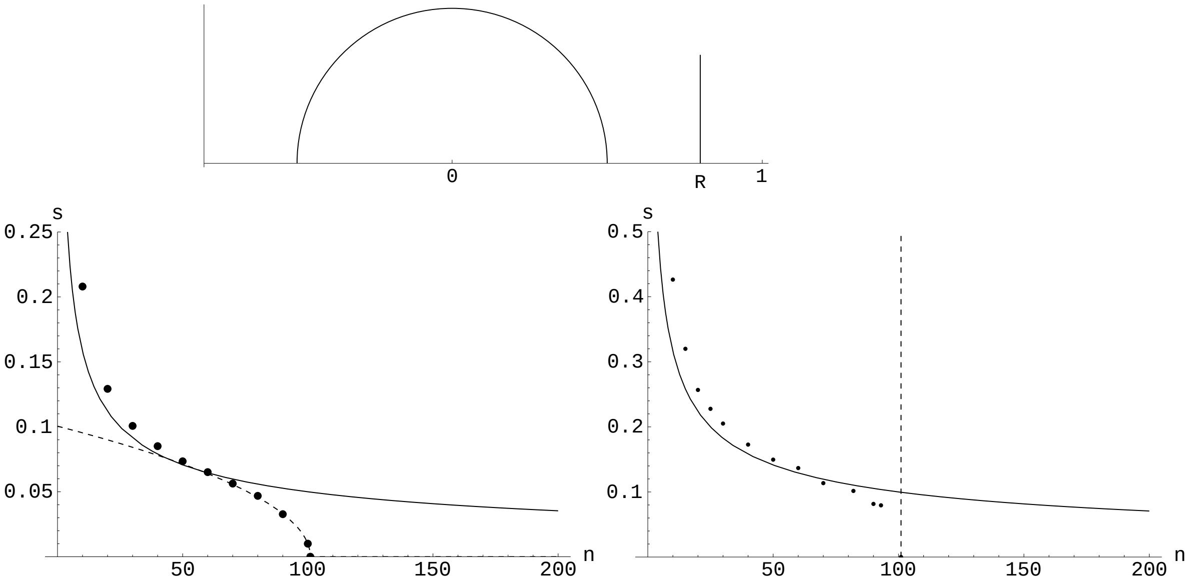

Figure 1: (a) Distribution of eigenvalues for large symmetric matrices with positive mean. The largest eigenvalue R splits off from the semicircle law maximum. Instabilities set in when R crosses the value 1. (b) Stability regions for symmetric ecologies with $m = 0.01$. Vertical axis: the standard deviation in the matrix elements. The solid curve is that predicted by Eq. (3), whereas the dotted one corresponds to Eq. (5). The points correspond to results of computer evaluation of the eigenvalues. (c) Same as (b) but for asymmetric interactions. Notice the difference in scales. Solid curve is the generalized Wigner law, and the dotted one is from Eq. (6).

We now consider several realistic improvements of the original model and show how stability is affected by having cooperative behavior in the system. This corresponds to the case when the overall benefit to be accrued by the entities exceeds the collective cost (i.e., a cooperative situation). In what follows, we first assume that the interactions are symmetric and bounded but with nonzero mean . For these interactions, the matrix A is symmetric, with entries chosen from a random distribution with nonzero mean μ. In this case, on average [11],

$$R = (n-1)\mu + \frac{\sigma^2}{\mu} \tag{4}$$

when μ is positive, to order $1/\sqrt{n}$, while all other eigenvalues remain within bounds of the semicircle law. Moreover, R is normally distributed around this value with variance $2\sigma^2$. This peeling off of the largest eigenvalue from the semicircle law is illustrated in Fig. 1a. Because of the non-zero variance, they will become unstable for a range of values of n around

$$n > 1 + \frac{\mu - \sigma^2}{\mu^2} \tag{5}$$

This result implies a shift towards a less stable situation, i.e., the system becomes unstable as it grows but at a lower threshold than in the zero-mean case. This can be observed in Fig. 1b where we plot the stability regions implied by the two theories along with results of computer evaluations that confirm their validity. As can be seen, there is a crossover between behaviors predicted by Eq. (3) and (5). Conversely, if μ is negative the system's stability will be determined by the criterion of Eq. (3) because the peeling eigenvalue is negative and the others remain within the semicircle to determine stability.

To elucidate the implications of these different models we consider the specific case studied by May [22], in which each species need not interact with all the others in the ecosystem. In this case, let p be the probability that any two species interact. As in the previous case, the strength of each existing link is taken from a distribution with mean m and variance s^2. Therefore, the corresponding matrix elements will have $\mu = mp$ and $\sigma^2 = s^2 p + m^2 p(1-p)$. We can then write $R = (n-1)mp + s^2/m + m(1-p)$, which should be compared with the zero-mean result, which gives $R = 2s\sqrt{np}$. Thus for fixed mean m and variance s^2, our analysis leads to an onset of instability that occurs much earlier than the case with zero mean, and it scales linearly with n, rather than the square root of it. In particular, unless the interactions are very weak or sparse, and the variance is very small, the system will be unstable for any reasonable value of n.

2.2 Asymmetric Matrices

An even more realistic model of an interacting ecosystem is provided by relaxing the assumption of symmetric interactions. This leads to an asymmetric matrix A for which the above results do not directly apply. In this case the stability of the ecosystem is determined by the largest real part of any eigenvalue. In the zero-mean case the generalized Wigner law [28], plus results of Juhasz [18], imply that the largest real part of the eigenvalues cannot scale much faster than $\sqrt{n}$. This implies that the stability is essentially the same as that given by Eq. (3), with the dominant effect of having the largest real part being a factor of 2 smaller than in the symmetric case. For the case of non-zero mean, and non-negative matrix elements, one obtains [18]

$$R = (n-1)\mu + O(\sqrt{n}) \tag{6}$$

which, within the mean-field theory, is the same as that provided by the symmetric case. Notice that even for the case of a general symmetric matrix with positive mean Eq. (6) provides a reasonable approximation. This is shown in Fig. 1c.

3 Ecosystems as Hierarchical Structures

In addition to these considerations, there are other interesting scenarios. For example, as the number of species considered, i.e., n, is increased, there may occur changes in the likelihood or strength of interactions among them. Thus p, the probability of a link existing, or m, the mean strength of interaction, depend on n. This changes the stability criteria we derived above. In particular, if the probability of interaction with a particular species decreases as the number of species increases, stability can be increased. This leads to several structured interactions in the large n limit.

3.1 Interactions between Levels

One important instance of such cases is provided by a hierarchically organized ecology consisting of multiple trophic levels [33]. In this case one expects that the system will become more stable to perturbations, because the corresponding hierarchical clustering tends to reduce the effective number of species interacting with any arbitrary one. Thus the introduction of a hierarchy moves the stability boundary above that of Fig. 1b. Alternatively, this can be thought of as effectively reducing the interaction probability or interaction strength. This increase in stability can be seen from the following argument.

Consider first the tree corresponding to a hierarchical structure, as shown in Fig. 2a. In this case the corresponding interaction matrix is shown in Fig. 2b. For the case of a constant branching ratio b, the number of species with which a given one directly interacts remains constant as the number of species increases. This constrains the structure of the corresponding interaction matrix A. Specifically, each row corresponding to an internal node will have b entries specifying interactions between species, whereas the remaining entries are zero; and rows corresponding to leaves will have a single nonzero entry. This allows us to obtain a bound on the magnitude of the largest eigenvalue of A using Gerschgorin's theorem [40], which states that

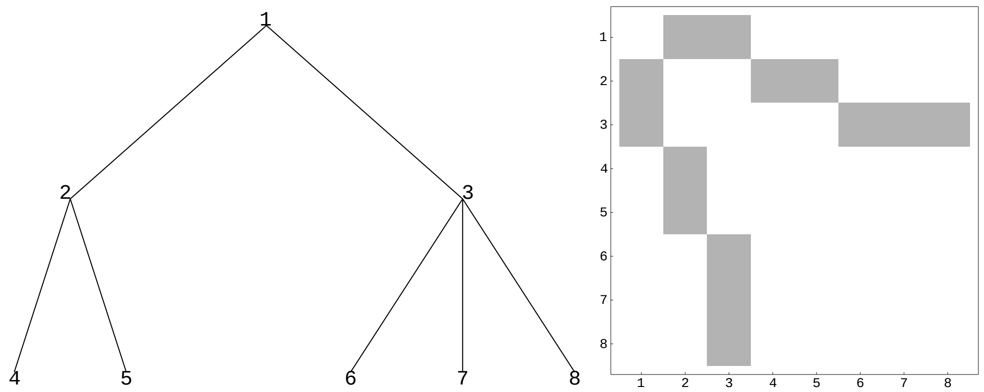

Figure 2: (a) A hierarchical structure. (b) Its corresponding interaction matrix. The shaded regions indicate the location of nonzero interaction values.

all eigenvalues λ of A are bounded by the largest row sum of magnitudes of elements in the matrix, i.e.,

$$|\lambda| < \max_i \sum_j^n |a_{ij}| \tag{7}$$

We now suppose that the magnitude of the interaction strengths, $|a_{ij}|$, are chosen from a distribution with mean $\bar{m}$ and variance $\bar{s}^2$. Note that an interacting system will have $\bar{m} > 0$. Thus, typically, the sums appearing in Eq. (7) for internal nodes will be normally distributed with mean $\bar{m}b$ and variance $\bar{s}^2 b$. The expected maximum value of the sum [29] over all n rows will then be given by

$$\langle|\lambda|\rangle < \bar{m}b + \bar{s}\sqrt{2b\ln n} \tag{8}$$

where we have increased and simplified the bound by replacing the contribution from the leaf nodes with the larger contribution from internal nodes. Because this grows much more slowly with n than Eq. (3) or (5), it illustrates the fact that hierarchically organized ecosystems are more stable than the unstructured organizations discussed above.

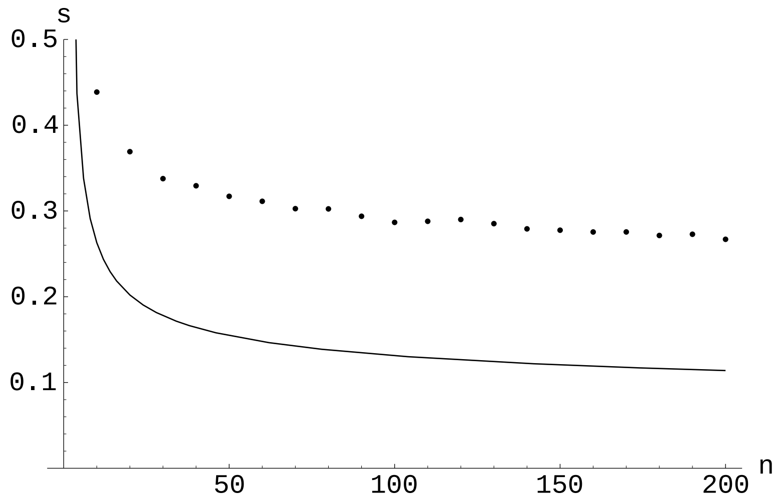

Figure 3: Stability region for a random hierarchical ecology with $\bar{m} = 0.01$. Solid curve: bound predicted by Eq. (9). Points are the actual stability boundary for symmetric interactions. Asymmetry produces a bound twice as high for these values of n.

These results assume the validity of a mean-field treatment of the structure i.e., one only needs to consider the average branching ratio of the tree. For systems which are less uniform a different stability criterion applies. Suppose that the hierarchical structure is that of a random tree. In this case the largest number of branches for any node grows as $\ln n / \ln \ln n$ [30] and a simplified upper bound on the row sum is provided by replacing b in Eq. (8) by $\ln n$. We thus have

$$\langle |\lambda| \rangle < (\bar{m} + \bar{s}\sqrt{2}) \ln n \tag{9}$$

This means that for a random system, structural fluctuations can cause it to be less stable than the regular tree, but still much more stable than the graphs representing non-hierarchical systems, as shown in Fig. 3. All of these stability results are summarized in Table 1.

Stability Bounds

	structure	regularity	mean	scaling
i)	graph	random	< 0	$\sqrt{n}$
ii)	graph	random	> 0	n
iii)	tree	regular		$< \sqrt{\ln n}$
iv)	tree	random		$< \ln n$

Table 1: Stability results for generic structures composed of n interacting entities. Scaling column shows how rapidly stability is lost as the system gets larger for fixed interaction strength.

3.2 Interactions within and between Levels

Finally, we consider the general system in which there is an overall hierarchical structure but each node of the tree corresponds to a collection of interacting species at the same level. In this case there may be interactions between parts of the tree at the same level, as well as between levels. A simple model would consider such a system to be a hierarchical structure in which the nodes of the tree correspond to the unstructured systems considered previously (i.e., macronodes). Depending on the relative strengths of the additional interactions, the instability could either develop locally, i.e., in a macronode when there are large interactions within a particular level, or globally throughout the tree if the extra interactions between levels are significant. Recently, Bachas and Huberman [1] related the complexity of the detailed structure of the hierarchy, as measured by its diversity [17, 3], to its dynamical behavior. This result suggests that there might be a quantifiable relationship between the diversity of a hierarchical structure and its stability, which remains to be investigated. Furthermore, recent results [2] suggest that the effective dimensionality of the space in which the interactions takes place and the overlap in food webs contribute to the nature of the structural representation of the community. We thus conclude that their stability will likewise be affected.

In situations where fixed points are no longer stable, other dynamical behaviors can occur, such as cycles and chaos, for which this theory has little to say [6]. Nervertheless, for those cases characterized by fixed points, our results provide a way of analytically extending dynamical studies of communities made up of a few species [13, 25] to larger cases. We have thus established a set of stability criteria for more realistic organizations and shown how hierarchical ones are the most robust. Because of their similarity to ecosystems, our results should also apply to several other systems, such as economic organizations and interacting computational processes.

Acknowledgements

The authors thank S. Rasmussen, R. M. May, F.R.S., and R. E. Ulanowicz for helpful comments and discussions.

References

[1] C. P. Bachas and B. A. Huberman. Complexity and ultradiffusion. *J. Physics*, A20:4995–5014, 1987.

[2] F. Briand and J. E. Cohen. Environmental correlates of food chain length. *Science*, 238:956–960, 1987.

[3] H. A. Ceccatto and B. A. Huberman. The complexity of hierarchical systems. *Physica Scripta*, 37:145–150, 1988.

[4] J. E. Cohen, F. Briand, and C. M. Newman. A stochastic theory of community foodwebs III: Predicted and observed lengths of food chains. *Proc. R. SOc. Lond.*, B228:317–353, 1986.

[5] J. E. Cohen and C. M. Newman. The stability of large random matrices and their products. *Annals of Probability*, 12:283–310, 1984.

[6] D. L. DeAngelis. Strategies and difficulties of applying models of aquatic populations and food webs. *Ecol. Modell.*, 43:57–73, 1988.

[7] D. L. DeAngelis, W. M. Post, and G. Sugihara. Current trends in food web theory. Report 5983, Oak Ridge National Laboratory, 1983.

[8] D. L. DeAngelis, W. M. Post, and C. C. Travis. Positive feedback in natural systems. *Biomathematics*, 15, 1986.

[9] D. L. DeAngelis and J. C. Waterhouse. Equilibrium and nonequilibrium concepts in ecological models. *Ecol. Monogr.*, 57:1–21, 1987.

[10] C. Elton. *Animal Ecology*. Macmillan, NY, 1927.

[11] Z. Furedi and K. Komlos. The eigenvalues of random symmetric matrices. *Combinatorica*, 1:233–241, 1981.

[12] M. R. Gardner and W. R. Ashby. Connectance of large dynamic (cybernetic) systems: Critical values for stability. *Nature Lond.*, 228:784–785, 1970.

[13] M. E. Gilpin and T. J. Case. Multiple domains of attraction in competition communities. *Nature*, 261:40–42, 1976.

[14] M. Granoveter. The strength of weak ties: A network theory revisited. In P. Marsden and N. Lin, editors, *Social Structure and Network Analysis*, pages 105–130. Sage, 1982.

[15] C. S. Holling. Simplifying the complex: the paradigms of ecological function and structure. *Eur. J. of Oper. Res.*, 30:139–146, 1987.

[16] B. A. Huberman, editor. *The Ecology of Computation*. North-Holland, Amsterdam, 1988.

[17] B. A. Huberman and T. Hogg. Complexity and adaptation. *Physica*, 22D:376–384, 1986.

[18] F. Juhasz. On the asymptotic behavior of the spectra of non-symmetric random (0,1) matrices. *Discrete Mathematics*, 41:161–165, 1982.

[19] C. J. Krebs. *Ecology*. Harper and Row, New York, 1972.

[20] R. Lande. Genetics and demography in biological conservation. *Science*, 241:1455–1460, 1988.

[21] R. L. Lindeman. The trophic-dynamics aspect of ecology. *Ecology*, 23:399–413, 1942.

[22] R. M. May. Will a large complex system be stable? *Nature*, 238:413–414, 1972.

[23] R. M. May. Stability and complexity in model ecosystems. In *Monographs in Population Biology*, volume 6. Princeton Univ. Press, 2nd edition, 1974.

[24] R. M. May. Ecology: The structure of food webs. *Nature*, 301:566–568, 1983.

[25] R. M. May. How many species are there on earth? *Science*, 241:1441–1449, 1988.

[26] J. M. McGlade. The evolution of spatially inhomogeneous populations. In W. Wolff, C.-J. Soeder, and F. R. Drepper, editors, *Ecodynamics*, pages 31–39. Springer-Verlag, Berlin, 1988.

[27] Ross E. McMurtrie. Determinants of stability of large randomly connected systems. *J. Theor. Biol.*, 50:1–11, 1975.

[28] M. L. Mehta. *Random Matrices and the Statistical Theory of Energy Levels.* Academic Press, New York, 1967.

[29] Alexander M. Mood, Franklin A. Graybill, and Duane C. Boes. *Introduction to the Theory of Statistics.* McGraw-Hill, New York, 3rd edition, 1974.

[30] J. W. Moon. On maximum degree in a random tree. *Michigan Mathematical Journal*, 15:429–432, December 1968.

[31] L. Nunney. Short-time delays in population models: A role in enhancing stability. *Ecology*, 66:1849–1858, 1985.

[32] E. P. Odum. *Fundamentals of Ecology.* W. B. Saunders, London, 1953.

[33] R. V. O'Neill, D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. A hierarchical concept of ecosystems. In *Monographs in Population Biology*, volume 23. Princeton Univ. Press, 1986.

[34] S. L. Pimm. Food web design and the effect of species deletion. *Oikos*, 35:139–149, 1980.

[35] S. L. Pimm. *Food Webs.* Chapman and Hall, London, 1982.

[36] A. C. Renfrew. Problems in the modelling of socio-cultural systems. *Eur. J. Oper. Res.*, 30:179–192, 1987.

[37] R. E. Ulanowicz. *Growth and Development: Ecosystems Phenomenology.* Springer-Verlag, New York, 1986.

[38] T. L. Vincent and L. R. Anderson. Return time and vulnerability for a food-chain model. *Theor. Popul. Biol.*, 15:217–231, 1979.

[39] E. P. Wigner. On the distribution of the roots of certain symmetric matrices. *Annls Math*, 67:325–327, 1958.

[40] J. H. Wilkinson. *The Algebraic Eigenvalue Problem.* Oxford University Press, 1965.