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PIVOTAL ASSUMPTIONS DETERMINING THE RELATIONSHIP BETWEEN STABILITY AND COMPLEXITY: AN ANALYTICAL SYNTHESIS OF THE STABILITY-COMPLEXITY DEBATE

DANIEL HAYDON*

Department of Zoology, University of Texas at Austin, Austin, Texas 78712

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Abstract.—The relationship between stability and complexity is examined in a class of models that has been used ubiquitously over the last twenty years to generate hypotheses concerning the structure and function of ecological communities. Previously established methods of analysis are examined and questionable assumptions identified. These include the use of "probability of stability" as a relevant measure of stability, the inclusion of unfeasible and unstable models in the Monte Carlo simulation samples, and the treatment of so-called self-regulatory terms in the models. When these models are reanalyzed under less restrictive assumptions, quite different results can be obtained. It is shown that stability (as measured by return time to equilibrium) can increase with various measures of complexity, which include connectivity, interaction strength, and trophic efficiency. Stability is reduced by the prevalence of donor control and by the number of species in a community.. These results can be understood in terms of a very general model by considering the behavior of so-called Gershgorin disks in the complex plane defined by the structure of the Jacobian matrix governing the dynamics around the equilibrium point.

This article addresses the use of a class of models that has been deployed ubiquitously in population and community ecology since the early 1970s to predict the structure of multispecies communities. The key assumption underlying the use of these models has been that communities that are in some sense "stable" will persist and, therefore, will be observed more often than those that are less so. Therefore, identifying structures and processes that enhance the stability of model communities will generate hypotheses concerning the properties of real-world communities. A particular focus of many studies that have used these models has been to elucidate the relationship between the "stability" and the "complexity" of communities. There has been much discussion of what type of stability confers this persistence on communities, on appropriate measures of complexity, and, to a lesser extent, on what assumptions the models make.

Early attempts at formalizing the meaning of ecological stability centered on the temporal constancy of species densities. MacArthur (1955) argued that unusual

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* Present address: Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom.

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variations in a species density would be corrected with least disturbance to other species if the choice of energy pathways through which corrective flows could take place was large. On the basis of this reasoning, MacArthur predicted stability would increase with species number and with the number of interspecific links in a community. Elton (1958, p. 145) perceived simple communities to be "more subject to destructive oscillations in populations . . . and more vulnerable to invasions." Together, these viewpoints laid out a credible and widely accepted intuitive foundation for the traditional ecological wisdom that complexity begets stability.

This paradigm was not seriously challenged until the early 1970s. In a series of papers (Gardner and Ashby 1970; May 1971, 1972, 1974; Daniels and Mackay 1974), it was demonstrated that the probability with which a system of connected linear (or linearized) differential equations possessed a stable equilibrium point decreased with various measures of their complexity. That is to say, such systems tend to be stable not because of, but in spite of, their complexity. The contrast between this mathematical result and the undisputed complexity and evident persistence of real-world ecological communities has been a heuristically productive paradox. However, before this paradox is confronted, three subsidiary questions should be addressed: (1) Is the "stability despite complexity" result both legitimate and robust? (2) Are such simple mathematical models sufficiently accurate representations of the dynamics of real communities that these observations require reconciliation? (3) Is the stability concept implicit in these models one that is relevant to the persistence of real communities? The last two questions remain largely doctrinal and are not easily approachable with any generality. I intend to concentrate largely on the first of these three questions.

THE GENERAL MODEL

Let the population dynamics of the ith species in an n species community be described by the following equation:

$$\frac{dN_i}{dt} = F_i(N_1, N_2, \ldots, N_n), \tag{1}$$

where N_i is the ith species' density, t is time, and F_i is a function describing the rate of change of species i. Solve for the equilibrium populations (N_i^*) by placing the growth rates of each population to zero, and investigate the dynamics around this equilibrium as follows. Let

$$N_i(t) = N_i^*(t) + x_i(t), \tag{2}$$

where x_i measures the initially small perturbation from the equilibrium point. By Taylor-expanding equation (1) around the equilibrium point and by discarding terms of second order and above, the following linearized approximation is obtained:

$$\frac{d\mathbf{x}}{dt} = \mathbf{G}\mathbf{x}, \tag{3}$$

where $\mathbf{x}$ is a vector of displacements from the equilibrium and $\mathbf{G}$ is the Jacobian matrix governing the dynamics around the equilibrium point, with elements

$$g_{ij} = \left.\frac{\partial F_i}{\partial N_j}\right|_{\mathbf{N}=\mathbf{N}^*}. \tag{4}$$

If the eigenvalue with the most positive real part, $\mathrm{Re}(\lambda_d)$, associated with the Jacobian matrix $\mathbf{G}$ is negative, then $x_i(t) \xrightarrow{t\to\infty} 0$, and the perturbation will die out. In this case, the equilibrium point is locally stable. If any of the eigenvalues has a positive real part then the perturbations will grow and the equilibrium is unstable.

The behavior of the model is usually investigated with the use of Monte Carlo simulations. The matrix $\mathbf{G}$ may be constructed in two significantly different ways. First, the elements may be assigned directly by random selection from prescribed distributions, and the equilibrium point *assumed* to be feasible (see, e.g., Gardner and Ashby 1970). This general method will henceforth be referred to as the technique of "direct assignment." Second, the elements may be assigned by calculation of the appropriate partial derivatives associated with a specified set of equations that has been parameterized with values chosen randomly from prescribed distributions, in which case the feasibility of the equilibrium can be established with certainty (see, e.g., Pimm and Lawton 1978).

THE EVALUATION OF STABILITY

The stability of these models has conventionally been assessed in two quite different ways. First, by sampling models with both stable and unstable equilibria, it is possible to calculate the proportion of models that possess stable equilibrium points. A sample of models that contained a higher proportion of stable equilibria would then be deemed to have greater stability than another sample with a lower proportion of stable equilibria (see, e.g., Gardner and Ashby 1970; Daniels and Mackay 1974; DeAngelis 1975). Alternatively, sampling may take place only over the set of models possessing stable equilibria, in which case stability can be assessed as the average time taken for a perturbation to fade to a certain fraction of its original magnitude (referred to as return time and estimated as $-1/\mathrm{Re}(\lambda_d)$; see, e.g., Pimm and Lawton 1978). The return time of these models is a direct measure of how quickly induced oscillations in the species' population densities die out, and it is, therefore, sufficiently close to the concept of stability envisioned by MacArthur and Elton to sensibly address the questions they raise.

As a direct measure of stability, the first of these techniques for evaluating stability is not rationally well founded. If existing real-world communities persist in the vicinity of stable equilibria, the probability with which they exist is not necessarily informative of their stability. Thus, if we wish to know if an existing (and, therefore, stable) complex ecosystem will on the whole be more or less resilient than an existing (and therefore stable) simple one, nothing necessarily relevant is learned from studying the probability with which either is stable. If existing ecosystems do not persist in the vicinity of stable equilibria, there is no logical premise for examining anything related to the stability of these models at all.

May (1974, p. 214) suggested that the probability with which an equilibrium point is stable might be positively correlated with the size of the domain of parameter space wherein it is stable. If this were so, properties of these models would be very easily related to their structural stability (see, e.g., May 1974; DeAngelis 1975; Goh and Jennings 1977; Nunney 1980; Yodzis 1981). However, there is at this time no published evidence that I know of to support the existence of a positive correlation between the structural stability and the probability of the existence of stable equilibrium points in dynamical systems.

Since the probability with which a dynamical system possesses a stable equilibrium point is not a direct measure of stability, and there would appear to be no evidence at present to assume that it is a valid indirect measure of stability, the case for its study is weak. Restricting the investigation of these models to those that possess stable feasible equilibrium points has important consequences for the hypotheses that the use of these models generates.

A NEW APPROACH TO THE ANALYSIS OF SIMPLE COMMUNITY MODELS

In the following analysis, use will be made of the following three theorems.

THEOREM 1. The sum of the eigenvalues of **G** equals the sum of the diagonal elements (the trace) of **G**.

THEOREM 2 (Gershgorin's first circle theorem). Every eigenvalue of **G** lies in at least one of the circles (disks) $C_1, \ldots, C_n$, defined over the complex plane, where C_i has its center at the diagonal entry g_{ii} and its radius,

$$r_i = \sum_{\substack{j=1 \\ j \neq i}}^{n} |g_{ij}|,$$

is equal to the sum of the absolute values of the off-diagonal elements along the rest of the row.

THEOREM 3 (Gershgorin's second circle theorem). If s of the circular disks of Theorem 2 form a connected domain that is isolated from the other disks, then there are precisely s eigenvalues within this connected domain. (Proofs of these theorems may be found in Wilkinson 1965, pp. 71–72.)

If some limited assumptions are made about how the eigenvalues are distributed over the disks referred to in Theorems 2 and 3, it is possible to use these theorems to construct hypotheses relating the behavior of the eigenvalues of a matrix to its structural properties. The critical assumption required to formulate such hypotheses is that the variance of the two-dimensional probability density function (p.d.f.) describing the distribution of the eigenvalues within the disks with respect to the real axis be proportional to the radius of the disks. For the case in which the matrix elements are selected independently from identical Gaussian distributions, this p.d.f. is uniform (Hwang 1986) and the assumption is met. For the case in which the matrix elements are selected from uniform distributions, numerical work (fig. 1) strongly suggests that this assumption will also be met. When the two-dimensional p.d.f. describing the distribution of the eigenvalues within the disks is proportional to the disk radius, it follows that, as the radii of the disks increase, the probability that an eigenvalue takes on a value much higher or lower than its expected value will also increase.

The dynamics of these systems can now be understood by considering the geometry of one or more domains formed by the existence of *n* disks in which *n* eigenvalues are required to fall. Three observations can now be made about the behavior of the largest eigenvalue.

First, consider a two-species case in which both diagonal terms are identically negative (fig. 2*A*). By Theorem 1, the eigenvalues must sum to $2g_{11}$; by Theorem 3, both eigenvalues must fall within the two (overlapping) disks. As the radii of the disks are increased, one eigenvalue is progressively more likely to be more negative than its expected value (g_{11}); thus, the other must be more positive than its expected value, since the two eigenvalues must sum to $2g_{11}$. This more positive than expected eigenvalue will become the eigenvalue that determines the stability of the system. Therefore, the stability of systems known to be stable can be expected to become progressively less so as the radii of the disks increase. As a greater proportion of the disks protrude into the positive real quadrant it would be expected that the relationship between the most positive (but still negative) eigenvalue and the radii of the disks would weaken in a fashion dependent on the nature of the two-dimensional p.d.f. describing the distribution of the eigenvalues within the disks (see fig. 3*Ai*).

Second, consider the two-species example illustrated in figure 2*B* in which the diagonal elements are different. One species is not self-regulated (which causes a zero to appear on the diagonal of the Jacobian), the other is assigned a negative self-regulation term. By Theorem 3, each disk must host precisely one eigenvalue, and they must sum to g_{11}. Assume that the model has a stable equilibrium point (i.e., that both eigenvalues are known to be negative). As the radii of the disks are increased, λ_1 is progressively more likely to be more negative than its expected value (zero); thus, λ_2 must be more positive than its expected value, if the eigenvalues are to sum to g_{11}. However, λ_1 is the most positive eigenvalue, and so, as the radii of the disks increase, a system known to be stable can be expected to become progressively more so (see fig. 3*Aii*).

The cause of the differences in the behavior of the two systems depicted in figure 2*A* and *B* is that, when all the diagonal elements are similar (i.e., the disks are centered in approximately the same place), any excessive negativity in an eigenvalue must be compensated for by an excessive positivity in another eigenvalue lying in the same domain, and so it will become the most positive eigenvalue. If there is variation in the diagonal elements of the matrix (i.e., if some disks are set well back into the negative real quadrant), eigenvalues in these more negatively located domains can compensate for any excessive negativity in eigenvalues residing in disks nearer the positive real quadrant without any chance of becoming the "most positive" eigenvalues themselves. It is transparently obvious in both cases that, as the disks increase in radius, the probability that both

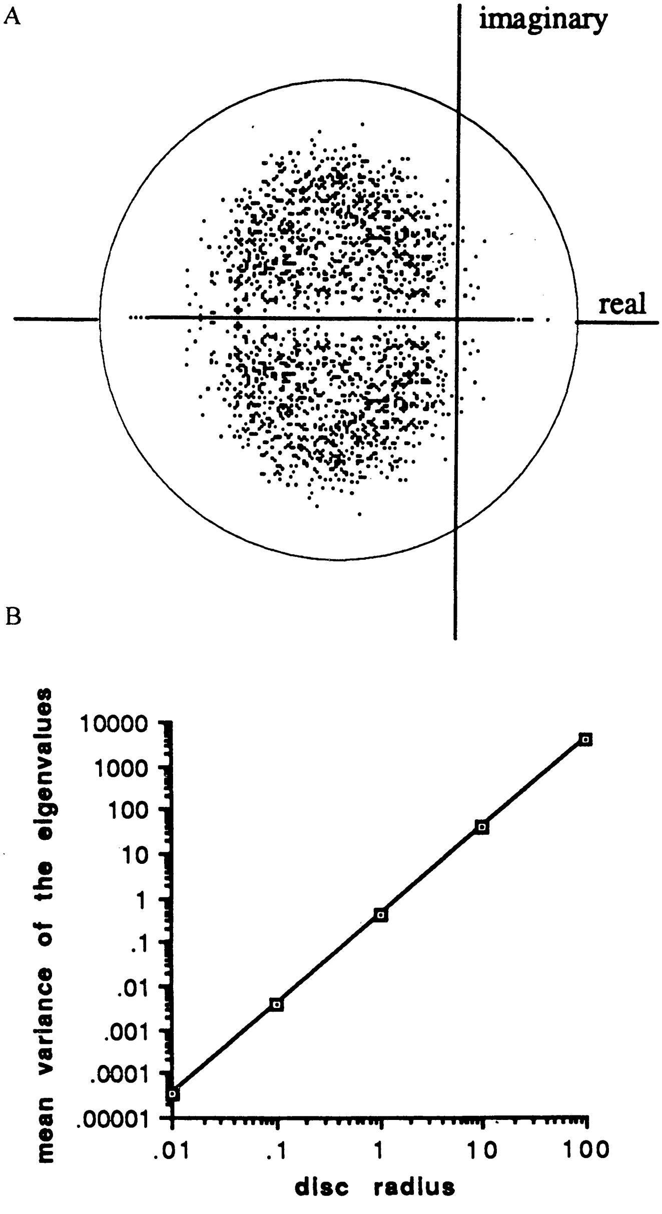

FIG. 1.—*A*, The distribution of the eigenvalues of 500 6 × 6 matrices, falling in six Gershgorin disks of identical radius and positioning. The diagonal elements are assigned the value of -1. Four randomly selected off-diagonal elements from each row were assigned values of v_1 and v_2, selected from uniform distributions $[-z, z]$, and of v_3 and v_4, equal to $\pm (z - |v_1|)$ and $\pm (z - |v_2|)$, where the terms were chosen to be negative (independently) with a probability of .5 and with $z = 1$. *B*, The variance of the p.d.f. describing the distribution of the eigenvalues over the disks increases with the radii of the disks (for $n = 6$, z varies from .005 to 50; off-diagonal elements were assigned in the manner described in *A*).

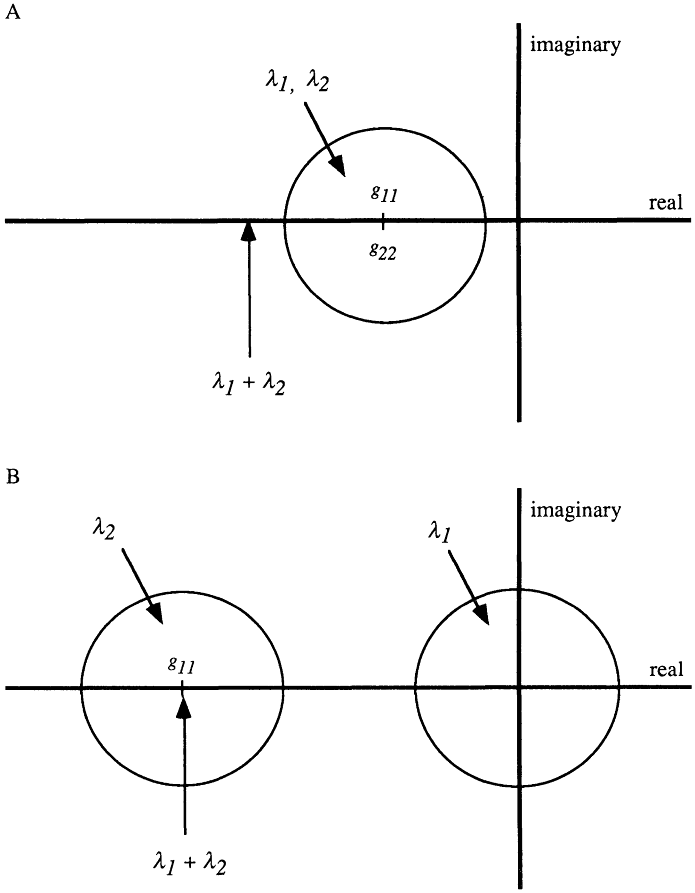

FIG. 2.—*A*, Two Gershgorin disks of the same radius and centered at the same point on the real axis. *B*, Two Gershgorin disks of the same radius; one disk is centered at the origin of the complex plane, the other is set back in the negative quadrant.

eigenvalues will be negative (and the equilibrium point stable) will decrease. It is also clear that, for disks of a similar radius, systems of the type depicted in figure 2*A* will probably be more stable than those of the type depicted in figure 2*B*.

Third, consider now the effect of adding another disk to either system while holding the number and average magnitude of off-diagonal elements constant. If it is centered to the left of the other disks (i.e., if $g_{33} < g_{11}$ and $g_{33} < g_{22}$), it will not, on the average, contribute a more positive eigenvalue than the two disks centered more positively and will not, therefore, determine the equilibrium point's stability. If the additional disk is centered somewhere between the other two disks (i.e., if $g_{22} \leq g_{33} \leq g_{11}$ or $g_{11} \leq g_{33} \leq g_{22}$), the probability of an eigenvalue acquiring a more positive value is increased. It is expected that under these circumstances increasing the number of disks cannot be stabilizing and will normally be destabilizing (fig. 3*Bi* and *Bii*). If for any reason the radii of the disks

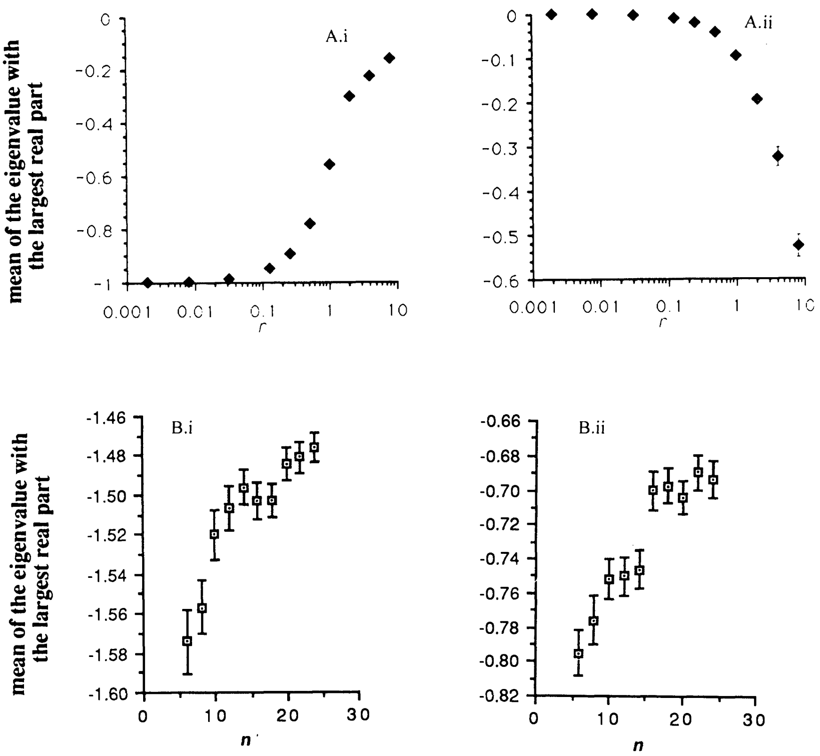

FIG. 3.—*A*, The relationship between the radii of Gershgorin disks (r) and the most positive eigenvalue of 200 6 × 6 matrices known to possess eigenvalues that are all negative: *Ai*, all g_{ii} are equal to -1; *Aii*, half the g_{ii} are equal to -2 and half are set equal to 0. Off-diagonal elements were assigned in the manner described in fig. 1*A* (z varies from .002 to 4). *B*, The relationship between the number of Gershgorin disks (n) and the most positive eigenvalue of $n \times n$ matrices known to possess eigenvalues that are all negative: *Bi*, all g_{ii} are equal to -1; *Bii*, half the g_{ii} are equal to -2, the remaining set is equal to 0. Off-diagonal elements were assigned in the manner described in fig. 1*B* ($z = 1$).

increase with the number of disks, then the outcome could be ambiguous because both stabilizing and destabilizing forces may be at work (such might be the case if the proportion of nonzero off-diagonal elements was held constant as the order of the matrix was increased as for a constant frequency of connectedness).

These observations encapsulate the behavior exhibited by the eigenvalues of a matrix in response to modifications of its elements. By combining these three behavioral components in an additive fashion, the conduct of the eigenvalues can be anticipated in situations intermediate to the extremes considered above. This approach to the consideration of the dynamics of these models is easily generalized to the n species case (at least intuitively). The effects on stability of increasing the radii of the disks depend entirely on the nature of the variability in the diagonal terms. Increasing the number of disks will, under most circumstances, be destabilizing.

GENERATING ECOLOGICAL HYPOTHESES: A SPECIFIC EXAMPLE

The assumption that it is possible to vary a single property of model communities without causing consistent and significant changes in the other parameters or variables of the model permits the straightforward association of ecological processes with the effect they can be expected to have on the radii of the disks. For example, consider a modified n-species generalized Lotka-Volterra model:

$$\frac{dN_i}{dt} = N_i\left(\gamma b_i + \sum_{\substack{j=1 \\ j>i}}^{n} \beta\epsilon a_{ij}N_j - \sum_{\substack{k=1 \\ k<i}}^{n} \kappa\epsilon a_{ik}N_k - a_{ij}N_i\right). \tag{5}$$

The a_{ij} terms are per capita interspecific and intraspecific interaction terms describing the effect of species j on species i, and the b_i terms describe the rates of change of each species in the absence of all other species. Four tuning parameters, γ (proportional to equilibrium population densities), κ (inversely proportional to donor control), β (proportional to ecological efficiency), and ϵ (proportional to interspecific interaction strength) are included so that the per capita effects of prey on predators, predators on prey, and equilibrium population densities (N_i^*) can be independently modified. The model is assumed to represent a community containing only predator-prey interactions and to be organized in a loopless hierarchical structure (this assumption allows the species to be numbered such that the Jacobian can be constructed with all of the negative elements above the diagonal—which permits the use of the summation notation in eq. [5]). The Jacobian governing the dynamics of the system linearized about its internal equilibrium point is

$$\mathbf{G} = \begin{bmatrix} -a_{11}N_1^* & -\epsilon\kappa a_{12}N_1^* & \cdots & -\epsilon\kappa a_{1n}N_n^* \\ \beta\epsilon a_{21}N_2^* & -a_{22}N_2^* & & \\ \vdots & \vdots & \ddots & \vdots \\ \beta\epsilon a_{n1}N_n^* & & \cdots & -a_{nn}N_n^* \end{bmatrix}. \tag{6}$$

If there are increases in the per capita interspecific interaction strengths (by increasing the magnitudes of ϵ), predator efficiency (by increasing the magnitude of β), the average equilibrium population densities (as would occur if there were increases in the levels of primary production or energy flux through the food web, achieved by increasing γ), or connectivity (C, which is defined as the frequency of nonzero elements in the Jacobian), one would expect corresponding increases in the radii of the disks in which the eigenvalues must fall. Similarly, increases in donor control (by decreasing κ) would cause the radii of the disks to decrease. The effect of these changes on the stability of the equilibrium will be determined by the variation in the magnitudes of the intraspecific regulatory terms (the a_{ii}'s) and the shape of the species abundance curve at equilibrium (the $\mathbf{N}^*$ vector).

Figures 4 and 5 illustrate the effect on the average stability of a large number of equilibria known to be both feasible and stable of varying C, n, γ, ϵ, β, and

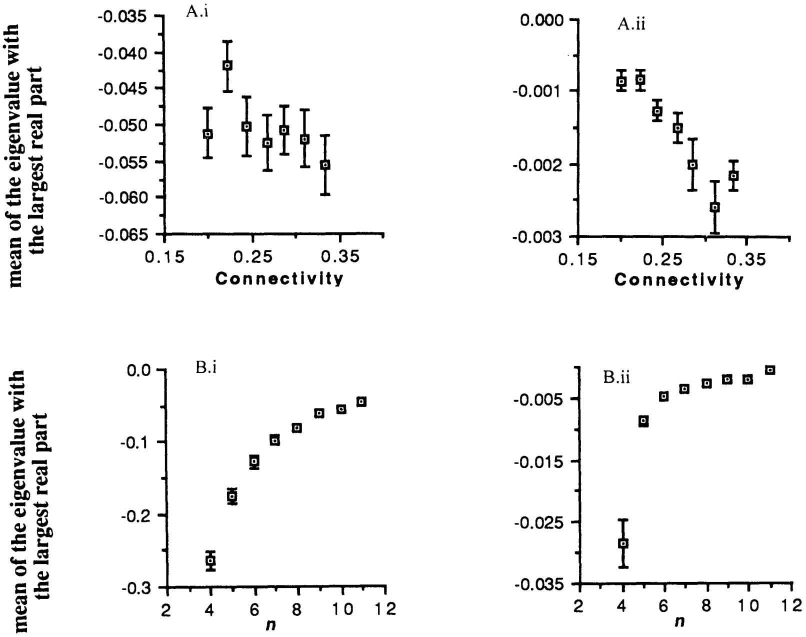

FIG. 4.—*A*, The relationship between connectivity (defined as the frequency of nonzero off-diagonal elements in the Jacobian **G**) and the eigenvalue with the largest real part of feasible food webs with stable equilibrium points; $n = 10$, $\beta = 1$, $\epsilon = 1$, $\gamma = 1$, $\kappa = 1$. *B*, The relationship between the number of species and the eigenvalue with the largest real part of feasible food webs with stable equilibrium points; $C = .467$, $\beta = 1$, $\epsilon = 1$, $\gamma = 1$, $\kappa = 1$. *Graphs in the first column* describe webs in which a_{ii} terms were constructed according to algorithm 1, whereas *graphs in the second column* describe webs in which a_{ii} terms were constructed according to algorithm 2 (see text). In the food web assembly algorithm, two species are designated as autotrophs ($b_i = 1.0$) and $n - 2$ are heterotrophs ($b_i = -.02$); a_{ij} is assigned randomly from a uniform distribution [0.0, 1.0] if *j* is prey to *i*, and [−1.0, 0.0] if *i* is prey to *j*. Feeding relationships are randomly assigned subject to the constraints that the web must not be composed of discrete subwebs, and that there should be no loops of the type *a* eats *b* eats *c* eats *a*. Webs were generated until 200 stable and feasible webs had been assembled.

κ. Simulations were performed with two different algorithms for the construction of the diagonal elements. Algorithm 1 (results on the left-hand side of the panels of figs. 4 and 5) selected species' self-regulatory terms (a_{ii}'s) from the uniform distribution [−constant, 0] (following, e.g., Gardner and Ashby 1970), and algorithm 2 (results on the right-hand side of the panels) selected only autotrophic species' self-regulatory terms from this distribution, whereas heterotrophs were left with no self-regulation (following, e.g., Pimm 1982). The first algorithm was adopted to generate disk structures akin to that depicted in figure 2*A* (variation in the diagonal elements was generated mostly by variation in the equilibrium population densities), whereas the second algorithm should generate a disk structure more like that depicted in figure 2*B* (with some variability in the diagonal

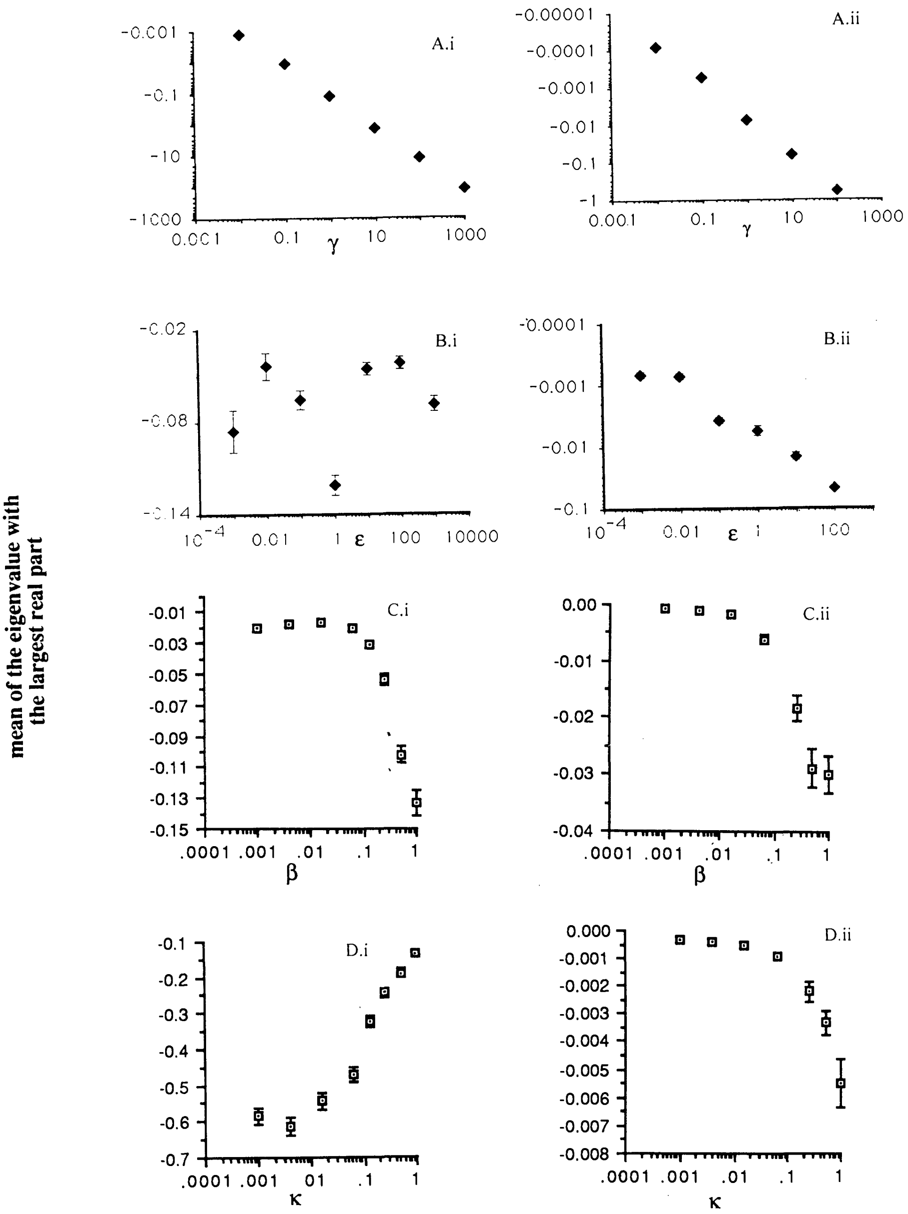

FIG. 5.—*A*, The relationship between γ (as it appears in eq. [5]) and the proportion of known feasible food webs with stable equilibrium points; $n = 6$, $\beta = 1$, $\epsilon = 1$, $C = .467$, and $\kappa = 1$. *B*, The relationship between ϵ (as it appears in eq. [5]) and the eigenvalue with the largest real part of feasible food webs with stable equilibrium points; $C = .467$, $\beta = 1$, $n = 6$, $\gamma = 1$, $\kappa = 1$. *C*, The relationship between β (as it appears in eq. [5]) and the eigenvalue with the largest real part of feasible food webs with stable equilibrium points; $C = .467$, $\epsilon = 1$, $n = 6$, $\gamma = 1$, $\kappa = 1$. *D*, The relationship between κ (as it appears in eq. [5]) and the proportion of known feasible food webs with stable equilibrium points; $C = .467$, $\beta = 1$, $n = 6$, $\gamma = 1$, $\epsilon = 1$. *Graphs in the first column* describe webs in which a_{ii} terms were constructed according to algorithm 1, whereas *graphs in the second column* describe webs in which a_{ii} terms were constructed according to algorithm 2 (see text). The food web assembly algorithm was the same as for the results described in fig. 4.

elements regardless of the equilibrium population densities). The selection of the other parameters in the simulations are detailed in the appropriate figure legends.

When heterotrophic self-regulation terms are set to zero (algorithm 2), stability increases with increasing connectivity (fig. 4*Aii*), equilibrium population densities (fig. 5*Aii*), interspecific interaction strengths (fig. 5*Bii*), ecological efficiency (fig. 5*Cii*), and reduced donor control (fig. 5*Dii*). When heterotrophic terms remain negative (algorithm 1), stability increases with equilibrium population densities (fig. 5*Ai*) and ecological efficiency (fig. 5*Ci*), behaves ambiguously with respect to connectivity (fig. 4*Ai*) and interspecific interaction strength (fig. 5*Bi*), and only decreases with reduced donor control (fig. 5*Di*). As predicted, increasing species number is always destabilizing (fig. 4*Bi* and *Bii*). It would appear that, with these parameter selection procedures and even when the diagonal elements are constructed according to algorithm 1, the diagonal elements of the Jacobian (**G**) generated by equation (5) possess sufficiently high variance that increasing the radii of the Gershgorin disks is generally a stabilizing phenomenon. These results are representative of a large body of simulation work presented elsewhere (Haydon 1992).

Since the radii of the disks are determined by the absolute value of the interspecific interaction terms, this analytic approach can be extended to apply to the stability of general ecological networks (those including competition and mutualism interactions). When there is a sign imbalance in the off-diagonal terms of the Jacobian (or when terms of one sign are consistently larger than terms of the other sign), the mean of the distribution from which the terms are drawn is in effect changed to some nonzero value. Computer simulations show that the effect of such a bias in the off-diagonal terms manifests itself as an asymmetry in the p.d.f., which describes the distribution of the eigenvalues within the disks. When there is a preponderance of positive terms, the distribution becomes positively skewed, which results in a greater likelihood of a more positive eigenvalue (fig. 6*A*); whereas, if the preponderance of terms is negative, the distribution becomes negatively skewed, which results in a greater likelihood of a more negative eigenvalue (fig. 6*B*). The variance of this p.d.f. is still proportional to the radii of the disks, so the proposed techniques are still applicable.

DISCUSSION

When the partial derivatives in the Jacobian are evaluated from the selected parameter values and calculated equilibrium densities (as in the numerical work presented above), establishing the effect of varying a parameter on the stability of an equilibrium point may be confounded because of the difficulty of controlling the position of the equilibrium point while tuning the selected parameter. If the species' equilibrium abundances are highly sensitive to the parameter that is varied, the investigator will be uncertain whether the observed changes in the stability of the equilibrium point are the direct consequence of changing the parameter or the indirect effects of the change in the position of the equilibrium point (the $\mathbf{N}^*$ vector) mediated through the change in the parameter. If the effect of the parameter change on the species' equilibrium population abundances is

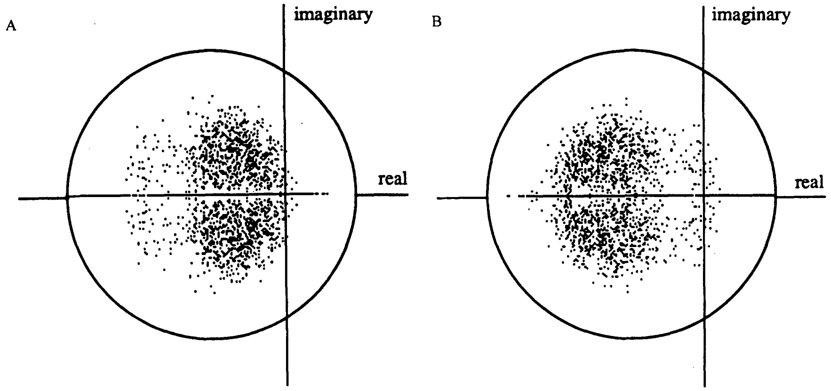

FIG. 6.—The distribution of the eigenvalues of 500 6 × 6 matrices, falling in six Gershgorin disks of identical radius and positioning. The diagonal elements are assigned the value of -1. Four randomly selected off-diagonal elements from each row were assigned values of v_1 and v_2, selected from uniform distributions $[-z, z]$, and of v_3 and v_4, equal to $\pm (z - |v_1|)$ and $\pm (z - |v_2|)$, where the terms are chosen to be negative (independently) with a probability of 0.1 (*A*) and of 0.9 (*B*), with $z = 1$.

consistent across the model community (as DeAngelis [1980] established for γ), the effects on stability are unequivocal: increasing equilibrium abundances increase disk radii and cause already negatively centered disks to become more so; therefore, enhanced stability always results. When the effect of parameter variation on species' equilibrium abundance is not consistent across the community, the consequences for stability may be much harder to predict. Techniques of direct assignment avoid this problem only when it is assumed that the equilibrium points are independent of parameter selection.

The behavior of these models is clearly qualitatively dependent on the nature of the diagonal elements of the Jacobian. Their treatment is worthy of careful attention. The diagonal elements of the Jacobian are often referred to as describing self-regulatory density-dependent processes. This is a little misleading, since it implies that these processes are entirely intraspecific. This impression is reinforced by the use of generalized Lotka-Volterra models; in these models, it is true that only purely intraspecific terms appear on the diagonal of the Jacobian. However, this is idiosyncratic to these particular equations; in fact, interspecific terms are present in the partial derivatives of these equations taken with respect to themselves, but, when these are evaluated at an equilibrium, they can be subtracted out. This is not possible if minor nonlinearities are added to the trophic interactions. Consider the modified generalized Lotka-Volterra model (otherwise similar to eq. [5]):

$$\frac{dN_i}{dt} = N_i\left(b_i + \sum_{\substack{j=1\\ j<i}}^{n} a_{ij}N_i^{1+x} - \sum_{\substack{k=1\\ k>i}}^{n} a_{ik}N_kN_i^x - a_{ii}N_i\right). \qquad (7)$$

If $x = 0$, all the predator functional responses are implicitly type 1 (with no satiation), and the usual generalized Lotka-Volterra equations are recovered. If $x < 0$, the functional responses all become of type 2; if $x > 0$, they are of type 3 (with no satiation). The diagonal elements of the Jacobian evaluated at an equilibrium are

$$g_{ii} = \left.\frac{\partial F_i}{\partial N_i}\right|_{\mathbf{N}=\mathbf{N}^*} = -a_{ii}N_i^* - \sum_{j>i}^{n} x a_{ij} N_j^* N_i^{*x} . \tag{8}$$

Even with no intraspecific interaction term present, the self-regulatory term may depend in a complicated fashion on other species in the community. Inclusion of this type of nonlinearity complicates the assignment of values to the diagonal elements of the Jacobian. (Since the terms in the summation in eq. [8] are negative when $x > 0$ [i.e., type 3 functional responses], this approach would clearly yield results consistent with Nunney's [1980] observation that type 3 functional responses should be a stabilizing influence on food webs; it is interesting that type 2 functional responses [$x < 0$, which render the summation terms positive] are devastating to the stability of the equilibrium). With these observations in mind, it is not clear how assigning identical values to the diagonal elements of the Jacobian can be easily justified.

It has been common practice (see, e.g., May 1974; Taylor 1988; Hogg et al. 1989) to assign a value of -1 to all the diagonal elements of the Jacobian. This allegedly results from the appropriate choice of timescale (May 1972). By rescaling time such that $t \rightarrow \tau = kt$ (where τ is transformed time and k is a constant used to rescale time), equation (3) can be rewritten as

$$\frac{d\mathbf{x}}{d\tau} = \frac{1}{k}\mathbf{G}\mathbf{x} . \tag{9}$$

It is clear that, unless the diagonal elements of $\mathbf{G}$ are all identical, k can not be chosen so that they all become -1. It may be possible to achieve this objective with a linear transformation by changing the variable x_i to y_i, such that

$$\mathbf{y} = \mathbf{M}\mathbf{x} \tag{10}$$

and $\mathbf{M}$ is chosen (possibly with some difficulty) so that the diagonal elements in the matrix $\mathbf{M}\mathbf{G}\mathbf{M}^{-1}$ (with the assumption that $\mathbf{M}^{-1}$ exists) are all equal to $-k$, and equation (3) now becomes

$$\frac{d\mathbf{y}}{dt} = \mathbf{M}\mathbf{G}\mathbf{M}^{-1}\mathbf{y} . \tag{11}$$

Time can now be rescaled as before, such that $t \rightarrow \tau = kt$ and, with both sides multiplied by $1/k$,

$$\frac{d\mathbf{y}}{d\tau} = \frac{1}{k}\mathbf{M}\mathbf{G}\mathbf{M}^{-1}\mathbf{y} . \tag{12}$$

This would render the diagonal elements of the transformed matrix all equal to -1. The stability of the system is now determined by the eigenvalues of the matrix $1/k\ \mathbf{MGM}^{-1}$ (which will be the same as those for $\mathbf{G}$, but which will be scaled by $1/k$). If these transformations are undertaken (or assumed to have been undertaken), it is only appropriate to correlate the eigenvalues of $1/k\ \mathbf{MGM}^{-1}$ with the structural properties of the matrix $\mathbf{G}$. Although $1/k\ \mathbf{MGM}^{-1}$ and $1/k\ \mathbf{G}$ are similar matrices (i.e., they possess identical eigenvalues), they are not the same matrix. Without knowledge of $\mathbf{M}$, the ecological details (such as connectivity, the sign structure of the interaction matrix, and the interaction strengths) of the dynamical system defined by equation (5) are not available. Obtaining the connectivity, trophic details, and mean square interaction strength from the elements of the matrix $1/k\ \mathbf{MGM}^{-1}$ has the effect of implicitly redefining the model under study to one in which

$$\left.\frac{\partial F_i}{\partial N_i}\right|_{\mathbf{N}=\mathbf{N}^*} = \left.\frac{\partial F_j}{\partial N_j}\right|_{\mathbf{N}=\mathbf{N}^*} = -1 \qquad (13)$$

for all i and j; that is, one in which the diagonal elements of the Jacobian are all identical. Studies that use techniques of direct assignment and assign identical values to the diagonal elements are not as general as they may appear.

Normalizing the Jacobian by dividing the elements of the ith row by g_{ii} will not preserve the original dynamics in any way.

The relative magnitudes of the off-diagonal elements would appear to be an unalterable property of the model under study. The dependence of the model's behavior on the variance of the trace of the Jacobian does not seem to be a trivial problem.

It is commonly believed that the stability of model ecosystems is inversely related to connectivity, interaction strength, and species richness (May 1974). It is also asserted that the stability of model food webs is enhanced by the existence of high degrees of donor control (DeAngelis 1975; Pimm 1982) and low trophic efficiencies (DeAngelis 1975). These observations have led ecologists to speculate that trade-offs must exist between the different components of complexity (see, e.g., May 1974; Lawlor 1978; Rejmanek and Stary 1979; Yodzis 1980). The analysis developed here suggests that, for a wide range of models, these results may be obtained only in rather special cases and that, in general, it is possible to argue that quite the reverse may often be true. Given sufficient variability in species' self-regulatory terms, it can be argued that communities should be composed of dense webs of strong, efficient, and reciprocal interactions linking highly populous species, especially if the community is destabilized by high-species richness. Numerical studies suggest that the variability in the self-regulatory terms need not be extravagant for this to be the case. On a different note, the same models suggest that relatively simple communities are indeed more vulnerable to species invasions than their complex counterparts (see, e.g., Post and Pimm 1983). The paradox resulting from the observations of Elton and MacArthur and previous analyses of model ecosystems could be largely illusory.

Ecologists have wrangled for decades over the extent to which population dynamics are density-dependent. The relationship between stability and complexity in model ecosystems appears to hinge on the between-species variability in the prevalence of this density dependence (it is ironic that ecologists find it easier to agree that there is interspecific variability in the density dependence governing species' population dynamics than to measure its precise extent). If these models are representative of the dynamics of real communities, it will be a very long time before it is possible to state the relationship between stability and complexity with any empirical generality.

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