

MAXIMALLY STABLE MODEL ECOSYSTEMS CAN BE HIGHLY CONNECTED

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Abstract. Community ecologists have long sought to understand the basis for two apparently conflicting observations. The first is the evident persistence of complex communities through time. The second is the theoretical result that, in general, complex model communities are less likely to be stable than simpler ones. Previous attempts to reconcile these observations have studied the average properties of model communities constructed under a variety of different assumptions. The problem with such studies is that the set of all possible models, even when subject to strict constraints, is very large relative to the subset that may be representative of real communities, and it is unclear which constraints to apply. Here, it is assumed that real communities are a highly restricted subset of all possible models, and attention is focused instead on properties of communities constructed to be as stable as they could be. Geometrically derived analytic results show that in general, communities constructed in this way require high levels of connectance, as measured by the product of the strength and frequency of interspecific interaction. In particular, connectance between weakly and strongly self-regulated elements of these communities is of critical importance.

Key words: *community stability vs. community complexity; connectance; connectivity; ecosystem models; ecosystem stability; eigenvalues; interaction strength; stability and complexity.*

INTRODUCTION

When Robert May (1971, 1972, 1974) first “kicked open the barn door” (Cohen et al. 1990: 67) on the relationship between ecological stability and complexity back in the 1970s he exposed a seemingly fundamental contradiction between prevailing ecological intuition espoused by MacArthur (1955) and Elton (1958) and mathematical fact. The ensuing “stampede of theoretical and empirical studies that thundered out” (Cohen et al. 1990: 67) of this particular barn has now largely subsided; yet, this contradiction—defined by some of the principal architects of modern ecology—remains to be convincingly resolved.

May’s (May, 1971, 1972, 1974) formulation is frequently criticized for three broadly different reasons. First, populations are not generally thought to be at equilibrium; second, belief persists that even if populations are found around equilibrium, these models are unrealistic, omitting details of autecology important to

understanding population dynamics; and last, stability is only evaluated with respect to arbitrarily small perturbations.

Of these concerns, only the last is necessarily serious. First, state variables considered to be at equilibrium can be measured over any appropriate spatial scale—and in particular, they do not have to represent local population densities. For example, results apply equally if variables under consideration are chosen to be proportions of available habitat in ecosystems occupied by species, areas over which guilds or groups of species range, or spatially averaged mean population densities—and none of these choices necessarily require an assumption that populations are at equilibrium at smaller scales. Second, while ecosystem variables are likely to have complicated functions governing their dynamics, May’s methods require only an approximate estimate of first-order terms of these functions obtained from a linearization around the equilibrium; thus, his results do not assume or require detailed knowledge of them.

As a result, some of May’s randomly generated interaction matrices are likely to describe local interactions at some scale where variables are reasonably stable about an equilibrium point, and in this respect can-

Manuscript received 31 March 1999; revised 29 September 1999; accepted 30 September 1999.

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not easily and justifiably be criticized as being unrealistic. However, the problem remains, as pointed out by Lawlor (1978), that parameter combinations representative of realistic model ecosystems probably constitute only a tiny fraction of full parameter space and that randomly assembled systems are vanishingly unlikely to reflect real ecosystems. Many previous studies reveal that it is unclear what constraints render model ecosystems more realistic (past examples have included equilibria that are feasible, stable, possessing realistic trophic structures, etc). With this difficulty in mind, I have asked instead what are connectance properties of model ecosystems that are as stable as mathematically possible? I conclude that the most stable possible systems are characterized by heightened connectance, but such systems require strongly self-regulated ecosystem variables to be connected with those more weakly self-regulated. Removal of either these strongly self-regulated elements, or their links with other elements of the ecosystem, will likely result in substantial ecosystem changes.

ANALYSIS

Proceed in the now-standard way (e.g., May 1974), by investigating the n eigenvalues of an $n \times n$ Jacobian matrix \mathbf{A} (with elements a_{ij}), that determine the linearized dynamics: $d\mathbf{x}/dt = \mathbf{A}\mathbf{x}$, where \mathbf{x} is a vector containing small perturbations made to a system of n undefined state variables near an assumed equilibrium. Use is made of the following three rules governing location of eigenvalues of any matrix: (1) Every one of the n eigenvalues of \mathbf{A} lies in at least one of the circles (discs), C_1, \dots, C_n , defined over the complex plane, where C_i has its center on the real axis at the diagonal entry a_{ii} and its radius is equal to the sum of absolute values of off-diagonal elements along the rest of the row. (2) If s of these circular discs form a connected domain that is isolated from other discs, then there are precisely s eigenvalues within this connected domain. (These two rules are known as Gerschgorin's first and second theorems.) (3) The sum of real parts of the eigenvalues of \mathbf{A} equals the sum of diagonal elements of \mathbf{A} ; thus positions of eigenvalues must "balance" about the center of these discs as measured with respect to the real axis (proofs and details provided in Wilkinson [1965]; this approach is further outlined in Haydon [1994]). For the equilibrium to be stable, the largest of the real parts of the eigenvalues must be negative. The more negative this leading eigenvalue is, the faster the system returns to equilibrium following (small) perturbations.

Strength and frequency of interspecific interactions indicated by the magnitude and frequency of non-zero off-diagonal elements define ecosystem connectance. The per capita amount of self-regulation of the i th sys-

tem variable near equilibrium is characterized by the magnitude of the diagonal (a_{ii}) element of the Jacobian matrix. In view of the central importance of diagonal elements of \mathbf{A} in what follows, it must be appreciated that, in general, the value of these diagonal elements will not be simple functions of parameters associated with the dynamics of purely the i th variable—but may contain contributions from any interaction in which the i th variable participates nonlinearly. (Thus, for example, concavity in a functional response often contributes negative quantities to these diagonal elements, while convex, type II responses often contribute positive quantities.)

First, following May's (1971, 1972, 1974) formulation, consider the special case in which all n discs are identically centered. This amounts to assuming all ecosystem variables are equally self-regulated. Note the trivial case in which off-diagonal terms are all zero, discs are single points on the real axis, and it follows that the eigenvalues must be the diagonal elements. The stability of the whole system cannot be more (or less) than the degree of self-regulation exhibited by each variable. Now introduce non-zero off-diagonal terms. The basis for May's result is immediately made transparent: as discs increase in radius, eigenvalues contained within them may be found at greater distances from disc centers, but because of rule three, eigenvalues more negative than the disc centers must be balanced by more positive eigenvalues. Increasing connectance "decouples" eigenvalues from their diagonal elements and inevitably results in the most positive eigenvalue becoming more positive (Fig. 1a). Thus, increasing system connectance cannot permit increased stability, and the probability of finding stable systems drops rapidly off with increased connectance. Increasing the numbers of discs (i.e., the number of variables constituting the ecosystem dynamics) increases the likelihood that any one eigenvalue will take on a more positive value (Fig. 1b), and thus decreases stability.

Next consider the more general case in which discs are not all centered at the same point, that is, permit differences between self-regulatory terms. What connectance properties are exhibited by the most stable systems? Examination of Fig. 1c and d immediately shows that only when discs have non-zero radii is it possible for dynamical systems to have a stability greater than that of their least self-regulated component. The extent to which this greater stability can be attained is governed by the connectance of these less self-regulated variables with the rest of the system. More highly connected systems (Fig. 1d) are *potentially* more stable than those that are less well connected (Fig. 1c). While May's result is accurate in identifying highly connected systems as less likely to be stable, connectance is an unambiguous requirement of

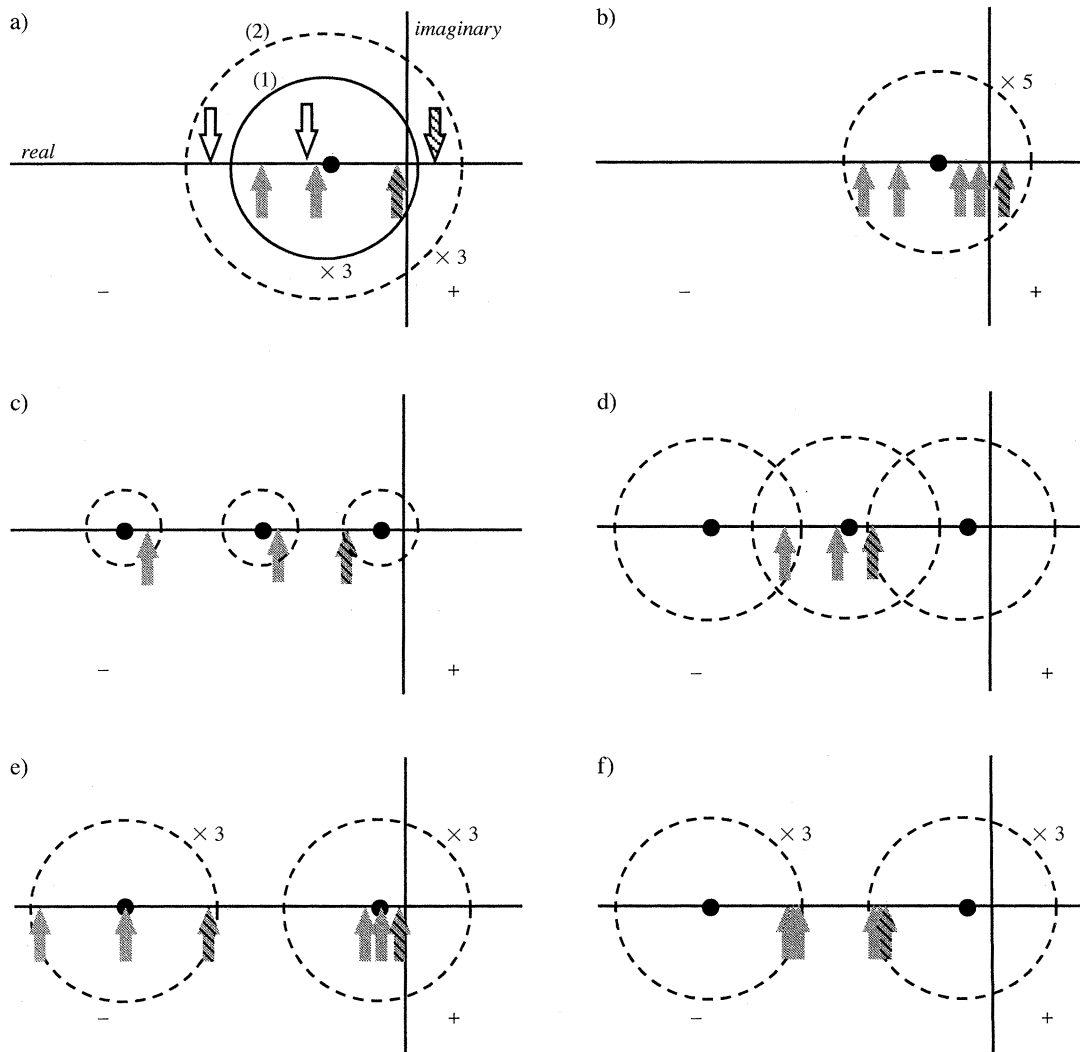


FIG. 1. Locating eigenvalues of matrices in the complex plane (axes cross at the origin). Positions and radii of discs are determined by a_{ii} elements and the quantities $\sum_{j=1, j \neq i}^n |a_{ij}|$ as stated by Gerschgorin's theorems (see *Analysis*). Eigenvalues are found within these domains subject to constraints of rules 2 and 3 outlined in text (see *Analysis*). Note that as a consequence of rule 3, in all six examples (a-f) the sum of real parts of all eigenvalues must equal the sum of diagonal elements of the matrix; this is equivalent to observing that real parts of eigenvalues and disc centers must share the same "center of gravity."

(a) Two cases with three discs super imposed. (1) Three smaller discs all of identical radius and position (superimposed on each other) containing three eigenvalues (denoted by grey arrows below the x -axis). Stability is determined by the real part of the largest eigenvalue (hatched arrows in the diagrams), which must be negative if the equilibrium is to be stable; the more negative this real part is, the more locally stable is the equilibrium. (2) Three superimposed discs with the radii of all three increased by the same amount; the most negative eigenvalue can now become more negative (as indicated by white arrows above x -axis), but in compensation, some eigenvalues must become more positive (in compliance with rule 3). Note that the real part of the most positive eigenvalue cannot be less than the value taken by the diagonal elements.

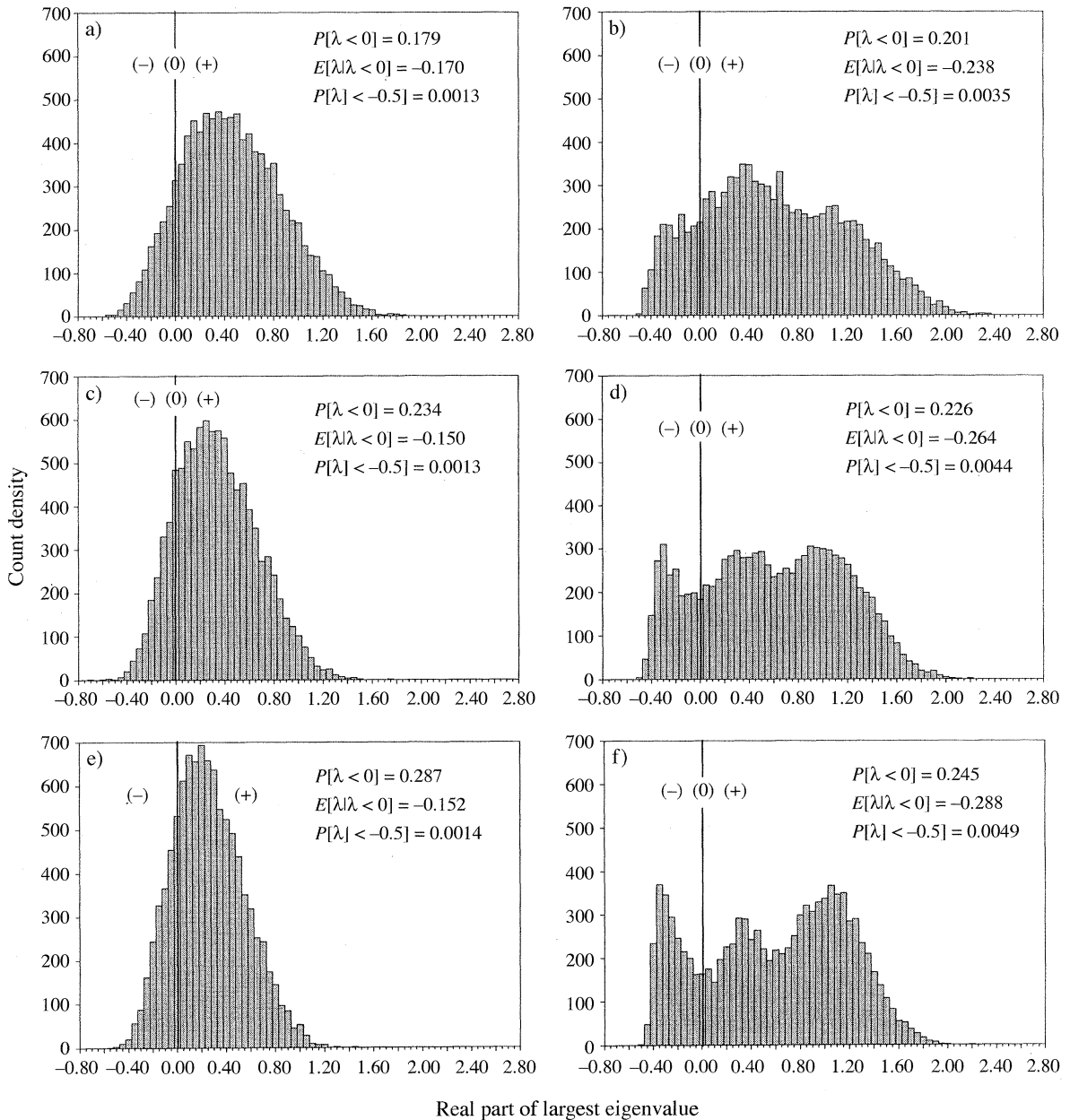
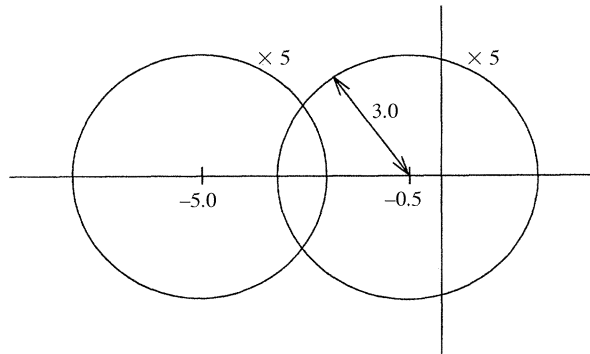
(b) Add two more discs to the system (two more state variables, and thus, two more eigenvalues); once again the most positive eigenvalue can become more positive.

(c) Let diagonal elements take on different values. Note that under some configurations the real part of the dominant eigenvalue can now be less than the most positive a_{ii} .

(d) Note that the larger the radii of discs, the more stable the most stable equilibria can be.

(e) Note the requirement for this form of interactive stabilization is that less and more self-regulated variables of the system must be connected. If the triplets of strongly self-regulated variables in (e) are not connected to the triplet of weakly self-regulated variables, then each must conform separately to rule 3, and there are in effect two systems each equivalent to that shown in (a).

(f) If the left and right disc systems are connected to each other, the system as a whole complies with the three rules, permitting greater stability.



Real part of largest eigenvalue

“more stable” systems. Systems that have been stabilized as a consequence of interactions will be referred to as “interactively stabilized.”

More insight can be obtained by noting that the three rules concerning location of eigenvalues can be validly applied to any fully disconnected subset of a larger system (see Fig. 1e and f). In order to realize the full potential for interactive stabilization in a system, weakly self-regulated variables must be connected to those that are more strongly regulated. Thus a key requirement of interactive stabilization is the precise location and magnitude of interactions between strongly and weakly self-regulated system variables.

Numerical analyses (Fig. 2) suggest that while stability is not simply or strongly related to number or strength of connections between weak and strong self-regulators, systems with more of this form of connectance do tend to be more stable than those with less. Furthermore, whether high connectance results from many weak, or few strong, interactions has only a small bearing on distributions of leading eigenvalues (see Fig. 2). This is consistent with a body of literature that focused on products of interaction strength and frequency (May 1974, McNaughton 1978, Rejmanek and Sibly 1979, Winemiller 1990).

This approach is not suitable for anticipating specific effects of removing links and variables from the system (the latter has been referred to as “species deletion stability,” see Pimm [1982]). The elements of the Jacobian matrix are partial derivatives evaluated at a specified equilibrium, and structural perturbations to the model are likely to change this equilibrium position. Furthermore, as described above, the *i*th diagonal element of the Jacobian matrix will not generally be a function only of the *i*th variable and parameters specific to it, but may be a function of any number of other variables and their parameters. However, the removal of strongly regulated and/or connected variables and links between strongly and weakly self-regulated variables carries a clear risk of initiating instability, while more limited consequences might be anticipated from

removal of weakly connected variables regardless of their self-regulatory capacity, links between weakly self-regulated variables, and weakly self-regulated variables.

DISCUSSION

Previous studies have focused on average stability properties of model dynamical systems constructed using different algorithms. That approach leaves open the possibility that real systems are somehow not average, and might not therefore conform to hypotheses generated by examining average model properties. This problem can be turned around by asking: What properties must ecosystems have to be as stable as mathematically possible? By examining the most extreme stability properties of dynamical systems, long-standing conceptual paradoxes can be more clearly understood. May's (1971, 1972, 1974) results regarding destabilizing influences of frequency and interaction strength refer only to the case when variation in the capacity of each system variable to self-regulate is small relative to variation in connectance. When these restrictions are removed, connectance becomes a required property of more stable systems — specifically, my analysis suggests that interactions binding less regulated ecosystem elements to those that are more regulated are critical properties of the most stable model ecosystems.

Mathematically this is a simple and obvious result—yet it provides a theoretical basis for a number of ecologically interesting speculations. First, it suggests that studying average properties of model dynamical systems may be quite misleading. Second, it will not be possible to understand the relationship between stability and complexity (as here defined) without understanding something about differential self-regulation of ecosystem variables. Third, ecosystems—especially those whose dynamics are governed by many variables—might require very particular connective configurations to remain stable, and therefore some links, weak or strong, may be critical to ecosystem stability.

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FIG. 2. Count density functions obtained from examining real parts of the largest eigenvalues (λ) of 10000 10×10 matrices assumed to be Jacobian matrices. Matrices were constructed randomly in the following manner: In each case half the diagonal elements were set to -5 , and half to -0.5 , and off-diagonal elements in a row sum to $|3.0|$. There are 3, 4, and 5 off-diagonal elements per row, in the top, middle, and lower panels, respectively. All but the last off-diagonal elements in each row are randomly selected from uniform distributions $[-1.0, 1.0]$; the last is chosen so that off-diagonal elements of the matrix row sum to $|3.0|$. In the right-hand panels (b, d, and f), all but the last-chosen off-diagonal elements in each row connect weakly self-regulated elements with more strongly self-regulated ones. In the left-hand panels (a, c, and e), all but the last off-diagonal elements link strongly self-regulated elements with strong ones, or weakly self-regulated elements with weak ones. The last off-diagonal elements are positioned randomly subject to the constraint that the resulting network be a single connected entity. This procedure results in all matrices having identical and constant disc structure (diagrammed above panels). Note that, regardless of overall connectance, matrices with leading eigenvalues more negative than the most positive diagonal entry (-0.5) are at least twice as likely in matrices in which weakly and strongly self-regulated elements are more often linked to each other (right-hand panels) compared to when such links are rare (left-hand panels).

In the absence of variability in self-regulatory capacity of ecosystem variables these models certainly suggest that stability is maintained *in spite* of interspecific interaction (e.g., Caswell 1976)—but when sufficient differential self-regulatory capacity exists, stability may be maintained *because of* such interaction.

While theory of this sort can only offer the most general of guidelines with respect to the likely fragility of ecosystems, it is consistent with the notion that ecosystem-conservation approaches are most safely attempted from a whole assemblage basis rather than a species-based approach, and considerable peril could result from loss of allegedly redundant species.

ACKNOWLEDGMENTS

I am grateful to P. Abrams, C.P. Baer, N. Colegrave, A. Chek, J. Ruesink, and M.E.J. Woolhouse for comments that improved this manuscript, and to Eric Pianka for his unwavering encouragement.

LITERATURE CITED

- Caswell, H. 1976. Community structure: a neutral model analysis. *Ecological Monographs* **46**:327–354.
- Cohen, J. E., F. Briand, and C. M. Newman. 1990. *Community food webs: theory and data*. Springer-Verlag, London, UK.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Macmillan, New York, New York, USA.
- Haydon, D. T. 1994. Pivotal assumptions determining the relationship between stability and complexity: an analytic synthesis of the stability–complexity debate. *American Naturalist* **144**:14–29.
- Lawlor, L. L. 1978. A comment on randomly constructed model ecosystems. *American Naturalist* **112**:445–447.
- MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* **36**:533–536.
- May, R. M. 1971. Stability in multispecies community models. *Mathematical Biosciences* **12**:59–79.
- May, R. M. 1972. Will a large complex system be stable? *Nature* **238**:413–414.
- May, R. M. 1974. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- McNaughton, S. J. 1978. Determinants of stability of large randomly connected systems. *Nature* **275**:251–252.
- Pimm, S. L. 1982. *Food webs*. Chapman & Hall, London, UK.
- Rejmanek, M., and P. Stary. 1979. Connectivity in real biotic communities and critical values for stability of model ecosystems. *Nature* **280**:311–313.
- Wilkinson, J. H. 1965. *The algebraic eigenvalue problem*. Oxford University Press, Oxford, UK.
- Winemiller, K. O. 1990. Must connectivity decrease with species richness? *American Naturalist* **134**:960–968.