# Qualitative Stability and Ambiguity in Model Ecosystems

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abstract: Qualitative analysis of stability in model ecosystems has previously been limited to determining whether a community matrix is sign stable or not with little analytical means to assess the impact of complexity on system stability. Systems are seen as either unconditionally or conditionally stable with little distinction and therefore much ambiguity in the likelihood of stability. First, we reexamine Hurwitz's principal theorem for stability and propose two "Hurwitz criteria" that address different aspects of instability: positive feedback and insufficient lower-level feedback. Second, we derive two qualitative metrics based on these criteria: weighted feedback ($wF_n$) and weighted determinants ($w\Delta_n$). Third, we test the utility of these qualitative metrics through quantitative simulations in a random and evenly distributed parameter space in models of various sizes and complexities. Taken together they provide a practical means to assess the relative degree to which ambiguity has entered into calculations of stability as a result of system structure and complexity. From these metrics we identify two classes of models that may have significant relevance to system research and management. This work helps to resolve some of the impasse between theoretical and empirical discussions on the complexity and stability of natural communities.

*Keywords:* community matrix, community structure, Hurwitz criteria, Lyapunov stability, qualitative stability, system feedback.

May's (1973, p. 641) statement that "increased complexity tends to beget diminished stability" has remained an inescapable and pivotal assertion in the diversity-stability debate. This conclusion was based on a comparison of the mathematical stability of two community matrix models: one, of minimal complexity, was qualitatively stable, and the other, of maximal complexity, had conditional stability. May asserted that while this comparison was somewhat artificial, its generalization to large models of natural systems was nonetheless useful. Particularly lacking, however, has been a meaningful generalization of model structure or complexity that considers the stable domain of parameter space that can be assumed by different models.

Traditional analyses of model stability have used system connectance (proportion of nonzero elements of the community matrix) to describe model complexity. Gardner and Ashby (1970) and May (1972, 1974) found that there is, for a given level of connectance, less scope for stability as system size increases. These results were challenged by analyses restricted to biologically plausible models (Lawlor 1978) or biased toward strong self-regulation in system variables (De Angelis 1975), by empirical evidence (Reagan et al. 1996), and by suggestion that connectance may be linked to robustness (Dunne et al. 2002). Connectance remains, however, a vague indicator of model complexity in specific circumstances because it provides little insight into the implications of system structure, either within or between models. May (1974, p. 216) called for some "quintessential number to be distilled" to make meaningful to empiricists the degree to which ecosystem complexity affects stability.

The lack of a useful descriptor of system structure has led to an impasse between theorists and empiricists in discussions of ecosystem diversity, complexity, and stability (Goodman 1975). Attempts to circumvent this impasse have led many ecologists to define their way out of the problem. Grimm and Wissel (1997) list 163 definitions of stability taken from the ecological literature. In both ecological and mathematical terms, however, the essential features of mathematical, or "Lyapunov," stability remain of practical importance and can be "understood generally as an ability of a living system to persist in spite of perturbations" (Logofet 1993, p. 1). Logofet (1993) argues that

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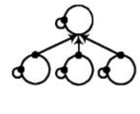
Lyapunov stability is a sufficient measure of ecological stability defined as stochastically bounded persistence (sensu Connell and Sousa 1983).

We suggest a reinterpretation of May's (1973) results and emphasize the equivalent conclusion that increased complexity tends to beget increased ambiguity. We discuss definitions of and criteria for Lyapunov stability and then investigate the degree to which model structure imparts ambiguity to those calculations. We derive weighted measures of stability and test them through quantitative simulations within a broad region of parameter space. These metrics emerge as a practical means to assess and classify the potential stability of models of varying size, structure, and complexity. Moreover, this work suggests that in theory, complexity is not hopelessly at odds with stability.

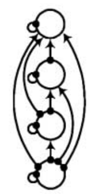
## Sign Stability of the Community Matrix

For a Lotka-Volterra system of $n$ interacting species, necessary conditions for Lyapunov stability can be derived from the sign pattern of the $\alpha_{ij}$ elements of the community matrix **A**. Rules simplifying the mathematics were derived by economists Quirk and Ruppert (1965) and adopted in ecology by May (1973, 1974, p. 71). The "Quirk-Ruppert" rules are (i) $\alpha_{ii} \leq 0$ for all $i$; (ii) $\alpha_{ii} \neq 0$ for at least one $i$; (iii) the product $\alpha_{ij}\alpha_{ji} \leq 0$ for all $i \neq j$; (iv) for any possible sequence of three or more variables, with indices $k$, $l$, $m$, … , $q$, $r$, such that $k \neq l \neq m \neq \cdots \neq q \neq r$, the cyclical product of their conjunct links $\alpha_{\mathrm{kl}}\alpha_{\mathrm{lm}} \ldots \alpha_{\mathrm{qr}}\alpha_{\mathrm{rk}} = 0$; and (v) the determinant of $\mathbf{A} \neq 0$. The rules are practical albeit incomplete formulations of stability criteria (Logofet 1993). Jeffries (1974) supplied an additional color test, which identifies a unique type of neutrally stable system. Jeffries' color test and the Quirk-Ruppert rules together provide both necessary and sufficient conditions for sign stability. A key point is that if a system is not sign stable, it is not necessarily unstable. Rather, it can be conditionally stable, but determining stability remains ambiguous because it is dependent on knowing the magnitude of community matrix elements.

May (1973) made use of the Quirk-Ruppert rules to illustrate differences in the stability of two four-variable models, a′ and b′,

model a′ 

$$\mathbf{A}_{a'} = \begin{bmatrix} - & + & + & + \\ - & - & 0 & 0 \\ - & 0 & - & 0 \\ - & 0 & 0 & - \end{bmatrix}$$

model b′ 

$$\mathbf{A}_{b'} = \begin{bmatrix} - & + & + & + \\ - & - & + & + \\ - & - & - & + \\ - & - & - & - \end{bmatrix} \tag{1}$$

which are depicted both as signed digraphs and community matrices. Model a′ satisfies all of the Quirk-Ruppert rules for stability as well as Jeffries' color test and is therefore qualitatively stable without condition (sign stable). Model b′ fails Quirk-Ruppert rule iv because of omnivory. Although Quirk-Ruppert rule iv easily identifies conditional stability in model b′, it provides no insight into the nature or severity of constraints on model parameters. We can, however, gain a deeper understanding of these conditions by examining Hurwitz's ([1895] 1964) principal theorem for Lyapunov stability.

## The Hurwitz Criteria for Lyapunov Stability

For a Lotka-Volterra system described by a set of $n$ linear first-order differential equations

$$d\mathbf{x}/dt = \mathbf{A}\mathbf{x}, \tag{2}$$

where **x** is a column vector of $n$ system variables (or populations), the behavior through time of variable $x_i$ following the disturbance of $x_j$ depends on the direct interaction between all system variables, as detailed in the Jacobian, or community, matrix **A**. Lyapunov ([1892] 1992) defined the stability of the dynamic motion of variables in terms of a local neighborhood surrounding a point of equilibrium. A system is said to be stable if, following a sudden and small perturbation to one or more of its variables, all variables converge toward their original equilibrium level. Lyapunov rigorously defined the stability of a system based on the eigenvalues ($\lambda$) of **A**, which are the roots of the characteristic (determinantal) equation formed by the equality

$$|\mathbf{A} - \lambda\mathbf{I}| = 0, \tag{3}$$

where **I** is the identity matrix and $|\ |$ denotes the matrix determinant. The resulting characteristic polynomial is of the form

$$a_0\lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + \cdots + a_n = 0. \tag{4}$$

Lyapunov's ([1892] 1992, p. 91) theorem I states, "When the determinantal equation corresponding to the system of differential equations of the disturbed motion has roots with negative real parts, the undisturbed motion is stable, and moreover in such a way that every disturbed motion for which the perturbations are sufficiently small will approach asymptotically the undisturbed motion," and theorem III states, "When among the roots of the determinantal equation there are some for which the real parts are positive, the undisturbed motion is unstable." Thus the system described by equation (2) can exhibit local, or Lyapunov, stability if and only if all eigenvalues of **A** have negative real parts:

$$\mathrm{Re}\lambda_i(\mathbf{A}) < 0 \quad i = 1, 2, 3, \ldots, n. \tag{5}$$

Additional theorems define neutral stability as existing where one or more roots have real parts equal to zero.

Hurwitz ([1895] 1964) presented the means, through a sequence of "Hurwitz determinants" ($\Delta_1, \Delta_2, \Delta_3, \ldots, \Delta_n$) constructed from the polynomial coefficients of the characteristic equation (4), to determine for a system of any size whether its eigenvalues all have negative real parts. Hurwitz's principal theorem ([1895] 1964, p. 73; commonly known as the Routh–Hurwitz criteria or conditions) states, "A necessary and sufficient condition that the equation $a_0\lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + \cdots + a_n = 0$, with real coefficients in which the coefficient $a_0$ is assumed to be positive, have only roots with negative real parts, is that the values of the determinants

$$\Delta_1 = a_1, \Delta_2 = \begin{vmatrix} a_1 & a_3 \\ a_0 & a_2 \end{vmatrix},$$

$$\Delta_3 = \begin{vmatrix} a_1 & a_3 & a_5 \\ a_0 & a_2 & a_4 \\ 0 & a_1 & a_3 \end{vmatrix}, \ldots, \tag{6}$$

$$\Delta_n = \begin{vmatrix} a_1 & a_3 & a_5 & a_7 & \cdots & a_{2n-1} \\ a_0 & a_2 & a_4 & a_6 & \cdots & a_{2n-2} \\ 0 & a_1 & a_3 & a_5 & \cdots & a_{2n-3} \\ 0 & a_0 & a_2 & a_4 & \cdots & a_{2n-4} \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ . & . & . & . & . & a_n \end{vmatrix}$$

all be positive." Where indices for the coefficients within Hurwitz determinants exceed $n$, the coefficients become 0; for example, for a three variable system in $\Delta_3$, both $a_4$ and $a_5$ are 0. Note that successive Hurwitz determinants are nested along the matrix diagonal. From expansion of matrix minors, dependency is created between successive Hurwitz determinants, which we will exploit to advantage in later analyses.

From rules for calculating determinants, we can gain an alternative interpretation of Hurwitz's principal theorem. Given the requirement of zero coefficients for indices $>n$, we see in the $n$th Hurwitz determinant that the last column will be all zeros except for the $\Delta_{nn}$ element, which will be $a_n$. Consequently, $\Delta_n = \Delta_{n-1}(a_n)$ and the requirement that $\Delta_{n-1}$ and $\Delta_n$ be positive is equivalent to the requirement that both $\Delta_{n-1}$ and $a_n$ be positive (Hurwitz [1895] 1964). Furthermore, Hurwitz ([1895] 1964) states that a necessary (but not sufficient) condition for the roots of the characteristic equation to have only negative real parts is that all polynomial coefficients $a_0, a_1, a_2, \ldots, a_n$ be positive. Since the sign of $a_0$ is arbitrary, this statement can also be interpreted as a condition wherein all coefficients are negative or, more generally, that they all are of the same sign.

We have recast Hurwitz's principal theorem into two criteria that we call the "Hurwitz criteria," which makes use of the alternate sign convention for $a_0$ and the interdependence of signs for $\Delta_n$ and $a_n$: (i) polynomial coefficients $a_0, a_1, a_2, \ldots, a_n$ are all of the same sign; (ii) Hurwitz determinants $\Delta_2, \Delta_3, \Delta_4, \ldots, \Delta_{n-1}$ all are positive, where $a_0 = +1$. The important contribution is the omission from criterion ii of the first and last Hurwitz determinants, which are both satisfied in criterion i. Criterion i is only a necessary condition for Lyapunov stability. Taken together, the two criteria (i and ii) provide both necessary and sufficient conditions for Lyapunov stability. This step is an important consideration in our study because it removes some of the interdependence of successive Hurwitz determinants. It is now possible to determine whether or not systems fall into two separate classes, namely, whether they primarily fail criterion i or ii. In general terms, it will be seen that criterion i fails due to the presence of positive feedback cycles, namely, cycles counteracting sign uniformity of the coefficients. Criterion ii fails due to relative weakness in low-level feedback, and it is important to realize that it can do so despite the absence of positive feedback. A discussion of feedback is necessary.

## System Feedback

Levins (1974, 1975) and Puccia and Levins (1985, 1991) provide a basic understanding of polynomial coefficients and Hurwitz determinants in terms of system feedback. Negative feedback cycles can be understood to provide stability. Conversely, positive feedback cycles are self enhancing and act to destabilize a system. Each $a_1$, $a_2$, $a_3$,

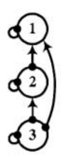
$\ldots$ , $a_n$ coefficient is taken to mean feedback ($F$) at each $n$th level of the system, which is synonymously subscripted as $F_1$, $F_2$, $F_3$, $\ldots$ , $F_n$. Here we employ the $a_0 = -1$ sign convention so that negative feedback can be equated with stability through Hurwitz criterion i. Overall feedback ($F_n$) is feedback at the highest system level and is equal to the system determinant. Hurwitz criterion i then means that system stability is dependent on each level of the system having negative feedback.

Hurwitz criterion ii addresses a balance between lower and higher levels of feedback such that a system is not driven too strongly by feedback at higher levels, which causes it to overcompensate. Substituting $-F_n$ for $a_n$ in the calculation of the second Hurwitz determinant, that is, $-F_0 = +1$, we gain the following inequality:

$$\Delta_2 = F_1F_2 + F_3 > 0. \tag{7}$$

Given that criterion i is met, then $F_1$, $F_2$, and $F_3$ are all negative. Therefore, to have a positive Hurwitz determinant, the overall feedback ($F_3$) must be less than the product of feedback at lower levels ($F_1F_2$). Stability therefore depends on lower levels of feedback not being overwhelmed by feedback at higher levels in the system.

An illustration of these calculations is made below using a maximally connected three-variable system that includes omnivory:

model c′ 

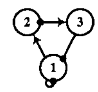

$$\mathbf{A}_{c'} = \begin{bmatrix} - & + & + \\ - & - & + \\ - & - & - \end{bmatrix} \tag{8}$$

Feedbacks for model c′ are

$$\begin{aligned} F_3 &= -\alpha_{1,1}\ \alpha_{2,2}\ \alpha_{3,3} - \alpha_{1,1}\ \alpha_{2,3}\ a_{3,2} \\ &\quad -\alpha_{2,1}\ \alpha_{1,2}\ \alpha_{3,3} - \alpha_{3,1}\ \alpha_{1,2}\ \alpha_{2,3} \\ &\quad -\alpha_{3,1}\ \alpha_{1,3}\ \alpha_{2,2} + \boldsymbol{\alpha_{1,3}\ \alpha_{3,2}\ \alpha_{2,1}}, \\ F_2 &= -\alpha_{1,1}\ \alpha_{2,2} - \alpha_{2,2}\ \alpha_{3,3} - \alpha_{1,1}\ \alpha_{3,3} \\ &\quad -\alpha_{2,1}\ \alpha_{1,2} - \alpha_{2,3}\ \alpha_{3,2} - \alpha_{3,1}\ \alpha_{1,3}, \\ F_1 &= -\alpha_{1,1} - \alpha_{2,2} - \alpha_{3,3}, \\ F_0 &= -1. \end{aligned} \tag{9}$$

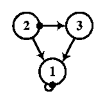
All feedback cycles in each level are negative except for a single cycle, at the highest level (in bold), that is the cyclical product of conjunct links associated with omnivory. Stability is achieved when the product of the three links in the positive omnivory cycle is relatively weak.

In model d′ and e′, Hurwitz criterion i is met unconditionally:

model d′ 


$$\mathbf{A}_{d'} = \begin{bmatrix} - & 0 & - \\ + & 0 & - \\ 0 & + & 0 \end{bmatrix}$$

$$\begin{aligned} F_3 &= -\alpha_{1,1}\ \alpha_{2,3}\ \alpha_{3,2} - \alpha_{2,1}\ \alpha_{1,3}\ \alpha_{3,2} \\ F_2 &= -\alpha_{2,3}\ \alpha_{3,2} \\ F_1 &= -\alpha_{1,1} \\ F_0 &= -1 \end{aligned}$$

model e′ 


$$\mathbf{A}_{e'} = \begin{bmatrix} - & + & + \\ 0 & 0 & - \\ 0 & + & 0 \end{bmatrix}$$

$$\begin{aligned} F_3 &= -\alpha_{1,1}\ \alpha_{2,3}\ \alpha_{3,2} \\ F_2 &= -\alpha_{2,3}\ \alpha_{3,2} \\ F_1 &= -\alpha_{1,1} \\ F_0 &= -1 \end{aligned} \tag{10}$$

In the conditions for $\Delta_2$, however, the product of $F_1$ and $F_2$ creates a term ($\alpha_{1,1}\ \alpha_{2,3}\ \alpha_{3,2}$) that is repeated in opposite sign in $F_3$ and thus canceled in the inequality of equation (7). Hence, $\Delta_2$ will always be nonpositive in models d′ and e′, and neither can be stable within any parameter space.

The above examples illustrate how the Hurwitz criteria can be used to provide equivalent interpretations of the Quirk-Ruppert rules and Jeffries' color test. Quirk-Ruppert rules i, ii, iii, and v are all satisfied when Hurwitz criterion i is met unconditionally, that is, with no positive feedback cycles occurring at any level in the system (the "rules" in question are simply explicit but redundant reformulations of this criterion). Quirk-Ruppert rule iv, which addresses the presence of long loops, is similarly met through Hurwitz criterion i but also by criterion ii. Models c′ and d′, for instance, are identified as not being sign stable by Quirk-Ruppert rule iv because they have feedback cycles that are the cyclical product of conjunct links. These cycles may or may not produce countervailing feedback and hence the conditions for Hurwitz criterion i, as they do in model c′ (eq. [9]) but do not in model d′ (eq. [10]). When cyclic conjunct links do not produce conditions undermining criterion i, there still will be conditions that can cause a failure of Hurwitz criterion ii. Model e′, in which Jeffries (1974) demonstrates the necessity of the color test, has no countervailing conditions in Hurwitz criterion i (which it passes), but it fails criterion ii unconditionally with a Hurwitz determinant that can only equal 0. This system can only be neutrally stable.

The Quirk-Ruppert rules and Jeffries' color test distinguish models that are sign stable from those that are not through visual inspection of signed digraphs and calculation of the system determinant. Although these criteria are clear-cut, they offer no insight into the stable domain of parameter space that given models can assume. From the Hurwitz criteria, however, we gain symbolic inequalities identifying the relative degree to which stable parameter space can be constrained. In small systems ($n \leq 5$), symbolic analysis of the Hurwitz criteria can yield penetrating insights into system dynamics, and it is the core of Levins's (1974, 1975) and Puccia and Levins's (1985, 1991) loop analysis. A practical limit is quickly reached, however, because of a factorial increase in terms of the polynomial coefficients. Complex systems of even moderate size can have an unreasonable number of logical contingencies within their characteristic polynomials. In particular, maximally connected systems have $n!$ feedback cycles at their highest level. While we cannot overcome the limit that large complex systems impose on our ability to comprehend the Hurwitz criteria symbolically, considerable information can still be gained from a qualitative analysis of system feedback. We propose two metrics to evaluate these criteria based solely on the sign structure of a system.

## Weighted Feedback and Weighted Determinants

Both Hurwitz criteria depend on a countervailing balance of feedback cycles or determinantal terms. Accordingly, we define ambiguity as the relative proportion of feedback cycles or determinantal terms that are of opposite sign. Through qualitative analyses we can therefore determine the degree to which each Hurwitz criterion is conditional or ambiguous based solely on interaction sign. We do this determination based on a ratio, or weight, of the net to the absolute number of cycles at each level in the system and a ratio of the net to the absolute number of terms within each Hurwitz determinant. The value of each feedback cycle and determinantal term is treated equally because we are only concerned with its sign. This approach then gives us two qualitative metrics based on the Hurwitz criteria, namely, weighted feedback ($wF_n$) for criterion i and weighted determinants ($w\Delta_n$) for criterion ii.

Considering model c′ (eq. [8]), ambiguity in $F_3$ (eq. [9]) arises from a net number of four negative cycles—given the cancellation of one negative and one positive cycle—divided by an absolute number of six cycles, which yields a weighted feedback of $wF_3 = -0.66$. In $F_2$ and $F_1$, all cycles are negative, and $wF_2$ and $wF_1$ both equal –1.0. In qualitative terms, weighted feedback ($wF_n$) represents the degree to which Hurwitz criterion i is ambiguous. Negative $wF_n$ values imply that negative feedback cycles outnumber positive feedback cycles (and vice versa). Values of $wF_n$ tending toward $-1.0$ imply unambiguous conditions for stability, those tending toward 1.0 imply unambiguous conditions for instability, and those near 0 imply wholly ambiguous conditions.

Conditions for stability arising within each Hurwitz determinant are also dependent on system structure and can be similarly considered through a ratio of the net to absolute number of terms, although in a less straightforward manner. Considering again the feedback of model c′ (eq. [9]), terms of the second Hurwitz determinant (eq. [7]) have a ratio of 13 net to 23 absolute terms, which gives a weighted determinant of $w\Delta_2 = 0.56$. Weighted determinants, however, cannot be considered in the same manner as weighted feedback. Even in a system that is sign stable, the ratio of net to absolute number of terms in a Hurwitz determinant can never equal 1.0. In model a′, which is unconditionally stable, the third Hurwitz determinant has a ratio of 784 net to 2,096 absolute terms, which gives an $n$th weighted determinant of $w\Delta_4 = 0.37$. Moreover, the relative magnitude of weighted determinants is greatly affected by system size. A five-variable version of model a′ has a ratio of 40,960 net to 244,740 absolute terms, which gives an $n$th weighted determinant of $w\Delta_5 = 0.17$. Nonetheless, models with structural links that create relatively greater feedback at higher levels in the system will have weighted determinants that are less than models (of the same number of variables) with relatively greater feedback at lower levels in the system. Thus, systems that are inherently unstable due to criterion ii will tend toward $w\Delta_n$ values that are negative. To circumvent the problem of relative magnitude and system size, we will show that weighted determinants can be judged in relation to values from standard models that are near 0.

Calculating weighted feedback and weighted determinants starts with a community matrix qualitatively specified by only the signed unity ($-1$, $+1$, 0) of its interaction terms (denoted as $°\mathbf{A}$). Qualitatively specified as such, equation (3) yields polynomial coefficients (denoted as $°a_n$) that are rendered in whole units of feedback cycles (denoted as $°F_n$). To calculate the absolute number of feedback cycles or terms within each polynomial coefficient, we

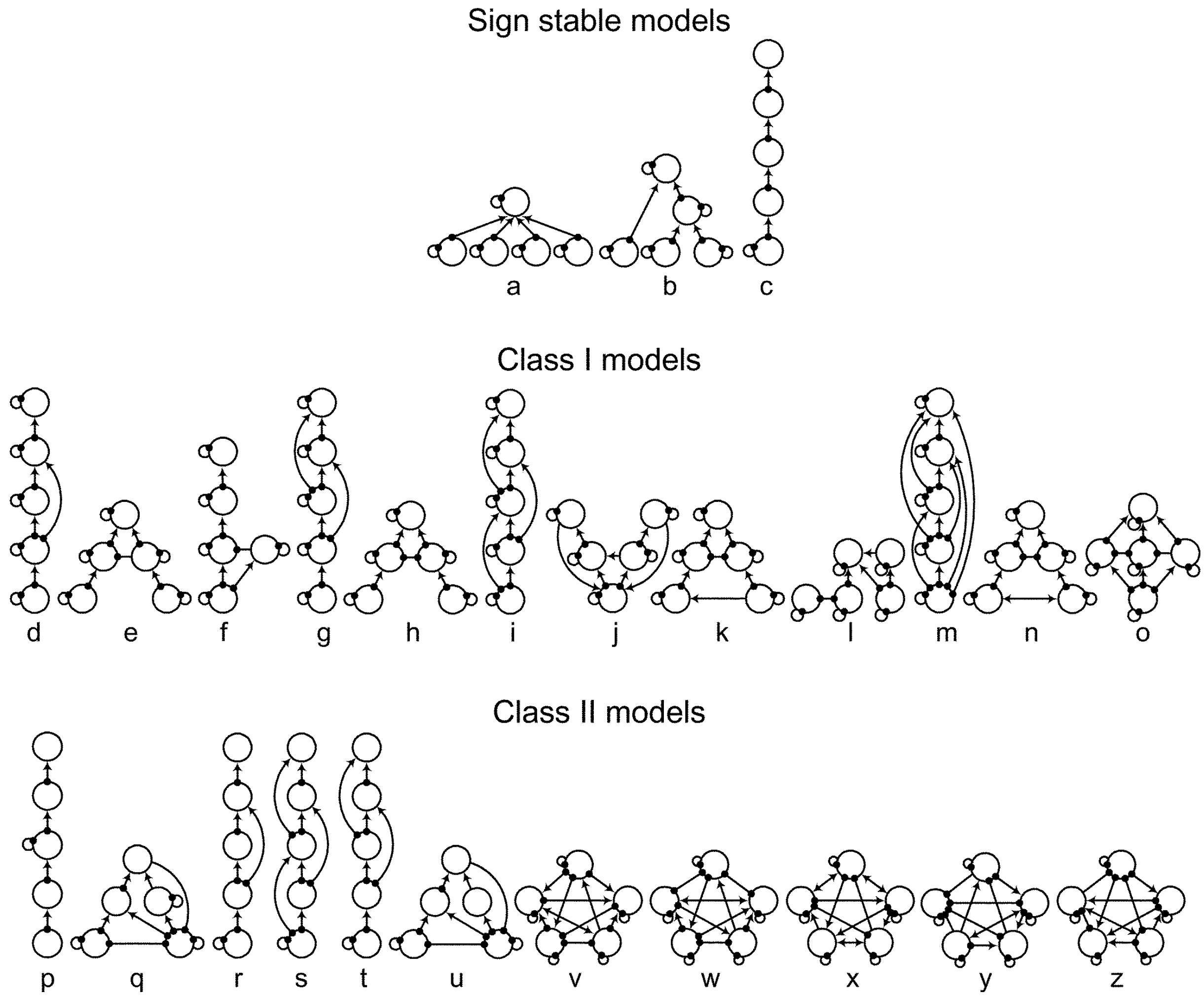



**Figure 1:** Signed digraphs of 26 five-variable model systems analyzed in computer simulations. Model j is a plankton community from Stone (1990) and model p is from Jeffries (1974). Model a is patterned after a four-variable model from May (1973), model l after a New England tidepool community from Puccia and Pederson (1983), model c after a general model from Pimm and Lawton (1978), and model o after an old-field (six-variable) food web from Schmitz (1997). Models v–z were randomly constructed by computer, and the remaining models were constructed by adding or removing links in models b, c, and e. Models a–c are sign (unconditionally) stable. Two classes of conditionally stable models, class I and class II, are distinguished based on qualitative properties discussed in the text and table 1.

make use of a system's adjacency matrix (denoted as $^{\bullet}\mathbf{A}$). This is merely a community matrix, including self effects where present, specified only by the absolute value of $^{\circ}\mathbf{A}_{ij}$ elements, that is, by 1 for all $^{\circ}\mathbf{A}_{ii}$ and $^{\circ}\mathbf{A}_{ij} \neq 0$ or by 0. From the adjacency matrix, we construct an absolute permanental equation

$$\overset{+}{|}{}^{\bullet}\mathbf{A} + \lambda\mathbf{I}\overset{+}{|} = 0 \tag{11}$$

that uses the matrix permanent to derive an absolute polynomial ($^{\bullet}a_0\lambda^n + {}^{\bullet}a_1\lambda^{n-1} + {}^{\bullet}a_2\lambda^{n-2} + \cdots + {}^{\bullet}a_n = 0$), the coefficients of which detail the absolute number of feedback cycles ($^{\bullet}F_n$) at each level in a system. The matrix permanent (also known as the plus determinant) is similar to the determinant, but it does not use subtraction in computation of matrix minors, for example,

$$\overset{+}{\left|\begin{matrix} a & b \\ c & d \end{matrix}\right|}^{+} = ad + bc,$$

nor does it employ alternating signs in expansion of matrix minors (Marcus and Minc 1964; Eves 1980; see app. A of

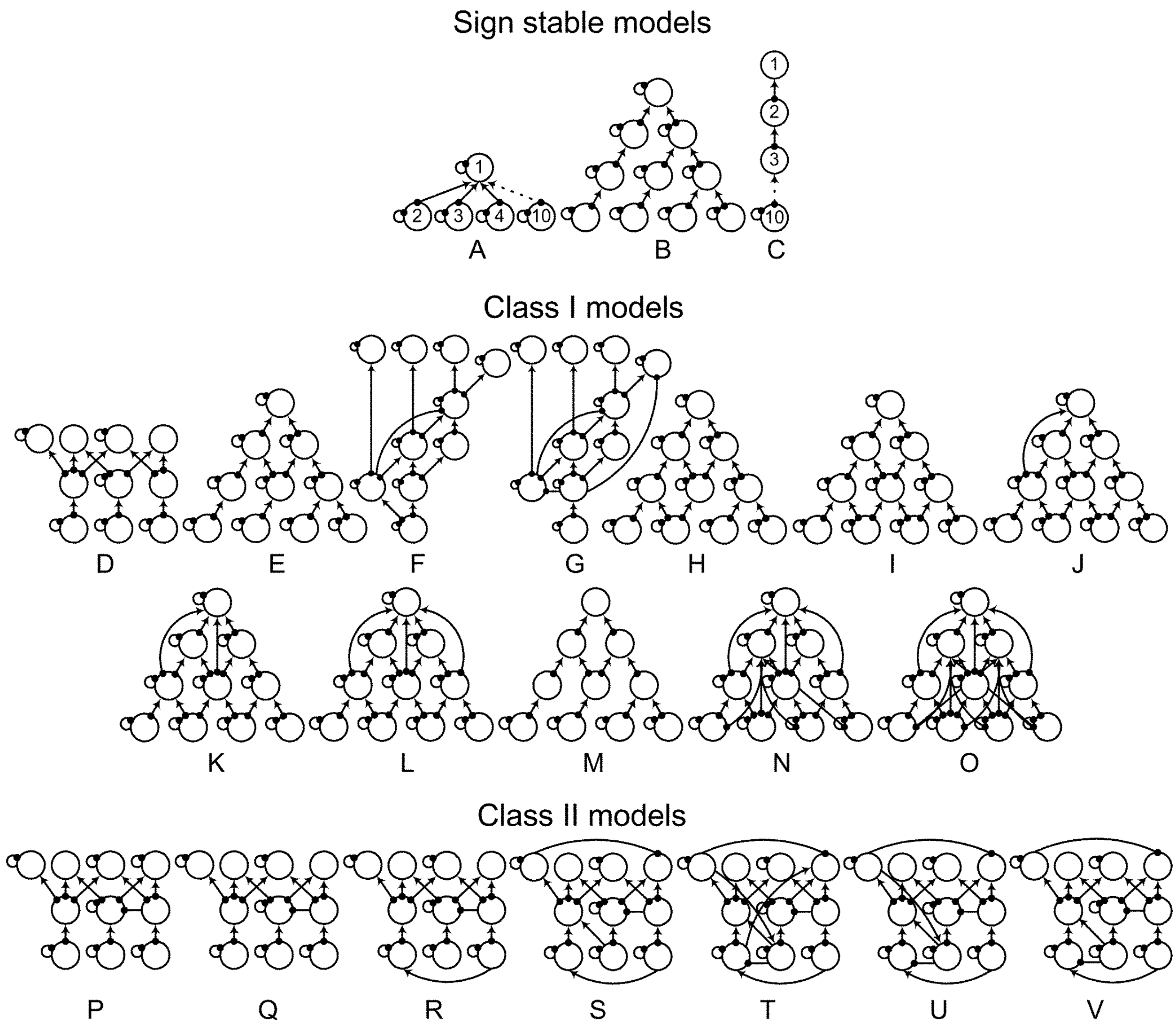



**Figure 2:** Signed digraphs of 22 10-variable model systems analyzed in computer simulations. Models F and G, respectively, are of mesotrophic and eutrophic Danish shallow lakes described by Jeppesen (1998) as discussed in Dambacher et al. (2002). Model P is an avian, fish, and benthic stream community adapted from Wright (1997). Remaining models were constructed by adding or removing links in models B or P. Models A–C are analogues of models a–c in figure 1 and are sign (unconditionally) stable. Conditionally stable models, class I and class II, are distinguished based on qualitative properties discussed in the text and table 1.

Dambacher et al. 2002 in *Ecological Archives* E083-022-A1).

Calculating weighted feedback at each level in the system then becomes the ratio of the net and absolute number of feedback cycles

$$wF_n = {}^{\circ}F_n / {}^{\cdot}F_n . \tag{12}$$

Using the permanent function and coefficients from the absolute polynomial, we calculate the absolute number of terms within each Hurwitz determinant by

$${}^{\cdot}\Delta_n = \left|\begin{matrix} {}^{\cdot}a_1 & {}^{\cdot}a_3 & {}^{\cdot}a_5 & \cdots & {}^{\cdot}a_{2n-1} \\ {}^{\cdot}a_0 & {}^{\cdot}a_2 & {}^{\cdot}a_4 & \cdots & {}^{\cdot}a_{2n-2} \\ 0 & {}^{\cdot}a_1 & {}^{\cdot}a_3 & \cdots & {}^{\cdot}a_{2n-3} \\ 0 & {}^{\cdot}a_0 & {}^{\cdot}a_2 & \cdots & {}^{\cdot}a_{2n-4} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \cdot & \cdot & \cdot & \cdot & {}^{\cdot}a_n \end{matrix}\right|^{+}_{+} . \tag{13}$$

Weighted determinants are calculated as the ratio of the net and absolute number of terms in Hurwitz determinants derived from the qualitatively specified systems

$$w\Delta_n = {}^{\circ}\Delta_n / {}^{\bullet}\Delta_n. \tag{14}$$

Weighted feedback ($wF_n$) and weighted determinants ($w\Delta_n$) are based on the network properties of the system. Taken together they provide a qualitative means to assess the relative degree to which ambiguity has entered into calculations of stability as a result of system structure and complexity. A computer program that calculates these metrics can be found in the revised Supplement 1 of Dambacher et al. (2002) in *Ecological Archives* E083-022-S1.

## Quantitative Simulations

### *Model Selection and Computer Programs*

We conducted quantitative simulations to distinguish the relative constraint that structural complexity can impart on stable parameter space. The qualitative metrics of weighted feedback and weighted determinants were tested in an array of five- and 10-variable models (figs. 1, 2) representing a broad range of complexity and conditional stability. Models were either taken from the literature or constructed from a few core models that were complicated with added links, including competitive (interference and resource), omnivorous, mutualistic, commensal, and predator-prey interactions. Models are identified alphabetically by lower- (five-variable) and uppercase (10-variable) characters. Models a–c and A–C are analogues. For each model a total of 5,000 quantitatively specified matrices were constructed based on the unchanging sign structure of the system. Nonzero elements of each matrix were quantitatively specified with a pseudorandom number generator that assigned interaction strength but not sign from an even distribution over two orders of magnitude (0.01–1.0); drawing on distributions over three or four orders of magnitude produced negligible differences in results. The stability of each quantitatively specified matrix was then assessed in terms of Hurwitz criterion i and ii, and the percentage of unstable matrices for each model was then compared to values of weighted feedback and weighted determinants.

For five-variable systems (fig. 1), all matrix calculations were symbolically detailed in terms of relative cell addresses along a single row in a spreadsheet program (Microsoft Excel 2000). The resulting spreadsheet had 250 columns and 5,000 rows of formulae, and a set of 5,000 matrices could thus be quantitatively specified and evaluated in 10 s (via Pentium III processor, 864 MHz). Stability analysis in 10-variable systems was done with an iterated computer algorithm (PV-WAVE, version 6.20, Visual Numerics, Boulder, Colo.). A set of 5,000 matrices could be evaluated in 31 s (via Pentium III processor, 450 MHz). The latter program was also used in a number of five-variable models to cross-verify results with the spreadsheet program.

### *Model Classification*

Based on Hurwitz criteria i and ii, we can consider two kinds of conditionally stable models: class I and class II (figs. 1, 2; table 1). Class I models are defined as having maximum values of weighted feedback occurring only at the *n*th, or highest, system level and $n-1$ weighted determinants that are greater than or equal to a standard value derived from a straight-chain system (of the same number of variables) that is self-regulated only at its basal variable, for example, models c (fig. 1) or C (fig. 2). Class II models are defined as having maximum values of weighted feedback that occur at lower levels in the system or having $n-1$ weighted determinants that are less than that of a model c–type system. As will be shown, model c–type systems have weighted determinants that in relative terms are near 0 and represent a threshold below which systems are prone to failing criterion ii. Class II models frequently have quantitatively specified matrices that fail Hurwitz criterion ii independently of Hurwitz criterion i; that is, they pass criterion i and fail criterion ii.

We use the term "potential stability" to mean the relative percentage of stable matrices generated from a random and evenly distributed parameter space. For brevity, we have tabulated only the details of five-variable models in table 1; the results of 10-variable models are similar. Results of both five- and 10-variable systems are given in figure 3.

### *The* n*th Weighted Determinant*

Our analysis follows the above discussion of Hurwitz's principal theorem and its division into two criteria. We start with the nested dependence of successive Hurwitz determinants, from which it could be expected that the *n*th Hurwitz determinant (table 1, sec. B) might account for most of the unstable matrices in quantitative simulations. Examining the number of nonpositive $\Delta_5$s and the total number of unstable matrices confirms this expectation for all five-variable models analyzed (table 1, secs. E and H). Thus, it follows that the *n*th weighted determinant ($w\Delta_n$) could account for stability of most of the quantitative matrices in our simulations. Figure 3*A* shows a strong curvilinear relationship between the percentage of stable matrices and $w\Delta_n$ for both five- and 10-variable systems. However, $w\Delta_n$ provides little insight into the potential stability of these models because matrices from models a–c and A–C, which are sign stable and thus 100% stable, have widely disparate $w\Delta_n$ values. In particular, $w\Delta_n$ values for models c and C are practically indistinguishable

**Table 1:** Summary of stability analysis for 26 five-variable model systems (fig. 1)

| | Sign stable models | | | Class I models | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | a | b | c | d | e | f | g | h | i | j | k | l | m | n | o |
| A. Weighted feedback: | | | | | | | | | | | | | | | |
| $wF_5$ | −1.00 | −1.00 | −1.00 | **−.82** | **−.78** | **−.60** | **−.50** | **−.45** | **−.35** | **−.29** | **−.23** | **−.20** | **−.13** | **−.05** | **0** |
| $wF_4$ | −1.00 | −1.00 | −1.00 | −.85 | −.82 | −.82 | −.68 | −.48 | −.59 | −.63 | −.43 | −.55 | −.33 | −.20 | −.15 |
| $wF_3$ | −1.00 | −1.00 | −1.00 | −.93 | −.91 | −.91 | −.88 | −.63 | −.84 | −.84 | −.63 | −.74 | −.67 | −.47 | −.51 |
| $wF_2$ | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −.87 | −1.00 | −1.00 | −.87 | −.86 | −1.00 | −.75 | −.88 |
| $wF_1$ | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 |
| B. Weighted determinant: | | | | | | | | | | | | | | | |
| $w\Delta_5$ | .17 | .13 | .0093 | .078 | .073 | .059 | .035 | .016 | .020 | .022 | .0090 | .012 | .0028 | .00070 | 0 |
| $w\Delta_4$ | .17 | .13 | **.0093** | .096 | .094 | .099 | .070 | .035 | .057 | .078 | .039 | .059 | .021 | .015 | .016 |
| C. Percent matrices with feedback at level $F_n \geq 0$: | | | | | | | | | | | | | | | |
| $F_5$ | 0 | 0 | 0 | .92 | 2.2 | 8.5 | 6.8 | 12 | 9.1 | 25 | 28 | 37 | 15 | 44 | 51 |
| $F_4$ | 0 | 0 | 0 | .26 | .62 | .78 | .86 | 9.6 | 1.3 | 3.4 | 12 | 11 | 2.6 | 31 | 31 |
| $F_3$ | 0 | 0 | 0 | 0 | .040 | .16 | .020 | 2.3 | .060 | .080 | 2.3 | 1.3 | .14 | 7.0 | 3.6 |
| $F_2$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | .08 | 0 | .16 | 0 |
| $F_1$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| D. Percent matrices failing criterion i: | | | | | | | | | | | | | | | |
| | 0 | 0 | 0 | .98 | 2.3 | 8.6 | 6.9 | 15 | 9.3 | 25 | 29 | 37 | 15 | 53 | 55 |
| E. Percent matrices with Hurwitz determinant $\Delta_n \leq 0$: | | | | | | | | | | | | | | | |
| $\Delta_5$ | 0 | 0 | 0 | 1.3 | 2.7 | 8.5 | 7.0 | 17 | 9.4 | 25 | 29 | 34 | 16 | 45 | 47 |
| $\Delta_4$ | 0 | 0 | 0 | .52 | .98 | .24 | .72 | 12 | .92 | .78 | 6.7 | 3.8 | 3.6 | 22 | 18 |
| F. Percent matrices failing criterion ii: | | | | | | | | | | | | | | | |
| | 0 | 0 | 0 | .52 | 1.0 | .44 | .76 | 12 | .98 | .96 | 7.4 | 4.1 | 3.7 | 23 | 19 |
| G. Percent matrices failing only criterion ii: | | | | | | | | | | | | | | | |
| | 0 | 0 | 0 | .38 | .62 | .060 | .40 | 6.1 | .38 | .24 | 2.7 | .72 | 2.0 | 2.2 | 2.7 |
| H. Percent matrices unstable: | | | | | | | | | | | | | | | |
| | 0 | 0 | 0 | 1.4 | 2.9 | 8.6 | 7.3 | 21 | 9.7 | 26 | 32 | 37 | 17 | 56 | 58 |

Note: Conditionally stable models, class I and class II, are designated by two characteristics: class I models have (1) maximum values of weighted feedback (bold font in sec. A) occurring at the highest level in the system and (2) values of the $n - 1$ weighted determinant ($w\Delta_4$) that are greater than or equal to $w\Delta_4 = .0093$ for model c (bold font in sec. B). A system is designated as class II if (1) maximum weighted feedback occurs at a lower level or (2) the fourth-weighted determinant is less than that of model c. For each model, 5,000 matrices were quantitatively specified by randomly assigning all $\alpha_{ii}$ and $\alpha_{ij}$ interaction terms from an even distribution varied by two orders of magnitude (0.01–1.0). Stability of each quantitatively specified matrix was judged by Hurwitz criteria i, negative feedback at all levels in the system, and Hurwitz criteria ii, all positive Hurwitz determinants.

from models, especially class II, with a large percentage of unstable matrices.

## *Maximum Weighted Feedback*

We consider next the implications of Hurwitz criterion i as assessed by weighted feedback in scaling-system stability. Maximum values of $wF_n$ are of concern because we are interested in identifying where conditions for overall negative (stabilizing) feedback are most compromised by countervailing conditions. By definition, class I models have a maximum value of weighted feedback only at their highest level, while in class II models it can (but need not) occur at a lower level. In figure 3*B*, class I models exhibit a strong negative curvilinear relationship ($r^2 > 0.6$) between the percentage of stable matrices and maximum $wF_n$ values for both five- and 10-variable systems. The left side of the curves is anchored by sign-stable models at 100% stable matrices. Models with maximum $wF_n > 0.5$ have a high percentage (>90%) of stable matrices. Given that weighted feedback is based on countervailing feedback cycles, a value of maximum $wF_n = 0$ should, on average, produce an equal number of stable and unstable matrices in class I models. Thus, the *y*-axis intercept should, theoretically speaking, be near 50%, as it is for the plot of five-variable models. However, the *y*-axis intercept for 10-variable models is closer to 75%, which is a result of the particular family of models selected for this analysis.

Weighted feedback can also be used to identify models prone to failing Hurwitz criterion ii, that is, class II models. From table 1, section C, nonnegative (destabilizing) feedback occurs most frequently at the same level in which maximum $wF_n$ values occur. When maximum $wF_n$ occurs at lower levels in a system (as in many but not all class II models), then it can be seen (table 1, sec. F) that there is an increased incidence of failure of criterion ii. Hence, where maximum $wF_n$ does not occur at the highest level in a system, then the lower level in which it does occur is most severely compromised by ambiguity or countervailing conditions. This insight conforms to the generality that instability in class II models can be caused by higher-level feedback being greater than lower-level feedback. In table 1, section A, one can consider the relative magnitudes of weighted feedback along each level in the system to-

| Class II models | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| p | q | r | s | t | u | v | w | x | y | z |
| **−1.00** | **−.25** | −1.00 | **0** | **0** | −.50 | −.25 | −.25 | −.21 | −.38 | −.28 |
| −1.00 | −.33 | **−.60** | −.20 | −.27 | **−.25** | **−.20** | **−.24** | **−.12** | **−.31** | −.19 |
| −1.00 | −.57 | −.67 | −.45 | −.56 | −.56 | −.41 | −.30 | −.13 | −.37 | **−.16** |
| −1.00 | −.75 | −1.00 | −1.00 | −1.00 | −.67 | −.68 | −.58 | −.44 | −.63 | −.53 |
| −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 | −1.00 |
| 0 | .0021 | .0071 | 0 | 0 | .00041 | −.000047 | −.00078 | −.00070 | −.0018 | −.0020 |
| **0** | **.0084** | **.0071** | **.0043** | **.0026** | **.00083** | **−.00019** | **−.0031** | **−.0034** | **−.0048** | **−.0070** |
| 0 | 25 | 0 | 49 | 50 | 11 | 11 | 8.8 | 15 | 6.3 | 11 |
| 0 | 19 | 12 | 23 | 22 | 28 | 17 | 11 | 28 | 11 | 21 |
| 0 | 4.0 | 6.8 | 12 | 11 | 6.7 | 2.8 | 10 | 32 | 8.2 | 29 |
| 0 | .46 | 0 | 0 | 0 | 2.5 | .28 | 1.1 | 5.7 | 1.3 | 3.5 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 34 | 17 | 57 | 54 | 38 | 21 | 19 | 48 | 16 | 38 |
| .080 | 48 | 67 | 66 | 66 | 66 | 55 | 75 | 84 | 70 | 84 |
| .080 | 36 | 67 | 49 | 56 | 63 | 54 | 73 | 83 | 71 | 83 |
| .080 | 39 | 68 | 63 | 68 | 69 | 54 | 73 | 85 | 71 | 86 |
| .080 | 22 | 51 | 29 | 34 | 37 | 39 | 59 | 44 | 58 | 52 |
| .080 | 55 | 68 | 85 | 88 | 75 | 64 | 78 | 92 | 75 | 91 |

gether as a sort of physical "moment" whereby stability is diminished as the moment increases in magnitude and is centered lower in the system.

### *The* n − *1 Weighted Determinant*

As we have just shown, maximum weighted feedback provides a scale by which to compare potential stability in class I models. It accounts for the majority of unstable matrices that are subject to failure by criterion i (table 1, secs. A, D, and H). It does not, however, reliably describe potential stability in class II models because these models are prone to fail criterion ii independently of criterion i, that is, pass i, fail ii (table 1, sec. G). Because the highest or *n*th Hurwitz determinant is interdependent with criterion i, we are led next to consider the $n-1$ weighted determinant in relation to the independence of criterion i and ii in unstable matrices. However, before doing so, we must first confront the difficulty of system size in judging relative values of weighted determinants. In figure 3*A*, we noticed that the highest degree of failure occurred with weighted determinants near to or less than 0. But, as stated earlier, proximity to 0 is confounded by the relative scale of the weighted determinants, which varies with system size; for example, the entire *x*-axis for weighted determinants of 10-variable models lies entirely to the left of the five-variable model c in figure 3*A*. We thus employ model c (or C) as a standard reference for being near 0. While model c is sign stable, its Hurwitz determinants are constituted by a delicate balance stemming from a minimal number of self-regulated variables.

In figure 3*C*, the $w\Delta_{n-1}$ value for model c (or C) sharply demarcates models with a high or low number of matrices failing only criterion ii. Below this threshold, class II models have a large percentage of matrices (>20% in models considered here, except for model p) that pass Hurwitz criterion i and fail criterion ii. Model p was used by Jeffries (1974) to demonstrate a system that could pass the Quirk-Ruppert rules yet be neutrally stable. This model is unique in having values of weighted feedback equal to −1.0 at every level in the system and *n*th and $n-1$ weighted determinants both equaling 0. These weighted determinants are composed of 76 terms equally divided in positive and negative sign. It should be noted that unstable matrices in model p were exceedingly rare, at most four out of 5,000, and all four were neutrally stable.

By definition, models with values of $w\Delta_{n-1}$ less than that of model c (or C) are designated as class II (table 1, sec. B). Although class II models with $w\Delta_{n-1}$ values greater than that of model c do exist, their matrices fail criterion ii independently of i about as frequently as class I models (fig. 3*C*). Class II models have two characteristics that contribute to a possible imbalance between higher and lower levels of feedback. First, where values of maximum weighted feedback do not occur at the highest level, then countervailing conditions are most severe at a lower level

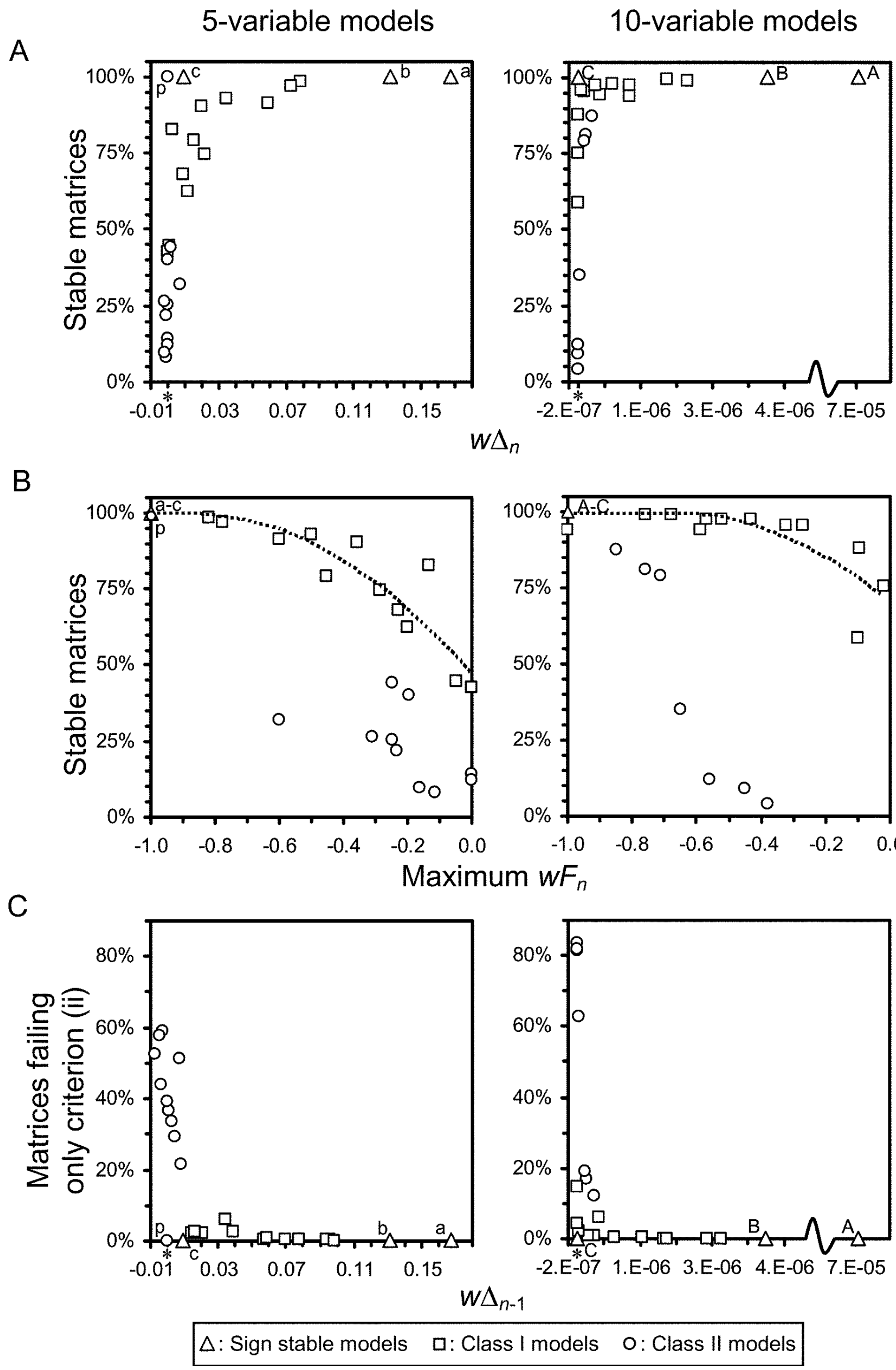



**Figure 3:** Stability analysis of five- and 10-variable model systems (figs. 1 and 2) in which interaction strengths of community matrix elements were randomly varied by two orders of magnitude (0.01–1.0) and assigned to 5,000 separate matrices. *A*, Percent stable matrices versus *n*th weighted determinant ($w\Delta_n$). *B*, Percent stable matrices versus maximum weighted feedback (maximum $wF_n$). Dotted lines drawn by hand show the relationship between maximum $wF_n$ and stability for sign stable and class I models. *C*, Relationship between the $n-1$ weighted determinant ($w\Delta_{n-1}$) and the percentage of quantitative matrices that were unstable only by criterion ii, that is, the percent passing criterion i but failing criterion ii. Zero on *x*-axes of *A* and *C* is denoted by an asterisk. Lower- and uppercase characters denote specific models discussed in the text.

in the system, which leads to domination by higher-level feedback. Second, small values of weighted determinants relative to a standard model c-type system indicate a nearly equal number of positive and negative terms in Hurwitz determinants such that nonpositive Hurwitz determinants, and hence unstable matrices, become more common in random parameter space.

## Discussion

Through the qualitative metrics of weighted feedback and weighted determinants, it is possible to scale meaningfully the effect that complexity has on the potential stability of two classes of conditionally stable models. This is accomplished through criteria i and ii derived from Hurwitz's ([1895] 1964) principal theorem and from Levins's (1974, 1975) and Puccia and Levins's (1985, 1991) concept of system feedback. These metrics were tested within a broad class of model ecosystems of varying size and complexity in a random and uniformly distributed parameter space. They emerge as a practical means of assessing potential model stability. While it is possible to explore other distributions of parameter space, we purposefully chose one that was numerically broad and with minimal assumptions, biological or otherwise.

We have approached the problem of system stability in this study and system predictability in other studies (Dambacher et al. 2002, 2003) strictly from a structural perspective. The advantages are that we circumvent quantitative considerations and gain some generality, but we have sacrificed the ability to explore interesting insights that arise from questions surrounding the magnitude of interactions. Recent studies have explored the importance and configuration of weak and strong links on the persistence of communities (McCann et al. 1998; Berlow 1999; McCann 2002), and we view the two approaches as complementary.

Class I models are prone to failure by criterion i due to positive (destabilizing) feedback occurring at one or more levels in the system, and their relative potential for stability can be judged by maximum weighted feedback. From the models we have studied thus far, class I models tend to have an abundance of pairwise relationships, particularly predator-prey, an abundance of self-regulated variables, and straight-chain or pyramidal trophic structures. We suggest that they might represent systems most commonly found in nature.

Class II models can be understood to be prone to failure by criterion ii, where feedback at higher levels in the system overwhelms feedback at lower levels, which leads to instability through overcompensation. The degree of stability of class II models can be judged by the qualitative metric of $n-1$ weighted determinants relative to a threshold value determined by a standard model c–type system. Class II models generally have a significant proportion of single links (amensal or commensal) within them, are less self-regulated, and are often less pyramidal in trophic structure. We suggest that they can encompass a type of system modified through human intervention wherein a paired relationship is damaged or a single link perceived as a cause-and-effect is introduced for management purposes, thus weakening lower-level feedback. These systems are of great concern from a manager's perspective, as they can give the appearance of stability because positive feedback, the cause of instability in class I models, can be negligible or even absent.

Although a consensus in ecology is that stability is ultimately at odds with complexity, we emphasize that this incompatibility is made most apparent when sign stability is used as the sole benchmark. Weighted feedback and weighted determinants are based on the network properties of system structure and can be used to assess and scale potential stability in large, complex systems. We found many complex models that were highly stable in quantitative simulations. These metrics may help resolve the impasse between theorists and empiricists in discussions of ecosystem diversity, complexity, and stability. Our results establish that if we can elucidate the structure of a community, we can, to a significant degree, assess its potential for stability.

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