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Stochastic structure and nonlinear dynamics of food webs: qualitative stability in a Lotka–Volterra cascade model

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Two competing models currently offer to explain empirical regularities observed in food webs. The Lotka–Volterra model describes population dynamics; the cascade model describes trophic structure. In a real ecological community, both population dynamics and trophic structure are important. This paper proposes and analyses a new hybrid model that combines population dynamics and trophic structure: the Lotka–Volterra cascade model (LVCM). The LVCM assumes the population dynamics of the Lotka–Volterra model when the interactions between species are shaped by a refinement of the cascade model. A critical surface divides the three-dimensional parameter space of the LVCM into two regions. In one region, as the number of species becomes large, the limiting probability that the LVCM is qualitatively globally asymptotically stable is positive. In the region on the other side of the critical surface, and on the critical surface itself, this limiting probability is zero. Thus the LVCM displays an ecological phase transition: gradual changes in the probabilities of various kinds of population dynamical interactions related to feeding can have sharp effects on a community's qualitative stability. The LVCM shows that an inverse proportionality between connectance and the number of species, and a direct proportionality between the number of links and the number of species, as observed in data on food webs, need not be directly connected with the qualitative global asymptotic stability or instability of population dynamics. Empirical testing of the LVCM will require field data on the population dynamical effects of feeding relations.

1. Introduction

Two competing models currently offer to explain a majority of empirical regularities observed in food webs (Lawton & Warren 1988; Lawton 1989). One model emphasizes dynamics, the other structure. The dynamical model of ecological communities – the Lotka–Volterra model – offers qualitative predictions about the long-run behaviour of the population sizes of interacting species, but is silent

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about how the interactions between species are determined (Pimm 1982). The Lotka–Volterra model is a system of nonlinear autonomous first-order ordinary differential equations. By contrast, the structural model, called the cascade model, describes many structural features of food webs or feeding relations among organisms (Cohen *et al.* 1990), but is silent about the population dynamics of the organisms. The cascade model is based on random directed graphs (digraphs). The Lotka–Volterra and the cascade models have evident shortcomings (some of which are mentioned below) and are by no means the only theoretical explanations for special aspects of structure in food webs (see Lawton (1989) for a review), but they are the two most general explanations proposed so far.

In a real ecological community, both population dynamics and trophic structure are important. There is an intellectual and empirical challenge in trying to connect the competing dynamic and structural models. Caswell (1988, p. 38) explicitly defends the connective role of theory in ecology.

This paper proposes and analyses a new hybrid model – called the Lotka–Volterra cascade model (LVCM) – that assumes the population dynamics of the Lotka–Volterra model when the interactions between species are shaped by a refinement of the cascade model (§2.3). Mathematical analysis of the LVCM combines the theory of large random digraphs with the qualitative theory of nonlinear differential equations to characterize the qualitative global asymptotic stability of ecological communities in the double limit of large time and large numbers of species. This form of stability describes a global tendency of hypothetical populations to approach an equilibrium, and may or may not have an important counterpart in the behaviour of real populations in Nature.

One major finding (§3.1) is that there exists a phase transition in qualitative global asymptotic stability, i.e. a sharp transition from a positive probability to a zero probability that the LVCM is qualitatively globally asymptotically stable (q.g.a.s.). This finding resembles a threshold property that May (1972, 1973) attributed to a much simpler, single-parameter model of community dynamics and structure, but differs in that our analysis is global and nonlinear. Unlike demonstrations in other models of an abrupt shift from one stable state to another as a result of a change in parameters or stochastic perturbations (see, for example, May 1977; Steele & Henderson 1984; Bondi 1985), our finding concerns transitions between stability and instability.

A second major finding (§4.1) is that, in the LVCM, the location of the phase transition in stability is not determined by a critical value of the product of the number of species and the connectance (defined in various ways). This finding differs from a conclusion that May (1972, 1973) drew about his model ecosystems. By contrast, in the LVCM, the location of the phase transition in stability is determined by a critical surface (described explicitly in §3.1) in a three-dimensional parameter space. On one side of the critical surface, there is a positive probability that the LVCM is q.g.a.s., while on the other side of the critical surface, and on the critical surface itself, there is a zero probability that the LVCM is q.g.a.s.

Efforts to link population dynamics and trophic structure in ecological theory have a venerable history (Hutchinson 1978; Pimm 1982). The LVCM and our analysis of it seem novel in two respects. First, the models for population dynamics

(Lotka–Volterra) and for trophic structure (cascade) each have some independent credibility, at least for some community ecologists; neither is an *ad hoc* construct for the purpose of achieving a synthesis. Second, the global behaviour of the fully nonlinear dynamic model is analysed. Previous efforts have often dealt with the local behaviour near equilibrium of linearized versions of dynamic models (see, for example, May (1972, 1973); Cohen & Newman (1988)) or have relied mainly on numerical simulations to demonstrate model behaviour (see, for example, Steele & Henderson (1984)).

Candour requires us to admit that both the Lotka–Volterra model and the cascade model have shortcomings, although each seems useful in limited circumstances. Among the defects of the Lotka–Volterra model as a description of the population dynamics of real populations are the assumptions that there are no mutualistic interactions between species (in the form of the model usually used by ecologists), that all interactions are strictly pairwise, and that the pairwise interactions follow a simple mass-action law specified by the product of abundances or biomasses. Among the defects of the cascade model as a description of the food webs of real communities are the assumption that trophic cycles (including cannibalism) are always absent, that feeding relations are static in time, and that each feeding relation is determined by a stochastic process independently of population abundances and independently of any other feeding relation. Both the Lotka–Volterra and the cascade models ignore genetic heterogeneity and age structure in populations as well as spatial and temporal heterogeneity (periodic or stochastic) in parameters, though each can be modified to accommodate these factors. This list of shortcomings of the Lotka–Volterra and cascade models does not purport to be exhaustive.

The LVCM shares the limitations of the Lotka–Volterra and cascade models, and has further limitations, described in §2.3. Thus the LVCM is not to be taken literally as a universal, realistic claim about Nature. The specific details of the LVCM are offered in the hope that the LVCM may lead to better models. The following developments illustrate how nonlinear dynamic models and stochastic structural models may be combined, analyzed, and related to observable facts about nature. Estimation of the LVCM's parameters and empirical testing of its predictions require field data on the population dynamical effects of feeding relations. A highly simplified lake food web is analysed to illustrate the empirical testing and use of the LVCM (§4.3).

2. MODELS: CASCADE, LOTKA–VOLTERRA, AND LOTKA–VOLTERRA CASCADE

We now describe the cascade model, the Lotka–Volterra model, and the hybrid Lotka–Volterra cascade model.

2.1. *The cascade model*

The cascade model (Cohen & Newman 1985*a*) assumes a community has n species. The species are assumed to be labelled or numbered $1, 2, \ldots, n$ (think of an ordering by increasing size). It is assumed that a species with a lower number can never eat a species with a higher number, but a species with a higher number has a probability c/n (where c is some positive constant less than n) of eating any species with a lower number, independently for all pairs of species. The most recent data indicate that the numerical value of c in nature is near 4 (Cohen 1990).

This model food web may be represented by a random digraph on n vertices, one vertex per species. A feeding relation is represented in this digraph by an arrow from a prey species to a predator species; the direction of the arrow shows the direction in which energy and materials flow. For any two vertices if $i < j$, there is no arrow (j, i) from vertex j to vertex i with probability 1. There is an arrow (i, j) from i to j with probability c/n, independently for all pairs i and j with $i < j$. We shall let W (for 'web') refer to this model of a random digraph, and let $P_W(i, j)$ denote the probability of an arrow (i, j) in W. Thus $P_W(i, j) = 0$ if $i > j$ and $P_W(i, j) = c/n$ for all $1 \leqslant i < j \leqslant n$.

This cascade model should not be confused with the model by the same name of Carpenter *et al.* (1985). The biological example in §4.3 below, based on the work of Carpenter and colleagues, will show a connection between their 'cascade' model and the Lotka–Volterra cascade model defined here.

2.2. *The Lotka–Volterra model*

The Lotka–Volterra model (as described by Redheffer & Zhou (1989)) assumes that the community has n species, labelled $1, 2, \ldots, n$. If u_i is the abundance or biomass of the ith species, then it is assumed that there exist a real $n \times n$ matrix $\mathbf{p} = (\mathbf{p}_{ij})$ and a real $n \times 1$ vector $\mathbf{e} = (\mathbf{e}_i)$, with both $\mathbf{p}$ and $\mathbf{e}$ independent of time t, such that, for all $t \in [0, \infty)$,

$$\frac{\mathrm{d}u_i}{\mathrm{d}t} = u_i\left(\mathbf{e}_i + \sum_{j=1}^{n} \mathbf{p}_{ij} u_j\right), \quad u_i(0) > 0, \quad i = 1, \ldots, n. \tag{1}$$

The coefficient $\mathbf{p}_{ij}$ measures the effect of species j on the growth rate of species i. It is assumed that (1) has a positive stationary solution, i.e. that there exists a constant $n \times 1$ vector $\mathbf{q} = (\mathbf{q}_i)$ such that

$$0 = \mathbf{e}_i + \sum_{j=1}^{n} \mathbf{p}_{ij} \mathbf{q}_j, \quad \mathbf{q}_i > 0, \ i = 1, \ldots, n. \tag{2}$$

As the values of the interaction coefficients in the matrix $\mathbf{p}$ in (1) can never be known exactly, but the signs of the coefficients can be determined more reliably, it is natural to consider the behaviour of (1) when the value of any interaction coefficient $\mathbf{p}_{ij}$ is changed to some other number with the same sign, whereas an interaction coefficient that is zero is left at zero. Under certain conditions, some of which will be described in a moment, the Lotka–Volterra model (1) bequeathes its stability to the whole family of equations obtained by replacing the interaction coefficients by others with the same signs. Under such conditions, (1) is said to be qualitatively stable. Qualitative stability is a natural concept for linking dynamic models with structural models based on random graphs, because structural models deal with the presence or absence of certain interactions, and not with the magnitudes of those interactions. What is surprising is that it is possible to say things about qualitative stability that connect usefully with structural food web models. Now we state these ideas more precisely.

For any real finite scalar s, define sign $(s) = +1$ if $s > 0$, sign $(s) = -1$ if $s < 0$ and sign $(s) = 0$ if $s = 0$. Define $\bar{p} \sim \mathbf{p}$ if and only if, for all i, j, sign $(\mathbf{p}_{ij}) =$ sign $(\bar{p}_{ij})$. Let $\bar{N}$ refer to the family of equations (1) when (i) $\mathbf{p}$ is replaced by any $n \times n$ matrix $\bar{p} \sim \mathbf{p}$, and (ii) $\mathbf{e}$ is replaced by any $n \times 1$ vector $\bar{e}$ such that $0 = \bar{e} + \bar{p}\bar{q}$ has a positive solution $\bar{q} > 0$. Positive initial conditions $u(0) > 0$ are assumed throughout. A result is considered 'qualitative' if it refers to all of $\bar{N}$.

A matrix $\mathbf{p}$ is defined to be sign semistable if, for every $\bar{p} \sim \mathbf{p}$, every eigenvalue of $\bar{p}$ has a non-positive (i.e., zero or negative) real part. Redheffer & Zhou (1989) proved results that contain the following as a special case.

THEOREM A. *Suppose* $\mathbf{p}_{ii} < 0$, *for* $i = 1, \ldots, n$. *If* $\mathbf{p}$ *is sign semistable, then every solution of every system in the family* $\bar{N}$ *is bounded, has a limit as* $t \rightarrow \infty$ *and that limit is independent of the initial condition.*

We need a converse of Theorem A.

THEOREM B. *If every solution of every system in the family* $\bar{N}$ *is bounded, has a positive limit* $\bar{q}$ *as* $t \rightarrow \infty$ *and that limit* $\bar{q}$ *is independent of the initial condition (though dependent on* $\bar{p}$ *and* $\bar{e}$*), then* $\mathbf{p}$ *is sign semistable.*

Proof. Suppose the nonlinear system (1) is globally asymptotically stable relative to the assumed positive stationary solution $\mathbf{q}$, i.e. every solution is bounded and has the limit $\mathbf{q}$ as $t \rightarrow \infty$ and that limit $\mathbf{q}$ is independent of the initial condition. Then no eigenvalue of its Jacobian matrix $J(\mathbf{q})$ evaluated at $\mathbf{q}$ can have positive real part (for if there were an eigenvalue of $J(\mathbf{q})$ with positive real part, there would exist a direction such that from this direction $\mathbf{q}$ would not be attractive). By direct calculation, $J(\mathbf{q})$ is the matrix with (i, j) element $\mathbf{q}_i \, \mathbf{p}_{ij}$. By the hypotheses of the theorem, if we take any $\bar{p} \sim \mathbf{p}$ and any $\bar{q} > 0$ and let $\bar{e} = -\bar{p}\bar{q}$, then also the matrix $(\bar{q}_i \, \bar{p}_{ij})$ cannot have eigenvalues with positive real part. Choosing $\bar{q}_i = 1$ for all i for each $\bar{p} \sim \mathbf{p}$, we conclude that the matrix $\mathbf{p}$ is sign semistable.

The combination of Theorems A and B shows that, assuming $\mathbf{p}_{ii} < 0$ for $i = 1, \ldots, n$, the matrix $\mathbf{p}$ of interaction coefficients is sign semistable if and only if every solution of every system in the family $\bar{N}$ is bounded and has a limit as $t \rightarrow \infty$ and that limit is independent of the initial condition. We shall say that a Lotka–Volterra system (1) with these characteristics is qualitatively globally asymptotically stable (q.g.a.s.).

There is a digraph D($\mathbf{p}$) associated with the matrix $\mathbf{p}$ of interaction coefficients. Following Jeffries *et al.* (1977, 1987) and Redheffer & Zhou (1989), we define the digraph D($\mathbf{p}$) of $\mathbf{p}$ as follows. D($\mathbf{p}$) has n vertices, an arrow (j, i) from vertex j to vertex i if $\mathbf{p}_{ij} \neq 0$ and $\mathbf{p}_{ji} = 0$, and a bidirectional arrow $\{i, j\}$ between i and j (equivalent to a pair of unidirectional arrows (j, i) and (i, j)) if $\mathbf{p}_{ij} \, \mathbf{p}_{ji} < 0$. (The case $\mathbf{p}_{ij} \, \mathbf{p}_{ji} > 0$ with $i \neq j$ will be excluded.) Whereas the food web digraph W represents feeding relations, the digraph D($\mathbf{p}$) represents population dynamical interactions. There seems to be no standard name for D($\mathbf{p}$), so we propose to call it the interaction digraph.

Quirk & Ruppert (1965) showed that $\mathbf{p}$ is sign semistable if and only if $\mathbf{p}_{ii} \leqslant 0$, $\mathbf{p}_{ij}\ \mathbf{p}_{ji} \leqslant 0$ for $i \neq j$, and $\mathrm{D}(\mathbf{p})$ has no k-cycles for $k \geqslant 3$. By using this fact in combination with Theorems A and B (and excluding the case $\mathbf{p}_{ij}\,\mathbf{p}_{ji} > 0$ with $i \neq j$), it is possible to determine whether a matrix $\mathbf{p}$ of interaction coefficients with negative diagonal elements determines a q.g.a.s. Lotka–Volterra system simply by inspecting the interaction digraph $\mathrm{D}(\mathbf{p})$ for the presence of k-cycles for any $k \geqslant 3$. This observation is the key to our main new mathematical result (§3.1).

With slightly different hypotheses, Bone *et al.* (1988, their Theorem 7.4) proved conclusions similar to those of theorem A. Instead of assuming that $\mathbf{p}_{ii} < 0$ for $i = 1, \ldots, n$, and that $\mathbf{p}$ is sign semistable, they assumed that $\mathbf{p}$ is sign stable (i.e. for every $\bar{p} \sim \mathbf{p}$, every eigenvalue of $\bar{p}$ has a negative real part) and that the digraph $\mathrm{D}(\mathbf{p})$ has a single strong component (i.e. every vertex of $\mathrm{D}(\mathbf{p})$ can be reached from every other vertex of $\mathrm{D}(\mathbf{p})$ by a directed path following the arrows in $\mathrm{D}(\mathbf{p})$). Now if $\mathbf{p}_{ii} < 0$, for $i = 1, \ldots, n$, and $\mathbf{p}$ is sign semistable, then $\mathbf{p}$ is sign stable, but a sign stable matrix may have many diagonal elements equal to zero. On the other hand, Theorem A allows $\mathrm{D}(\mathbf{p})$ to have many strong components.

2.3. *Lotka–Volterra cascade model*

The Lotka–Volterra cascade model (LVCM) links the cascade model to the Lotka–Volterra model by discriminating among the possible population dynamical effects caused by each feeding link. In principle, when species j eats species i, there could be a positive, a negative, or no effect on the population growth rate of species j, and a positive, a negative, or no effect on the population growth rate of species i, for a total of nine possible pairs of effects. As a first approximation to portions of reality, the LVCM ignores the five possible pairs of effects where j eating i hurts the population growth rate of species j or helps the population growth rate of species i. Thus if species j eats species i, the LVCM supposes that one of four biological effects occurs:

(i) the feeding has no effect on the growth of species j but hurts the growth of species i; or

(ii) the feeding helps the growth of species j but has no effect on the growth of species i; or

(iii) the feeding helps species j and hurts species i; or

(iv) the feeding has no effect on the growth of either j or i.

Corresponding to each biological effect, assume that:

(i) $\mathbf{p}_{ji} = 0$ and $\mathbf{p}_{ij} < 0$, so (j, i) is an arrow of $\mathrm{D}(\mathbf{p})$; or

(ii) $\mathbf{p}_{ji} > 0$ and $\mathbf{p}_{ij} = 0$, so (i, j) is an arrow of $\mathrm{D}(\mathbf{p})$; or

(iii) $\mathbf{p}_{ji} > 0$ and $\mathbf{p}_{ij} < 0$, so $\{i, j\}$ is a bidirectional arrow of $\mathrm{D}(\mathbf{p})$; or

(iv) $\mathbf{p}_{ji} = \mathbf{p}_{ij} = 0$, so no arrow of any kind exists between i and j in $\mathrm{D}(\mathbf{p})$.

Because of (iv), the event:

(iv′) no arrow of any kind exists between vertices i and j in $\mathrm{D}(\mathbf{p})$; represents two biologically distinct situations: predation without dynamic effects (described by (iv)) (e.g. the old lady who accidentally swallowed a fly), and the absence of predation (i.e. the absence of an edge (i, j) in W).

The LVCM assumes that events (i), (ii), (iii) and (iv′) occur, independently for each pair $i, j = 1, \ldots, n$ such that $i < j$, with probabilities, respectively, r/n, s/n, t/n, and $1-(r+s+t)/n$, where r, s, t are non-negative constants that do not depend on n. (Predation without dynamic effects (iv) occurs with probability $c/n-(r+s+t)/n$.)

More formally, for $n = 1, 2, \ldots$, let N_n be the system (1) with randomly chosen coefficients where, with probability 1, $\mathbf{p}_{ii} < 0$ for $i = 1, \ldots, n$ and the pairs $\{\mathbf{p}_{ji}, \mathbf{p}_{ij}\}$ for each $i, j = 1, \ldots, n$ with $i < j$ are chosen independently with

(i) $\operatorname{prob}\{\mathbf{p}_{ji} = 0 \text{ and } \mathbf{p}_{ij} < 0\} = r/n,$

(ii) $\operatorname{prob}\{\mathbf{p}_{ji} > 0 \text{ and } \mathbf{p}_{ij} = 0\} = s/n,$

(iii) $\operatorname{prob}\{\mathbf{p}_{ji} > 0 \text{ and } \mathbf{p}_{ij} < 0\} = t/n,$

(iv′) $\operatorname{prob}\{\mathbf{p}_{ji} = 0 \text{ and } \mathbf{p}_{ij} = 0\} = 1-(r+s+t)/n,$

and the vector $\mathbf{e}_n = (\mathbf{e}_i)_{i=1}^{n}$ is chosen (depending on $\mathbf{p}_n = (\mathbf{p}_{ij})_{i,j=1}^{n}$) so that for some vector $\mathbf{q}_n > 0$ (also depending on $\mathbf{p}_n$), $0 = \mathbf{e}_n + \mathbf{p}_n \mathbf{q}_n$. The sequence of systems $\{N_n\}_{n=1}^{\infty}$ defines the LVCM.

Pimm's (1982) studies of Lotka–Volterra models derived from hypothetical food webs represented each trophic link by a linkage of type (iii), with the further quantitative assumption that $|\mathbf{p}_{ij}| > \mathbf{p}_{ji}$. Lawton (1989, pp. 56–57) argues that dynamic links of types other than (iii) need to be considered, and reviews examples of links of type (ii), called 'donor control,' and of type (iv). Lawton (1989, p. 55) suggests that links of type (i) 'may occur with very polyphagous predators, where individual species of prey have trivial effects on the predator's dynamics, [but] the problem has received no attention in the food web literature.' His examples, and others, make it clear that dynamic links of types in addition to (iii) should be considered in a dynamic food web model.

In some respects, the LVCM is an even more limited model of community dynamics than the Lotka–Volterra model. As examples, the LVCM excludes a favourable effect of predation on the prey species (evidence for which is reviewed by Bianchi *et al.* (1989)); pairs of coefficients such that $\mathbf{p}_{ij} < 0$ and $\mathbf{p}_{ji} < 0$, which could represent competition between species i and j; and pairs of coefficients such that $\mathbf{p}_{ij} > 0$ and $\mathbf{p}_{ji} > 0$, which could represent mutualism between species i and j (examples of which are described by Kawanabe (1987)). Thus the LVCM is not the last word on models that relate deterministic, dynamic descriptions with stochastic, structural descriptions of communities.

3. MATHEMATICAL ANALYSIS: THE CRITICAL SURFACE FOR QUALITATIVE GLOBAL ASYMPTOTIC STABILITY

The LVCM has what physicists call a phase transition. As the parameters of the LVCM cross a certain critical surface, the probability of being qualitatively globally asymptotically stable changes from positive to zero. The critical surface for the phase transition in the stability of the LVCM is exactly the same as the critical surface for a phase transition when a giant strongly connected component suddenly appears in the digraph D(**p**) (Łuczak & Cohen 1990). The following theorem shows where the critical surface is and how the LVCM behaves on either side of the surface as well as on it.

3.1. *Theorem: limiting probability of qualitative global asymptotic stability*

Let x: $[1, \infty) \to (0, 1]$ be the smallest root of $x(z)\,\mathrm{e}^{-x(z)} = z\,\mathrm{e}^{-z}$.

(i) If

$$r+t < 1 \quad \text{and} \quad s+t < 1 \tag{3}$$

or

$$r+t \geqslant 1 \quad \text{but} \quad s+t < x(r+t) \tag{4}$$

or

$$s+t \geqslant 1 \quad \text{but} \quad r+t < x(s+t) \tag{5}$$

then

$$\lim_{n\to\infty} \text{prob}\,\{N_n \text{ is q.g.a.s.}\} = \lim_{n\to\infty} \text{prob}\,\{\mathbf{p}_n \text{ is sign semistable}\} = \rho > 0 \tag{6}$$

where

$$\rho = \begin{cases} \mathrm{e}^{(r+t)(s+t)/2}\, \dfrac{(r+t)\,\mathrm{e}^{s+t} - (s+t)\,\mathrm{e}^{r+t}}{r-s}, & r \neq s. \\ \mathrm{e}^{(r+t)^2/2}\,\mathrm{e}^{r+t}\,(1-r-t), & r = s. \end{cases} \tag{7}$$

When $(r+t)(s+t) > 0$, then $\rho < 1$.

(ii) If

$$r+t \geqslant 1 \quad \text{and} \quad s+t \geqslant x(r+t) \tag{8}$$

or

$$s+t \geqslant 1 \quad \text{and} \quad r+t \geqslant x(s+t) \tag{9}$$

then $\lim_{n\to\infty} \text{prob}\,\{\mathbf{p}_n \text{ is sign semistable}\} = 0$.

Informally speaking, a critical surface divides the three-dimensional parameter space $\{(r, s, t) | r \geqslant 0, s \geqslant 0, t \geqslant 0\}$ of the LVCM into two regions. In region (i), where (3) or (4) or (5) holds, as the number of species becomes large, the probability that the LVCM is qualitatively globally asymptotically stable (q.g.a.s.) approaches a positive limit, which is given explicitly by (7). In region (ii), where (8) or (9) holds, as the number of species becomes large, the probability that the LVCM is q.g.a.s. approaches zero.

3.2. *Proof of the theorem*

(i) By Theorems A and B, it suffices to show that, under the hypotheses, $\lim_n$ prob $\{\mathbf{p}_n$ is sign semistable$\} = \rho$ with $\rho > 0$ given by (7). By the assumptions of the LVCM, $\mathbf{p}_{ii} < 0$ and $\mathbf{p}_{ij}\,\mathbf{p}_{ji} \leqslant 0$ for $i \neq j$ with probability 1. Hence by the theorem of Quirk & Ruppert (1965) (quoted above after Theorems A and B), it suffices to show that $\lim_{n\to\infty}$ prob $\{\mathrm{D}(\mathbf{p}_n)$ has no k-cycles for $k \geqslant 3\} = \rho$ with $\rho > 0$. Now $\mathrm{D}(\mathbf{p}_n)$ is precisely the digraph denoted by $\mathrm{D}_n(r, s, t)$ in the main theorem of Łuczak & Cohen (1990). They proved that under the hypotheses (3–5), the number of cycles (i.e. directed cycles of length $\geqslant 3$) in $\mathrm{D}_n(r, s, t)$ is asymptotically Poisson distributed as $n \to \infty$ with a finite mean λ given by (A 1) in the Appendix. Starting from their expression, in the Appendix we derive the formulae (A 8) and (A 18), which immediately give (7) with $\rho = \mathrm{e}^{-\lambda}$.

(ii) When $s+t > x(r+t)$ or $r+t > x(s+t)$, part (ii) of the main theorem of Łuczak & Cohen (1990) asserts that $\lim_n$ prob $\{\mathrm{D}_n(r, s, t)$ contains a k-cycle for some $k \geqslant 3\} = 1$. By the theorem of Quirk & Ruppert (1965), it follows that $\lim_n$ prob

$\{\mathbf{p}_n$ is sign semistable$\} = 0$. Now assume that $s+t = x(r+t)$. (A similar argument will apply when $r+t = x(s+t)$.) Then it suffices to show that $\rho \to 0$ as $s \uparrow x(r+t)-t$. This follows easily from (7).

3.3. *Illustration of the critical surface*

The asymptotic ($n \to \infty$) probability that every $\bar{N}_n$ is globally asymptotically stable (g.a.s.) is ρ, given by (7) where $\rho > 0$ and is zero otherwise. Figure 1 plots the level contours of ρ as a function of $r+t$ and $s+t$. The probability of sign semistability is zero in the large region in the upper right of the figure and approaches one near the coordinate axes. The top curve in figure 1 is the frontier of stability, the curve that separates the region of zero probability of sign semistability from the region of positive probabilities of sign semistability; this curve plots the function $x(.)$ given at the start of §3.1. Figure 2 plots ρ in the special case $r = s < 1$ as a function of $r+t \in [0, 1]$. Figure 2 may be viewed as a partial cross-section through the surface in figure 1 along the diagonal $r+t = s+t$. When $r = s$ and $r+t > 1, \rho = 0$. Thus for $r+t > 1$, the derivative of ρ is evidently zero, but as $r+t$ approaches 1 from below, the derivative of ρ approaches $-e^{\frac{3}{2}}$. The transition from the region of positive probability to the region of zero probability of sign semistability is abrupt in the sense that the derivative of ρ changes discontinuously as the frontier of stability is crossed. Figure 3 plots a perspective view of the critical surface; $\rho = 0$ in the flat region in the foreground, where $r+t$ and $s+t$ are large, and takes positive values near the coordinate axes in the rear.

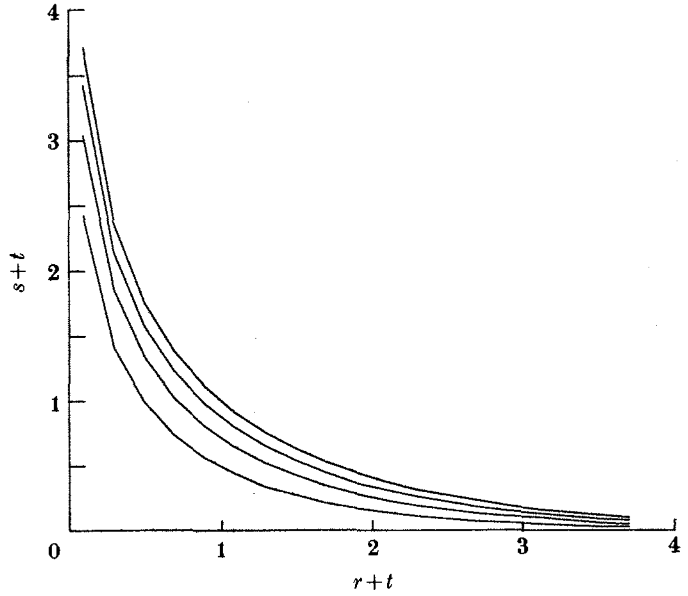

FIGURE 1. Contours of the probability of sign semistability or qualitative global asymptotic stability in the Lotka–Volterra cascade model, in the limit as the number of species approaches infinity, as a function of $r+t$ and $s+t$. The limiting probability is 0 in the region on and above the top curve. The curves below the top one show the contours where the limiting probability is 0.25, 0.5 and 0.75, respectively. The limiting probability is 1 along the $(r+t)$-axis and along the $(s+t)$-axis. Thus small values of $r+t$ and $s+t$ assure a high limiting probability of qualitative global asymptotic stability.

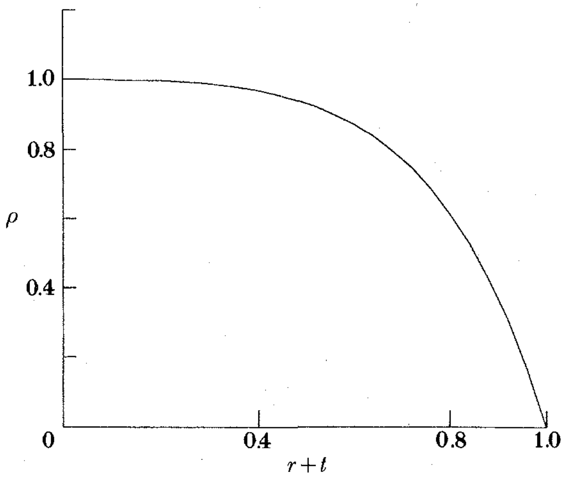

FIGURE 2. The probability of sign semistability or qualitative global asymptotic stability in the Lotka–Volterra cascade model, in the limit as the number of species approaches infinity, as a function of $r+t$, assuming $r = s$. Small values of $r+t$ assure a high probability of global asymptotic stability. For values of $r+t = s+t > 1$ (not shown in this figure), the probability is zero.

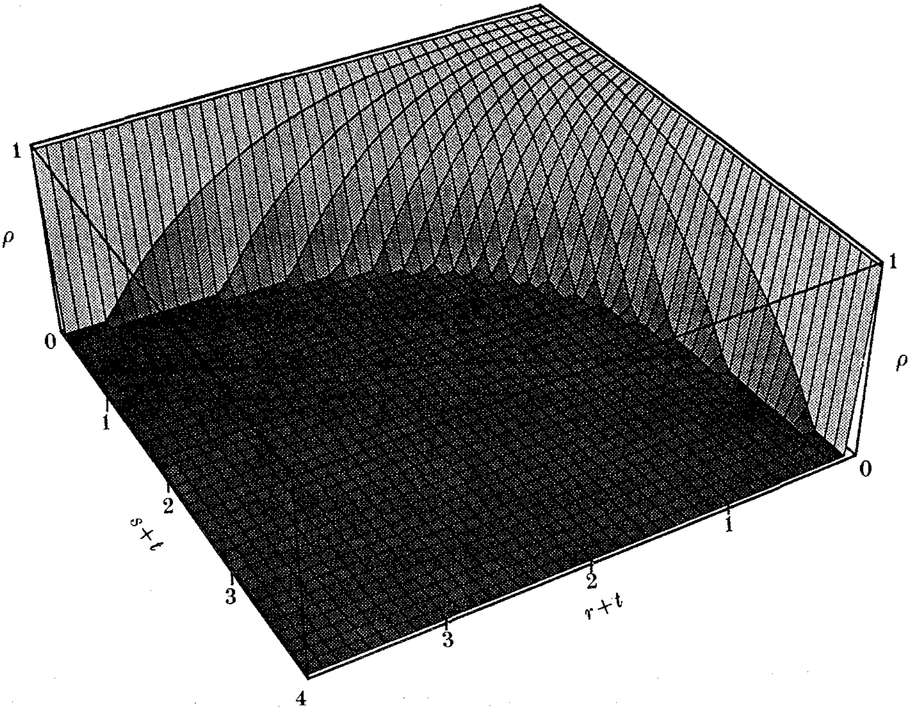

FIGURE 3. Perspective view of the probability of sign semistability or qualitative global asymptotic stability in the Lotka–Volterra cascade model, in the limit as the number of species approaches infinity, as a function of $r+t$ and $s+t$. The limiting probability is 0 in the flat region in the foreground. Small values of $r+t$ and $s+t$ assure a high limiting probability of qualitative global asymptotic stability.

4. BIOLOGICAL INTERPRETATION

4.1. *Connectance, species-link scaling, and stability: May's criterion*

An influential milestone in the history of efforts to link population dynamics and trophic structure was the claim by May (1972; 1973, p. 65) that the global stability of a linearized dynamic model is determined by $\lim_{n\to\infty} nCa^2$. Here n is the number of species, as usual; the connectance C (the fraction of all possible links that actually occur) depends on n; and a^2 (the mean squared interaction strength) is often assumed to be a constant independent of n. May asserted that if $\lim_{n\to\infty} nCa^2 > 1$, then his linear model is unstable with a probability that tends to one, while if $\lim_{n\to\infty} nCa^2 < 1$, then his linear model is stable with a probability that tends to one.

Without additional hypotheses, May's claim is not mathematically correct for his model, though it does hold for related models (Cohen & Newman 1984, 1985*b*). However, empirically testable consequences follow from the suppositions that a^2 is a constant independent of n, that $\lim_{n\to\infty} nCa^2$ exists and that real communities move to the frontier of stability where this limit equals one. Then, for large n, connectance C must be inversely proportional to the number of species n, as is observed approximately (Rejmánek & Starý 1979; Pimm 1982). If each non-zero element or each symmetrically located non-zero pair of elements in the community matrix of May's model corresponds to a fixed number of trophic links, then an inverse proportionality between C and n is equivalent to a direct proportionality between the expected number of trophic links and the number of species, as is observed approximately (Briand & Cohen 1984).

In retrospect, May (1984, p. 7) commented, and we agree: 'It is lunacy to imagine that the dynamical behaviour of real communities bears anything but the vaguest metaphorical relation to the linearized stability properties of the conventional "community matrix"' found in Levins (1968) and May (1973). We agree, even if May's comment applies to models of ours (Cohen & Newman 1984, 1985*b*, 1988) as well as to a model of his. (See also the review by Pimm (1984).)

Nevertheless, this background raises two interesting questions for the LVCM. First, does the LVCM predict an inverse proportionality between connectance and the number of species, or equivalently a direct proportionality between the number of trophic links and the number of species? Secondly, does $\lim_{n\to\infty} nC$ determine the stability of the LVCM? That is, if $\lim_{n\to\infty} nC$ exists in the LVCM, is there a constant K (analogous to a^{-2} in May's claim) such that the limiting probability that the LVCM is q.g.a.s. is positive if $\lim_{n\to\infty} nC < K$ and the limiting probability that the LVCM is q.g.a.s. is zero if $\lim_{n\to\infty} nC > K$?

We now show that the answer to the first question is yes; to the second, no. In the LVCM, there are two plausible ways to count links and two corresponding definitions of connectance. We define $\#\{.\}$ to mean the number of elements in the set $\{.\}$. Let the number of links in $D(\mathbf{p})$, counting bidirectional arrows as one link, be $L_1 = \#\{(\mathbf{p}_{ij}, \mathbf{p}_{ji}) | i \neq j \text{ and } |\mathbf{p}_{ij}| + |\mathbf{p}_{ji}| > 0\}$ and let $C_1 = L_1/[n(n-1)/2]$. Let the number of links in $D(\mathbf{p})$, counting bidirectional arrows as two links, be $L_2 = \#\{\mathbf{p}_{ij} | i \neq j \text{ and } |\mathbf{p}_{ij}| > 0\}$ and let $C_2 = L_2/[n(n-1)]$. It is easy to see that

$$\left.\begin{aligned}\lim_{n\to\infty} nC_1 &= r+s+t,\\ \lim_{n\to\infty} nC_2 &= \frac{r+s+2t}{2},\end{aligned}\right\} \tag{10}$$

$$\left.\begin{aligned}\lim_{n\to\infty} \frac{L_1}{n} &= \frac{r+s+t}{2},\\ \lim_{n\to\infty} \frac{L_2}{n} &= \frac{r+s+2t}{2}.\end{aligned}\right\} \tag{11}$$

Thus according to either definition of connectance, in the LVCM there is an inverse proportionality between connectance and the number of species, and a direct proportionality between the number of links and the number of species, for very large numbers of species. These conclusions are built into the LVCM by the assumption that the arrows of types (i), (ii) and (iii) in the interaction digraph occur with a probability inversely proportional to the number n of species, because the number of possible links in the definitions of connectance C_1 and C_2 is asymptotically proportional to n^2.

A single one of the limits in (10) does not suffice to determine the limiting probability of qualitative global asymptotic stability in the LVCM. For example, from the connectance C_1, suppose $r+s+t = 4$. If $r = 4$ while $s = t = 0$, then (4) holds, and the limiting probability is one that the LVCM is q.g.a.s. But if $r = s = 1$ and $t = 2$ (so that $r+s+t = 4$ still holds), then (8) holds (since $s+t > 1 \geqslant x(r+t)$), so the limiting probability is zero that the LVCM is q.g.a.s. Similarly, from the connectance C_2, suppose $(r+s+2t)/2 = 2$. If $r = 4$ while $s = t = 0$, then (4) holds, and the limiting probability is one that the LVCM is q.g.a.s. But if $r = s = t = 1$ (so that still $(r+s+2t)/2 = 2$), then (8) holds (because $s+t > 1 \geqslant x(r+t)$), so the limiting probability is zero that the LVCM is q.g.a.s.

The LVCM shows that an inverse proportionality between connectance and the number of species, and a direct proportionality between the number of links and the number of species, need have no simple connection with the qualitative global asymptotic stability or instability of population dynamics. Because the LVCM distinguishes four dynamic effects of a trophic link, multiple parameters (r, s, t) are required to describe the relative frequencies of these effects. The phase transition in the LVCM model occurs across a critical surface in parameter-space, rather than at a critical value of a single parameter, as claimed in May's (1972) model.

4.2. *Reconciliation with the cascade model*

According to the cascade model, the probability of a feeding link from any trophic species i to any trophic species j with $i < j$ is approximately $4/n$. According to the LVCM, the probability of an arrow (in either direction or both) between any two distinct vertices in the interaction digraph $\mathrm{D}(\mathbf{p}_n)$ of $\mathbf{p}_n$ (counting bidirectional arrows as one, since a bidirectional arrow represents a single trophic link) is $(r+s+t)/n$. If the trophic species of the cascade model may be identified with the species of the LVCM, then consistency between the cascade model and the LVCM requires that

$$r+s+t \leqslant 4, \tag{12}$$

with equality unless some predator–prey links affect the dynamics of neither predator nor prey populations [the event (iv) in §2.3]. On the assumption that at least some observed ecological communities have a positive probability of being q.g.a.s., we now consider how (12) can be reconciled with the hypotheses (3–5) of the theorem, part (i).

If (3) holds, then $r+s+2t \leqslant 2$. Therefore at least half of observed trophic links must be without any dynamic consequences.

If (4) holds, the maximal possible value of t occurs when $s = 0$. In this case, the maximal value of t satisfies $t = x(r+t)$. Assuming equality in (12) and $s = 0$ gives $r+t = 4$, hence $t = x(4)$. Numerical solution of this equation gives the approximate solution $t = 0.08$. Therefore $r = 4-t = 3.92$ approximately. The overwhelming majority of trophic links hurt the prey population but have no dynamic impact on the predator population.

If (5) holds, a symmetrical argument with r and s exchanged leads to the symmetrical conclusion that the overwhelming majority of trophic links help the predator population but have no dynamic impact on the prey population. Both of the last two conclusions follow from assuming equality in (12), and need not follow if many trophic links are without any dynamic consequences.

Mathematical analysis alone is insufficient to determine which, if any, of the conditions (3–5) is closest to reality, assuming that a real ecological community has a positive probability of being q.g.a.s. Empirical studies are required to discriminate among the possibilities.

4.3. *Simplified biological example: a lake food web*

A highly simplified example illustrates the possibilities for using data to test the LVCM and for using the LVCM to interpret data. The food web shown in figure 4*a* is based on studies of lakes in the north-central United States (Carpenter 1988;

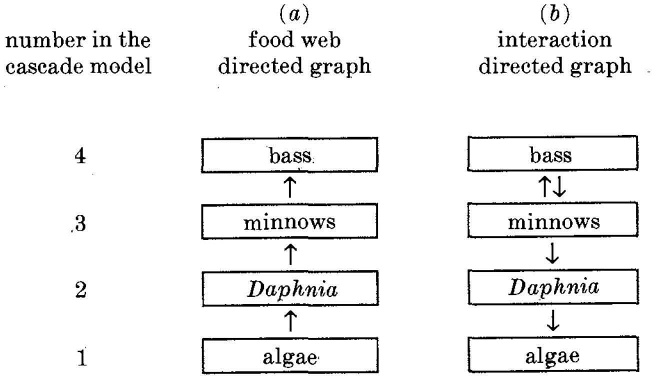

FIGURE 4. Schematic food web (*a*) and interaction digraph (*b*) of a lake in the north-central United States, based on drastic simplification of the reports of Carpenter (1988), Carpenter & Kitchell (1987), and Carpenter *et al.* (1985). In (*a*), arrows show the direction of flow of food from prey to predator. In (*b*), arrows show the direction of influence of one population on the per capita growth rate of the other population. Other interaction-directed graphs are equally plausible descriptions of this lake; see text for further details.

Carpenter & Kitchell 1987; Carpenter *et al.* 1985; and their references), but makes no pretence of doing justice to the complexity of the web as described in the original reports. In this strictly illustrative caricature of a web, large-mouth bass represent piscivores; minnows represent zooplanktivores (including invertebrate zooplanktivores such as *Chaoborus*); *Daphnia* represent zooplankton (including rotifers); and algae represent the aggregated edible phytoplankton. This simplification omits phosphorus altogether.

Carpenter *et al.* (1985, p. 636) write: 'An increase in piscivore density cascades through the food web in the following way. Vertebrate zooplanktivores are reduced while planktivory by invertebrates increases, shifting the herbivorous zooplankton community toward larger zooplankters and higher biomass. Chlorophyll *a* concentration declines.'

Based on this verbal description, the equations of Carpenter (1988, pp. 122–123), and the schematic food web of Carpenter & Kitchell (1987, p. 419), we infer that the signs of the interaction coefficients in a Lotka–Volterra model for the populations of bass (abbreviation: B), minnows (M), *Daphnia* (D) and algae (A) are:

$$\operatorname{sign}(\mathbf{p}) = \begin{array}{c} \\ A \\ D \\ M \\ B \end{array} \begin{array}{c} \begin{array}{cccc} A & D & M & B \end{array} \\ \begin{pmatrix} -1 & -1 & 0 & 0 \\ 0 & -1 & -1 & 0 \\ 0 & 0 & -1 & -1 \\ 0 & 0 & +1 & -1 \end{pmatrix} \end{array}. \tag{13}$$

The minnows are assumed to have a positive effect on the per capita population growth rate of the bass (sign $(\mathbf{p}_{BM}) = +1$) because no other food source for piscivores is shown in the web of Carpenter & Kitchell (1987, p. 419). The bass are assumed to have a negative effect on the per capita population growth rate of the minnows (sign $(\mathbf{p}_{MB}) = -1$) because, in the model of Carpenter (1988, p. 123), 'the survivorships of the small fishes decline linearly as piscivore biomass increases.' The remaining off-diagonal signs are derived or guessed similarly. The diagonal elements $\mathbf{p}_{ii}$ are assumed to be negative in this illustration because, even in the absence of limits on population growth set by food supplies or predators, at sufficiently high equilibrium densities intraspecific crowding and interference competition seem likely to intervene. The interaction digraph D($\mathbf{p}$) derived from (13) is shown in figure 4*b*.

As Stephen R. Carpenter (personal communication, 30 July 1989) pointed out, 'several sign configurations for the matrix $\mathbf{p}$ may be defensible.... [Other] equally reasonable configurations would be: (i) all predators are helped by consuming prey, so all subdiagonals ($\mathbf{p}_{BM}$, $\mathbf{p}_{MD}$, $\mathbf{p}_{DA}$) are positive. (ii) All compartments are regulated mainly by their predators, and are satiated by available food. Available food for a compartment is the compartment it eats plus 'alternate' foods not represented in the model. For example, *Daphnia* eat detritus and algae; minnows eat periphyton and zooplankton; bass eat benthos and minnows.' These alternative configurations would change the conclusions of the following illustrative analysis based on (13). More seriously, according to Carpenter (personal communication, 30

July 1989), 'the dynamics of (1) do not resemble those of lake communities.' We emphasize that this example is illustrative.

The sign matrix (13) and the interaction digraph satisfy the criteria of Quirk & Ruppert (1965) for sign semistability. (The criteria for sign semistability, but not the hypotheses of Theorem A, are satisfied even if some or all of the diagonal signs in (13) are changed from -1 to 0.) Whatever may be the numerical values of the interaction coefficients ($\mathbf{p}_{ij}$), so long as they have the sign pattern (13), the solutions of the Lotka–Volterra equations will be q.g.a.s., according to Theorem A. We now investigate whether arbitrarily large Lotka–Volterra systems with the same *statistical* properties will have a positive probability of being q.g.a.s.

The parameters of the LVCM may be estimated by simple counting. We denote the statistical estimates, based on data, of the model's parameters r, s and t by $\hat{r}$, $\hat{s}$, and $\hat{t}$, respectively. The number of species is $n = 4$. There are six pairs of off-diagonal elements. Of these, two correspond to 'down' arrows ($\{\mathbf{p}_{\mathrm{DM}} < 0, \mathbf{p}_{\mathrm{MD}} = 0\}$ and $\{\mathbf{p}_{\mathrm{AD}} < 0, \mathbf{p}_{\mathrm{DA}} = 0\}$) so $\hat{r}/n = \frac{2}{6}$ or $\hat{r} = \frac{4}{3}$. Similarly, there are no pairs of off-diagonal elements corresponding to 'up' arrows so $\hat{s} = 0$. There is one pair of off-diagonal elements corresponding to a bidirectional arrow ($\{\mathbf{p}_{\mathrm{MB}} < 0, \mathbf{p}_{\mathrm{BM}} > 0\}$) so $\hat{t}/n = \frac{1}{6}$ or $\hat{t} = \frac{2}{3}$. Thus $\hat{r}+\hat{t} = 2 > 1$ and $\hat{s}+\hat{t} = 0+\frac{2}{3} > x(\hat{r}+\hat{t}) = x(2) = 0.4064$. If the estimates of r, s and t did not change as n increased without limit, then (8) would apply, and the LVCM with these parameter values would have a zero limiting probability of being q.g.a.s. Obviously, parameter estimates based on $n = 4$ have high variance and do not provide much information about what would actually happen in the limit of large n.

Suppose, still for illustration, that $r = \frac{4}{3}$ and $s = 0$. Biologically, we are supposing that the trophic links arise only when (i) the predator hurts the prey or when (iii) the predator hurts the prey and the prey helps the predator, but not when (ii) the prey helps the predator but is not itself hurt. Then the critical value of t (which is the probability of bidirectional effects (iii)), that is, the value of t that separates the region of possible limiting stability from the region of instability is, according to (4) and (8), the solution of $t = x(\frac{4}{3}+t)$. Numerically we find $t = 0.48$ approximately. Estimating $c = 2L/(n-1)$ by formula (6.9) of Cohen & Newman (1985*a*, p. 435), where L is the number of trophic links in the web ($L = 3$ in figure 4*a*) gives $c = 2$ (lower than the typical value of 4; Cohen 1990). Assuming, for the sake of discussion, that the web is in the region of possible stability and therefore $t < 0.48$, it follows that the probability of predation without dynamic effects

$$[c-(r+s+t)]/n,$$

is at least $[2-(\frac{4}{3}+0.48)]/4 = 0.05$ approximately. Such predictions could be checked against observations.

5. Conclusions and prospects

5.1. *Synopsis of results*

A globally asymptotically stable (g.a.s.) Lotka–Volterra model approaches a positive limit independent of the initial conditions. For some, but by no means all, ecological communities, this property may usefully formalize what is meant by ecological stability (Pimm 1984). A Lotka–Volterra model is qualitatively g.a.s. (q.g.a.s.) if all Lotka–Volterra models with interspecific and intraspecific interaction parameters that share the sign pattern of the given model are also g.a.s.

The Lotka–Volterra cascade model (LVCM) assumes that the effects of any one species on the per capita growth rate of any other (the dynamic interactions) are present or absent according to a stochastic process like the one that determines whether any one species eats or is eaten by any other (the trophic interactions). Three parameters (r, s, t) determine the dynamic consequences of each predator–prey link or feeding relation that would be recorded in a food web. If n is the number of species, a trophic link hurts the prey but does not help the predator with probability r/n, helps the predator but does not hurt the prey with probability s/n, and helps the predator and hurts the prey with probability t/n. Here 'helps' means 'increases the population's per capita growth rate' and 'hurts' means 'decreases the population's per capita growth rate.'

Although we have derived the Lotka–Volterra cascade model from the cascade model by partitioning food web links according to their dynamic effects (or lack of effects), the LVCM can also be viewed as a free-standing model in its own right, independent of any derivation from a food web model.

Under the assumptions of the Lotka–Volterra cascade model, we have shown that, as the number of species becomes arbitrarily large, the probability of producing a q.g.a.s. Lotka–Volterra model approaches a limiting probability, which depends on the model's three parameters. A critical surface divides the parameter space $\{(r, s, t) | r \geqslant 0, s \geqslant 0, t \geqslant 0\}$ of the LVCM into two regions. In the region of possible stability, which lies below the critical surface, as the number of species becomes large, the limiting probability that the LVCM is q.g.a.s. is positive. Except when $r+t = 0$ or $s+t = 0$, this limiting probability is strictly less than one, so that there is a positive limiting probability that not every Lotka–Volterra model with the given pattern of interaction parameters will be g.a.s., even though each species is assumed to have negative density-dependence ($\mathbf{p}_{ii} < 0, i = 1, \dots, n$). Above or on the critical surface, the limiting probability that the LVCM is q.g.a.s is zero.

The critical surface between the region of possible stability and the region of instability reveals the trade-offs (3–9) among the three key probabilities of the LVCM. The higher the probability (t/n) of dynamic links that both help the predator and hurt the prey, the lower must be the probabilities of the other kinds of link. For a fixed probability of bidirectional dynamic links that both help the predator and hurt the prey, there is a trade-off between the probability (r/n) of dynamic links that hurt the growth of the prey only and the probability (s/n) of dynamic links that help the growth of the consumer only. As either probability increases from zero, the maximum possible value of the other that is consistent with a positive probability of being q.g.a.s. declines.

The LVCM sheds new light on May's (1972, 1973) criterion for the asymptotic stability of a linearized model of community dynamics. The LVCM implies an inverse proportionality between connectance and the number of species, and a direct proportionality between the number of links and the number of species, but the limit of the product of the number of species times connectance does not determine whether the limiting probability of being q.g.a.s. is zero or positive.

Thus the scaling of links with species needs have no simple connection with the qualitative global asymptotic stability or instability of population dynamics.

5.2. *Mathematical prospect*

The theory of the qualitative stability of linear and nonlinear systems has made great progress since the pioneering paper of Quirk & Ruppert (1965). Jeffries *et al.* (1987) and Jeffries (1988*b*) review and extend this progress. The qualitative stability of linear systems is closely connected to the qualitative stability of Lotka–Volterra systems (as demonstrated in slightly different ways by Bone *et al.* (1988, their Theorem 7.4) and Redheffer & Zhou (1989)). An open scientific opportunity is to exploit recent discoveries about the qualitative stability of linear systems (such as those in Jeffries *et al.* (1987)) and of nonlinear systems (such as those of Jeffries (1988*a*) and Redheffer (1989)) to give new information about stochastic families of nonlinear dynamical systems like the Lotka–Volterra cascade model.

5.3. *Biological prospect*

Food webs alone are not enough to predict dynamic behaviour. Field ecologists need to determine, by experiments or observations, at least the matrix of the signs of the population dynamical effects of feeding relations, as illustrated by (13). When species j eats species i, what are the consequences for the population growth rates of species j and of species i? Do the interaction digraphs of most real ecological communities fall in the region of (r, s, t)-space where, according to the Lotka–Volterra cascade model, they have a positive limiting probability of being qualitatively globally asymptotically stable?

Information about qualitative global asymptotic stability could assist the design of managed ecological systems such as closed ecological life support systems for space travel, nature reserves, and complex chemostats, microcosms and mesocosms. Qualitatively globally asymptotically stable systems may be desirable for practical and aesthetic reasons, because perturbations that do not change the signs of the interactions between species will not alter the existence of a long-run globally stable equilibrium. If future empirical studies confirm its usefulness, the LVCM would suggest designs that maximize (subject to some constraints) the probability of being q.g.a.s., asymptotically for large numbers of species; those are designs that satisfy the hypotheses of §3.1 (i) with large values of ρ. The Lotka–Volterra cascade model would suggest avoiding ecological designs that have little chance of being q.g.a.s., asymptotically for large numbers of species; those are designs that satisfy the hypotheses of §3.1 (ii).

Apart from its potential uses in ecological design, the LVCM warns of the possibility that gradual, smooth changes in the probabilities r, s, and t of various kinds of dynamic interactions related to feeding can have abrupt effects on the long-run probability of qualitative global stability or instability of ecological communities.

APPENDIX 1: EVALUATION OF ρ

Under the hypotheses (4) and (5) Łuczak & Cohen (1990) obtained the following expression for λ, the asymptotic mean number of cycles (i.e., directed cycles of length $\geqslant 3$) in the digraph $\mathrm{D}(\mathbf{p}_n)$ (denoted $D_n(r, s, t)$ in Łuczak & Cohen (1990)) as $n \to \infty$:

$$\lambda = \sum_{k=3}^{\infty} \frac{1}{k!} \sum_{u=1}^{k-1} C(k, u)(r+t)^{k-u}(s+t)^u. \tag{A 1}$$

Here $C(k, u)$ is the number of directed cycles of length k that pass through each vertex of the set $\{1, \dots, k\}$ with exactly u 'up arrows', i.e. arrows that go from a smaller vertex i to a larger vertex $j > i$. In this Appendix, we will obtain a simple closed-form expression for the infinite series in (A 1) when $(r+t)(s+t) > 0$.

We define an integral operator G (acting on functions $u(x)$ in the Hilbert space $L^2([0, 1], \mathrm{d}x)$) by

$$(Gu)(x) = \int_0^1 g(x, y)\, u(y) \mathrm{d}y, \quad g(x, y) = \begin{cases} a \equiv r+t, & x > y, \\ b \equiv s+t, & x < y. \end{cases} \tag{A 2}$$

For $k \geqslant 2$, G^k is trace class and its trace may be evaluated as

$$\begin{aligned} \operatorname{tr}(G^k) &= \int_0^1 \dots \int_0^1 g(x_1, x_2)\, g(x_2, x_3) \dots g(x_{k-1}, x_k)\, g(x_k, x_1)\, \mathrm{d}x_1 \dots \mathrm{d}x_k \\ &= \sum_{\pi} \int \dots \int_{0<x_1< \dots <x_k<1} g(x_{\pi 1}, x_{\pi 2}) \dots g(x_{\pi k}, x_{\pi 1})\, \mathrm{d}x_1 \dots \mathrm{d}x_k \\ &= \sum_{\pi} \frac{1}{k!} a^{k-u(\pi)} b^{u(\pi)} \\ &= \frac{1}{(k-1)!} \sum_{u=1}^{k-1} C(k, u)\, a^{k-u} b^u, \end{aligned} \tag{A 3}$$

where the first two sums are over all permutations π of $\{1, \dots, k\}$ and $u(\pi)$ denotes the number of up arrows of π, i.e. the number of pairs $(\pi i, \pi(i+1))$, $i = 1, \dots, k$, such that $\pi i < \pi(i+1)$ (here $\pi(k+1) = \pi 1$ by definition). We shall see below that G has a complete set of eigenfunctions $\{f_n : n \in \mathbf{Z}\}$ with eigenvalues $\{\lambda_n : n \in \mathbf{Z}\}$; it then follows from (A 1), (A 3) and the identity, $\operatorname{tr}(G^2) = ab$, that

$$\begin{aligned} \rho = \mathrm{e}^{-\lambda} &= \mathrm{e}^{ab/2} \exp\left(-\sum_{k=2}^{\infty} \frac{1}{k} \operatorname{tr}(G^k)\right) \\ &= \mathrm{e}^{ab/2} \exp\left(\sum_n \sum_{k=2}^{\infty} -\frac{1}{k}(\lambda_n)^k\right) \\ &= \mathrm{e}^{ab/2} \exp\left(\sum_n [\lambda_n + \ln(1-\lambda_n)]\right) \\ &= \mathrm{e}^{ab/2} \prod_n \mathrm{e}^{\lambda_n}(1-\lambda_n) \equiv \mathrm{e}^{ab/2} \Delta(G), \end{aligned} \tag{A 4}$$

where n runs over the integers $\mathbf{Z}$ in the summations and products above. Absolute convergence of the infinite series and products appearing in (A 4) is guaranteed by (4) and (5).

To find the eigenvalues and eigenfunctions, we take the eigenvalue equation,

$$\lambda f(x) = (Gf)\ (x) = a \int_0^x f(y)\, \mathrm{d}y + b \int_x^1 f(y)\, \mathrm{d}y, \tag{A 5}$$

differentiate it and evaluate it at $x = 0$ and 1. This yields

$$\lambda f'(x) = (a-b)f(x), \tag{A 6}$$

$$\lambda f(0) = b\int_0^1 f(y)\,\mathrm{d}y, \quad \lambda f(1) = a\int_0^1 f(y)\,\mathrm{d}y. \tag{A 7}$$

When $a = b$, the kernel $g(x, y)$ in (A 2) is the constant a; hence one eigenfunction is $u_0(x) \equiv 1$ with eigenvalue a and the orthogonal complement of u_0 is an eigenspace of eigenvalue 0. Hence for $a = b$, we have

$$\mathrm{e}^{-\lambda} = \mathrm{e}^{a^2/2}\mathrm{e}^{a}(1-a), \quad a = b. \tag{A 8}$$

Henceforth, we assume that $a \neq b$. In this case, (A 6)–(A 7) yield

$$f(x) = \mathrm{e}^{(a-b)x/\lambda}, \quad \frac{a}{b} = \frac{f(1)}{f(0)} = \mathrm{e}^{(a-b)/\lambda}, \tag{A 9}$$

where we have chosen the normalization $f(0) = 1$. Then the eigenvalues λ_n are given by

$$\lambda_0 = \frac{a-b}{\ln(a/b)} \in (0, \infty), \quad \frac{a-b}{\lambda_n} = \frac{a-b}{\lambda_0} + \mathrm{i}2n\pi \tag{A 10}$$

and the eigenfunctions are, of course,

$$f_n(x) = \mathrm{e}^{(a-b)x/\lambda_n} = e^{(a-b)x/\lambda_0 + \mathrm{i}2n\pi x}. \tag{A 11}$$

Because the set $\{\mathrm{e}^{\mathrm{i}2n\pi x} : n \in \mathbf{Z}\}$ is complete in $L_2([0, 1], \mathrm{d}x)$, it follows that so is $\{f_n(x) : n \in \mathbf{Z}\}$. Thus

$$\Delta(G) \equiv \prod_n \mathrm{e}^{\lambda_n}(1-\lambda_n) = \prod_n \mathrm{e}^{w/w_n}(1-w/w_n) \equiv h(w), \tag{A 12}$$

where, again, the products are over all $n \in \mathbf{Z}$, with

$$w_n = \ln(a/b) + \mathrm{i}2n\pi, \quad w = a-b. \tag{A 13}$$

The function h is an entire function of exponential order 1 with (simple) zeros exactly at the w_n. Because this is also the case for the function $\sinh([w-\ln(a/b)]/2)$, it follows that

$$h(w) = Ke^{cw}\sinh\left(\frac{w-\ln(a/b)}{2}\right) \tag{A 14}$$

for some constants K and c, which must be chosen so that h given by (A 14) has $h(0) = 1$ and $h'(0) = 0$, as implied by (A 12). We thus obtain

$$K = \left[\sinh\left(\frac{-\ln(a/b)}{2}\right)\right]^{-1} = \frac{2(ab)^{\frac{1}{2}}}{b-a}, \tag{A 15}$$

$$c = \frac{1}{2}\coth\left(\frac{1}{2}\ln\frac{a}{b}\right) = \frac{1}{2}\frac{a+b}{a-b}. \tag{A 16}$$

Inserting these expressions into (A 14), setting $w = a-b$ and doing some straightforward algebra, we obtain

$$\Delta(G) = \frac{a\,\mathrm{e}^{b} - b\,\mathrm{e}^{a}}{a-b}. \tag{A 17}$$

Thus, with $a = r+t$ and $b = s+t$,

$$\rho = e^{-\lambda} = e^{ab/2}\frac{a\,e^{b} - b\,e^{a}}{a-b}, \quad a \neq b. \tag{A 18}$$

The expression in (A 18) can be shown to converge to that in (A 8) when $b \to a$.

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