



Global Stability, Local Stability and Permanence in Model Food Webs

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The dynamical theory of food webs has been based typically on local stability analysis. The relevance of local stability to food web properties has been questioned because local stability holds only in the immediate vicinity of the equilibrium and provides no information about the size of the basin of attraction. Local stability does not guarantee persistence of food webs in stochastic environments. Moreover, local stability excludes more complex dynamics such as periodic and chaotic behaviors, which may allow persistence. Global stability and permanence could be better criteria of community persistence. Our simulation analysis suggests that these three stability measures are qualitatively consistent in that all three predict decreasing stability with increasing complexity. Some new predictions on how stability depends on food web configurations are generated here: a consumer–victim link has a smaller effect on the probabilities of stability, as measured by all three stability criteria, than a pair of recipient-controlled and donor-controlled links; a recipient-controlled link has a larger effect on the probabilities of local stability and permanence than a donor-controlled link, while they have the same effect on the probability of global stability; food webs with equal proportions of donor-controlled and recipient-controlled links are less stable than those with different proportions.

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Introduction

The relationship between stability and complexity of food webs has been a central issue in theoretical ecology. An influential theory, based on the local asymptotic stability (LAS) analysis of randomly assembled Lotka–Volterra model food webs, suggested that complexity reduces stability (May, 1972). This theory has been challenged for two reasons.

First, LAS may not be an appropriate criterion for food web persistence. LAS holds only in an arbitrarily small neighborhood of the equilibrium (Lewontin, 1969; Haydon, 1994) and

depends on the interaction coefficients which could vary considerably in real food webs. Moreover, LAS excludes complex dynamical behaviors such as periodic and chaotic solutions, which may be consistent with community persistence (Hutson & Law, 1985; Anderson *et al.*, 1992; Law & Blackford, 1992; Law & Morton, 1993; Hastings, 1988, 1996).

Second, randomly generated community matrices may allow biologically unrealistic structures such as an absence of autotrophs (Lawlor, 1978; Lawton, 1989; Hall & Raffaelli, 1993). Many efforts have been made towards incorporating structural features of real food webs into the pool of community matrices of dynamic models (DeAngelis, 1975; Yodzis, 1981; Pimm, 1982),

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including the “Lotka–Volterra cascade model” (LVCM, Cohen *et al.*, 1990b). The LVCM combines the trophic structure of the cascade model with the population dynamics of the Lotka–Volterra model. The model distinguishes among four types of dynamical effects caused by feeding links, namely, consumer–victim, donor-controlled and recipient-controlled interactions and links with no dynamical effects. The dynamical effects of consumer–victim interactions received much attention in previous studies. Some authors (Pimm, 1982; Hawkins, 1992) suggested that donor-controlled interactions are quite common in nature and that they have normally less destabilizing effects than consumer–victim interactions. More detailed work has yet to be done on the effects of these different types of interactions on stability in a more general context of complex food webs.

Qualitative global asymptotic stability (QGAS) and permanence are two alternative measures of stability. QGAS depends only on the sign pattern of the community matrix, but is independent of the values of the interaction coefficients as well as of the initial states (Cohen *et al.*, 1990b). Permanence measures the boundedness of the trajectory of a system within the region of state space where all species have positive abundances. Permanence includes complex dynamical behaviors such as periodic and chaotic motions (Law & Blackford, 1992; Law & Morton, 1993; Morton *et al.* 1995). Previous investigations of the permanence of Lotka–Volterra systems have mainly focused on community assembly (Law & Blackford, 1992; Law & Morton, 1993, 1996). They did not provide an explicit and systematic measurement of the probability of permanence in relation to the complexity of food webs.

The purposes of this paper are to examine, first, whether these three criteria of community persistence, QGAS, LAS, and permanence, predict qualitatively consistent relationships between food web stability and complexity, and second, how the stability determined by these three criteria are affected by the configuration of different types of trophic links. We use the LVCM with a finite number of species as the model system for this investigation. Until recently (Chen & Cohen, 2001), the LVCM was studied only in the limit of an infinite number of species (Cohen *et al.*, 1990b).

The Model and Methods of Analysis

THE LOTKA-VOLTERRA CASCADE MODEL

In the Lotka–Volterra model,

$$\dot{x}_i = x_i \left(e_i + \sum_{j=1}^n p_{ij} x_j \right), \quad x_i(0) > 0, \quad i = 1, \dots, n, \quad (1)$$

where x_i is the abundance or biomass of species i , \dot{x}_i is the derivative with respect to time, e_i is the intrinsic rate of increase or decrease of species i in the absence of all other species, p_{ij} is the inter-specific interaction coefficient between species i and species j . All the p_{ij} make up the community matrix $P = (p_{ij})_{i,j=1}^n$. We assume that the system [eqn (1)] has a positive equilibrium, i.e., a constant $n \times 1$ vector $Q = (q_i)_i^n$ such that $e_i + \sum_{j=1}^n p_{ij} q_j = 0$, with $q_i > 0$ for all i .

A LVCM system is a Lotka–Volterra model with its trophic structure defined by rules of the cascade model: for each pair of species $i, j = 1, \dots, n$ with $i < j$, species i has a probability of zero of eating species j , while species j has a probability of c/n ($0 < c < n$) of eating species i (Cohen & Newman, 1985; Cohen *et al.*, 1990a, b).

The LVCM supposes that one of the four dynamical effects occurs between each pair of species, independently for each pair of species $i, j = 1, \dots, n$ with $i < j$, with probabilities:

- (i) recipient-controlled interaction, $Pr\{p_{ij} < 0 \text{ and } p_{ji} = 0\} = r/n$;
- (ii) donor-controlled interaction, $Pr\{p_{ij} = 0 \text{ and } p_{ji} > 0\} = s/n$;
- (iii) consumer–victim interaction, $Pr\{p_{ij} < 0 \text{ and } p_{ji} > 0\} = t/n$;
- (vi) neither species has a dynamical effect on the other, or there is no trophic link between species i and j , $Pr\{p_{ij} = 0 \text{ and } p_{ji} = 0\} = 1 - (r + s + t)/n$.

Here $r, s, t \geq 0$ and $r + s + t \leq n$. The LVCM also assumes that all the species are self-limited (Cohen *et al.*, 1990b), i.e., $Pr\{p_{ii} < 0\} = 1$, $i = 1, \dots, n$. Biologically, a recipient-controlled link means that the predator diminishes the rate of increase of the prey population but does not enjoy any augmentation in the rate of increase of its own population as a result of feeding on the

prey. This situation is typically seen in the relationship between a generalist predator species and a prey species. A donor-controlled link means that the predator benefits from feeding on a prey, but the prey suffers little damage from the predator. This relation is quite common in plant–herbivore and host–parasite interactions. A consumer–victim link helps the consumer and hurts the victim; this is the common reciprocal relationship between a predator and its prey.

In this study, all sample food webs are stochastically assembled. Hence we define a food web configuration as the vector of probabilities $(r/n, s/n, t/n)$ and not as the particular realization of trophic links in a simulation. We denote $C^r = r/n$, $C^s = s/n$ and $C^t = t/n$ as the partial connectance of r , s and t links, respectively.

There are two ways to count links (L) and two corresponding definitions of connectance (C) in the LVCM (Cohen *et al.*, 1990b). Connectance refers to the expected fraction of all possible links that actually occur. If food webs are looked upon as undirected graphs, then only a single undirected link is recognized between any two interacting species and, hence, the undirected connectance is defined by $C_u = E(L_u)/[n(n - 1)/2]$ (L_u is the number of undirected links and $E(L_u)$ is the expected number of undirected links). A t link is counted as a single undirected link, equivalent to an r or s link ($r \sim s \sim t$), which gives $C_u = (r + s + t)/n$, $E(L_u) = n(n - 1)C_u/2 = (n - 1)(r + s + t)/2$. If food webs are regarded as directed graphs and cannibalism is ignored, then the directed connectance is defined by $C_d = E(L_d)/[n(n - 1)]$. A t link is counted as two directed links, equivalent to an r link plus an s link ($t \sim r + s$), which gives $C_d = (r + s + 2t)/(2n)$, $E(L_d) = n(n - 1)C_d = (n - 1)(r + s + 2t)/2$.

SIMULATION

Numerical simulations are conducted on randomly constructed LVCM food webs with $n = 10$ species and varying connectance to determine the probability of stability, as measured by QGAS, LAS and permanence, respectively, in relation to connectance and configuration of model food webs. The probabilities $r/10, s/10$ and $t/10$ are varied systematically. For each combination of the probability values, a random

community matrix $P = (p_{ij})_{i,j=1}^n$ is generated. Each non-zero element of $P = (p_{ij})$ is assigned a uniformly distributed random value within the interval of $(0, 1)$ for each non-zero p_{ji} and a value within the interval of $(-1, 0)$ for each non-zero p_{ij} and each p_{ii} for all i, j with $i < j$. Assuming that a positive equilibrium vector $Q = (q_i)_{i=1}^n$ exists, the Jacobian matrix of the LVCM is $Df = \text{diag}(Q) \cdot P$. For simplicity, we chose $q_i = 1$, for $i = 1, \dots, n$, so that $Df = P$. This approach is equivalent to normalizing the system by replacing x_i by $y_i = x_i/q_i$ for all i . This makes the equilibrium of y_i be 1 for all i and replaces the matrix of interaction coefficients P by $P' = P \text{diag}(Q)$. The Jacobian matrix at the equilibrium 1 for the normalized system is then P' . We just generate P' within the interval of $(0, 1)$. Both endpoints 0 and 1 of the uniform distribution are arbitrary choices in this case.

For each configuration of r, s and t , 10,000 such stochastic systems are generated, and the relative frequency with which these systems are qualitatively globally asymptotically stable and locally asymptotically stable is used to approximate the probability of having QGAS and LAS. Similarly, we also fix the connectance ($C^t = 0.4$) and vary the number of species (n) to determine the probability of stability in relation to the number of species in model food webs. The upper bound of the standard deviation of each relative frequency p is

$$S.D. = \sqrt{pq/n} \leq \sqrt{0.5 \cdot 0.5/10000} = 0.005.$$

The identification of permanence is computationally expensive, so we simulate only 1000 sample systems to estimate the probability of permanence (except for Table 1).

MEASURES OF STABILITY

Several conditions determine the QGAS of the Lotka–Volterra model (Quirk & Ruppert, 1965; Bone *et al.*, 1988; Redheffer & Zhou, 1989; Logofet, 1993). Logofet listed five conditions (1993) for determining the QGAS of the Lotka–Volterra model:

- (i) $p_{ii} \leq 0$ for all i and at least one $p_{ii} < 0$;
- (ii) $p_{ij}p_{ji} \leq 0$ for any $i \neq j$;
- (iii) the digraph $D(P)$ has no k -cycles for $k \geq 3$;

TABLE 1

Frequency of randomly assembled Lotka – Volterra cascade model systems having local asymptotic stability (LAS) and satisfying the sufficient condition for permanence. The model food webs all have ten species. Values outside the parentheses are the frequency of webs with $t/10 = 0.5$. Values inside the parentheses are the frequency of webs with $r/10 + s/10 = 0.5$ (and $r/10 = s/10$)

	LAS		Total
	Yes	No	
Permanence	Yes 7758 (2522)	122 (534)	7980 (3056)
	No 515 (183)	1605 (6761)	2020 (6944)
Total	8273 (2705)	1727 (7295)	10000

(iv) there exists a non-zero term in the standard expansion of the determinant

$$\det(P) = \sum \operatorname{sgn}(\sigma) \prod_{i=1}^n p_{\sigma(i)i}, \quad (2)$$

where σ is a permutation of the numbers $\{1, 2, \dots, n\}$ and $\operatorname{sgn}(\sigma) = \pm 1$ is the sign of σ ;

(v) the trophic graph fails the color test. A trophic graph is an undirected graph with a node corresponding to each species and an undirected edge between any two nodes, if and only if, at least one of the two corresponding species eats the other species. A trophic graph is said to pass the color test if each of its vertices can be colored black or white in such a way that: (1) all self-limited vertices are black; (2) there exist white vertices, each of which is linked to at least another white vertex; (3) if a black vertex is linked to a white one, then it is also linked to at least another white vertex. If not so, the graph fails the test.

Conditions (i), (ii), (iv) and (v) are immediately satisfied in the LVCM since $p_{ii} < 0$ for all i and $p_{ij}p_{ji} \leq 0$ for any $i \neq j$. The determination of QGAS in the LVCM reduces to checking that the digraph of a LVCM food web has no k -cycles for $k \geq 3$.

The LAS is determined by the eigenvalues of the Jacobian matrix of the LVCM. A system is said to have LAS, if and only if, all the eigen-

values of its Jacobian matrix are negative or have a negative real part, i.e. $\operatorname{Re}(\lambda_i) < 0$ for all i .

Permanence measures the ability of a system to stay bounded inside the positive orthant of the state space. A system is said to be permanent if the boundary (include the infinity) is a repeller (Hofbauer & Sigmund, 1998), that is, if there exists constants $0 < \delta_l < \delta_u$ such that $x_i(0) > 0$ for all $i = 1, \dots, n$ implies $\delta_l < \lim_{t \rightarrow +\infty} \inf x_i(t) < \lim_{t \rightarrow +\infty} \sup x_i(t) < \delta_u$ for $i = 1, \dots, n$ (Hofbauer & Sigmund, 1998). A sufficient condition for permanence is the existence of an average Lyapunov function (Hofbauer, 1981; Hutson, 1984; Jansen, 1987). For a Lotka–Volterra system with a unique positive equilibrium ($x_i^* > 0$ for all i) and no trajectory tending to infinity, the test of an average Lyapunov function is reduced to solving the linear programming problem (Jansen, 1987):

Minimize z
subject to

$$\sum_{i=1}^n h_i \left(e_i + \sum_{j=1}^n p_{ij} y_j^{B(k)} \right) + z \geq 0,$$

and $h_i > 0$ for all $i = 1, \dots, n$.

Here h_i , $i = 1, \dots, n$, and z are the variables in the linear programming problem and $y_j^{B(k)}$ ($j = 1, \dots, n$ and $k = 1, \dots, m$) is the equilibrium density of species j at the k -th boundary equilibrium. As $k = 1, \dots, m$, the m boundary equilibria yield m linear constraints. The boundary is a repeller and, hence, the system is permanent if the optimum z_{min} is negative. For more information on the sufficient condition for permanence of the Lotka–Volterra systems, see Jansen (1987), Law & Blackford (1992) and Law & Morton (1993). We solved this linear programming problem using software of the MOSEK optimization toolbox for Matlab (by EKA Consulting APS).

The second way to check whether the boundary is a repeller is numerical invasibility analysis, done by deleting species one at a time and seeing if the deleted species has a positive per-capita rate of change at the boundary equilibrium. The second approach could sometimes be computationally less expensive, but with efficient linear programming software such as MOSEK, the first approach is faster.

A way to determine the persistence (not permanence) of a dynamical food web model is to simulate numerically its trajectories from a large number of initial conditions. Unfortunately, for this approach, some non-permanent systems may have a non-zero probability of survival for the necessarily finite duration of the numerical simulation while some permanent systems may not persist when started from some starting points (Law & Morton, 1993). This numerical approach is computationally very expensive.

Currently, conditions that are both necessary and sufficient for permanence in Lotka–Volterra systems with more than three species are not known. Jansen’s (1987) condition is only a *sufficient* condition for permanence in Lotka–Volterra systems with more than three species. It may miss an unknown proportion of permanent systems. For large Lotka–Volterra systems, it is so far not clear how large a proportion of permanent systems may go undetected (Law & Morton, 1992). Below, when we say the probability of permanence for brevity, we refer to the probability that systems will satisfy the sufficient condition of Jansen (1987).

Results

COMPLEXITY-STABILITY IN LVCM

We plot the probability surfaces of QGAS and LAS in the LVCM having ten species with respect to $r + t$ and $s + t$ [Fig. 1(b and c)]. Like the asymptotic ($n \rightarrow \infty$) probability surface (Cohen *et al.*, 1990b) [Fig. 1(a) here], the two probabilities of stability in the LVCM with $n = 10$ decrease with increasing $r + t$ and $s + t$ (Fig. 1). The asymptotic probability of QGAS as $n \rightarrow \infty$ shows a sharp transition from a positive value to zero as t increases (Fig. 2). In contrast, the probabilities of QGAS, LAS and permanence for the LVCM food webs with ten species show a gradual transition from a positive value toward zero with increasing t (Fig. 2). When all links are consumer–victim (t) links ($r = s = 0$), the probability of QGAS is smaller than the probability of permanence which is, in turn, smaller than the probability of LAS [Fig. 2(a)]. However, when all the links are an equal number of r and s links ($r = s$ and $t = 0$), the probability of permanence

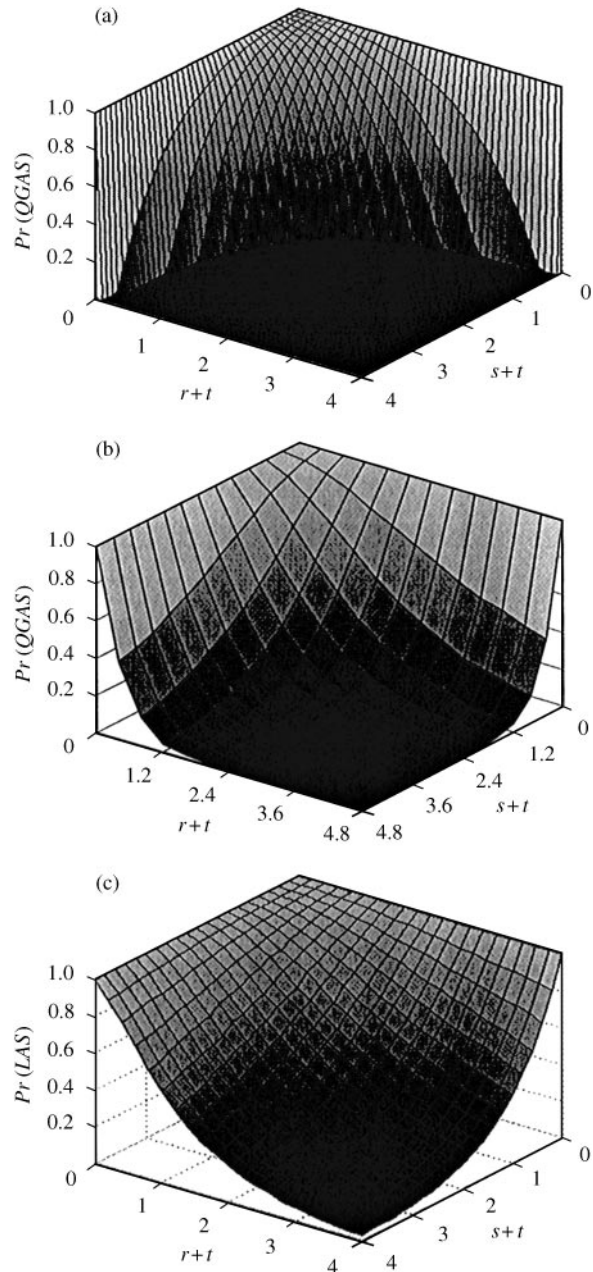


FIG. 1. Perspective view of the probability of stability in the Lotka–Volterra cascade model (LVCM), as measured by different stability criteria, as a function of $r + t$ and $s + t$. (a) Asymptotic ($n \rightarrow \infty$) probability of qualitative global asymptotic stability ($Pr(QGAS)$) (redrawn from Cohen *et al.*, 1990). (b) $Pr(QGAS)$ in the LVCM with $n = 10$ species. (c) Probability of local asymptotic stability ($Pr(LAS)$) in the LVCM with $n = 10$. Graphs (b) and (c) are plotted with $t = 0$, each representing the lower bound of a family of qualitatively similar surfaces.

becomes greater than the probability of LAS [Fig. 2(b)]. Table 1 also shows that with ten species and the same directed connectance, the subset of webs that have permanence but not

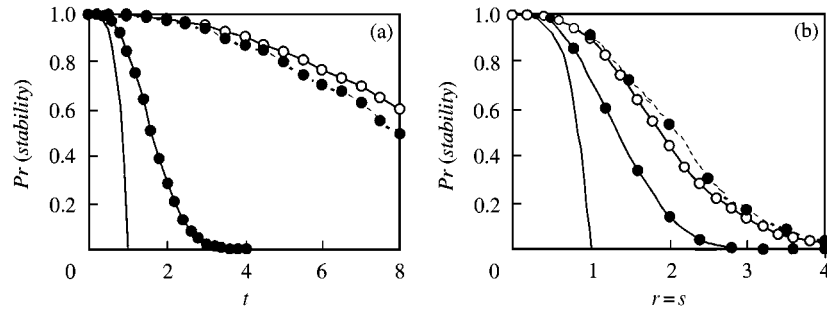


FIG. 2. The probabilities of stability of the Lotka–Volterra cascade model (LVCМ), as measured by different criteria: (a) with respect to t , assuming $s = r = 0$. (b) with respect to r and s , assuming $r = s$ and $t = 0$. The four curves are the asymptotic ($n \rightarrow \infty$) probability of qualitative global asymptotic stability (—), the probability of the qualitative global asymptotic stability (●—●), the probability of local asymptotic stability (○—○) and the probability of permanence (●—●) in LVCМ with ten species.

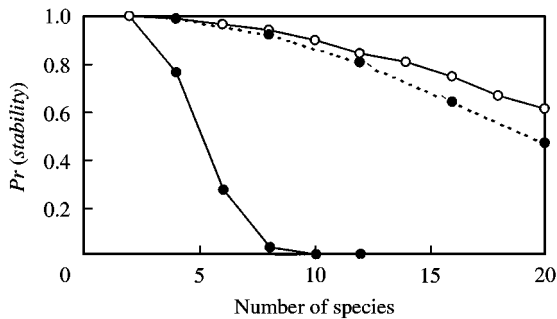


FIG. 3. The probabilities of stability ($Pr(stability)$) of the Lotka–Volterra cascade model, as measured by different criteria, with respect to the number of species (n). The three curves represent the probability of qualitative global asymptotic stability (●—●), the probability of local asymptotic stability (○—○) and the probability of permanence (●—●), respectively. In each case, the LVCМ food webs are assembled with t links only with an undirected connectance of 0.4.

LAS is smaller than the subset of webs that have LAS but not permanence for model webs with t links, while the opposite is true for model webs with the same probability of r and s links.

When the number of species n is increased while the undirected connectance is fixed at $C_u = t/n = C^t = 0.4$, with $r = s = 0$, the probabilities of QGAS, LAS and permanence of the LVCМ all decrease (Fig. 3). With increasing n , the probability of QGAS drops very sharply. The probabilities of LAS and permanence decrease more slowly (Fig. 3).

QUALITATIVE GLOBAL ASYMPTOTIC STABILITY AND FOOD WEB CONFIGURATION

For the LVCМ with $n \rightarrow \infty$, the limiting probability of QGAS is uniquely determined by the

values of $r + t$ and $s + t$ irrespective of the proportion of t in those values (Cohen *et al.*, 1990b). A t link has the same effect on the probability of QGAS as do an r link plus an s link. Since a t link represents a pair of directed links, a coupled positive–negative pair of unidirectional links has exactly the same effect on the asymptotic probability of QGAS as does an uncoupled positive–negative pair of unidirectional links.

In contrast, in LVCМ food webs with ten species, with equal directed connectances, i.e., $t/n = (r + s)/(2n)$, the LVCМ food webs with t links ($r = s = 0$) have greater probabilities of QGAS than do the webs with paired r and s links ($r = s$ and $t = 0$) [Fig. 4(a)].

On the other hand, if a t link is counted as an undirected link, given equal undirected connectances, i.e., $t/n = (r + s)/n$, the LVCМ food webs with t links ($r = s = 0$) have smaller probabilities of QGAS than do food webs with paired r and s links ($r = s$ and $t = 0$) [Fig. 4(b)].

This result leads to our prediction 1: when food webs are looked upon as directed graphs, then consumer–victim links, equivalent to coupled pairs of directed links, lead to a higher probability of QGAS than do the same number of pairs of donor-controlled and recipient-controlled links; when food webs are regarded as undirected graphs, then consumer–victim links lead to a lower probability of QGAS than do the same number of donor-controlled and recipient-controlled links, assuming there are equal numbers of donor-controlled and recipient-controlled links.

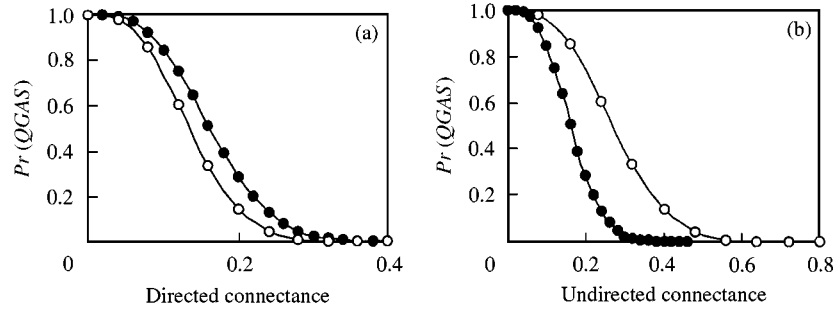


FIG. 4. The probabilities of qualitative global asymptotic stability ($Pr(QGAS)$) of the Lotka–Volterra cascade model in food webs connected by t links (●—●) and by paired r and s links (○—○). (a) Given equal directed connectances, i.e., $t/n = (r + s)/(2n)$, $Pr(QGAS)$ is greater in webs with t links than $Pr(QGAS)$ in webs with paired r and s links. (b) Given equal undirected connectance, i.e., $t/n = (r + s)/n$, $Pr(QGAS)$ is smaller in webs with t links than $Pr(QGAS)$ in webs with paired r and s links.

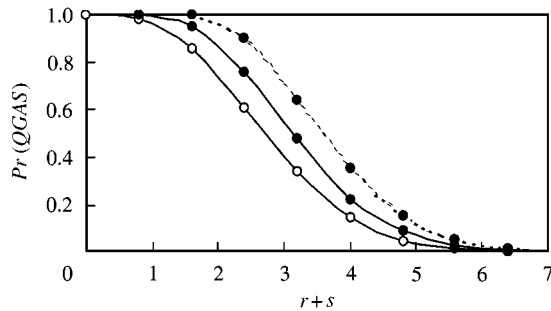


FIG. 5. The probability of qualitative global asymptotic stability ($Pr(QGAS)$) in the Lotka–Volterra cascade model with $n = 10$. For the same values of $r + s$, the probability becomes larger as the absolute value of difference between r and s increases. Here $t = 0$ for all three cases. The three curves represent the $Pr(QGAS)$ with $|r - s| = 0$ (○—○), $|r - s| = 0.4$ (●—●) and $|r - s| = 0.8$ (●---●), respectively.

Like the asymptotic probability surface [Fig. 1(a)], the probability surface of QGAS with ten species is symmetric with respect to $r + t$ and $s + t$ [Fig. 1(b)]. If we transect the probability surface, given by a specific value of t , by a plane $s = c$ and a plane $r = c$ (where c is a positive constant), respectively, the two resulting curves coincide.

Like the asymptotic probability, with the same value of $(r + t) + (s + t)$, the probability of QGAS in the LVCM with $n = 10$ decreases as the difference between r and s becomes smaller, and reaches the minimum when $r = s$ (Fig. 5).

This result gives our prediction 2: a donor-controlled link and a recipient-controlled link have an identical effect on the probability of QGAS in the LVCM; with fixed values of t and $r + s + t$, food webs with more even proportions

of r (recipient-controlled) links and s (donor-controlled) links are less likely to be QGAS than webs with less even proportions of these two types of unidirectional links. Results omitted for brevity also show that the second part of prediction 2, that webs with more even proportions of donor-controlled and recipient-controlled links are less likely to be stable than those with less even proportions, applies equally to LAS and to the lower bound of, or sufficient condition for, permanence.

LOCAL ASYMPTOTIC STABILITY AND FOOD WEB CONFIGURATION

As with the probability of QGAS for LVCM food webs with ten species, the probability of LAS is not uniquely determined by the values of $r + t$ and $s + t$. The probability increases with the proportion of t in the combination of $r + t$ and $s + t$. In Fig. 6, we compare the probability of LAS in food webs with t links ($r = s = 0$) with the probability of LAS in food webs with r and s links ($r = s$ and $t = 0$). The comparison is based on equal directed connectances [Fig. 6(a)], i.e., $t/n = (r + s)/(2n)$, and equal undirected connectances [Fig. 6(b)], i.e., $t/n = (r + s)/n$, respectively. In both cases, the LVCM food webs with t links ($r = s = 0$) have greater probabilities of having LAS than do the webs with paired r and s links ($r = s$ and $t = 0$) (Fig. 6).

This result yields our prediction 3: when regarded as coupled pairs of directed links, consumer–victim links produce a higher probability of LAS than the same number of pairs of

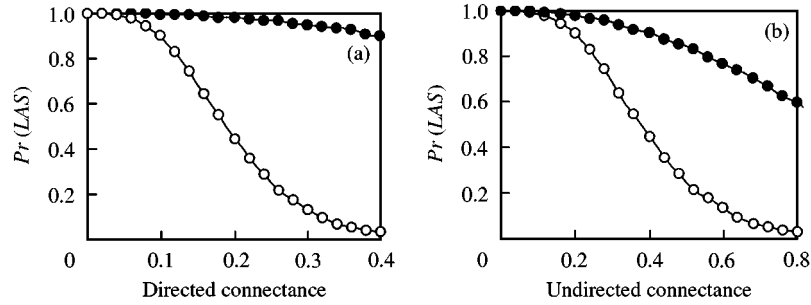


FIG. 6. The probability of local asymptotic stability ($Pr(LAS)$) of the Lotka–Volterra cascade model in food webs connected by t links ($\bullet\text{---}\bullet$) and by paired r and s links ($\circ\text{---}\circ$). (a) Given equal directed connectances, i.e., $t/n = (r + s)/(2n)$, $Pr(LAS)$ is greater in webs with t links than $Pr(LAS)$ in webs with paired r and s links. (b) Given equal undirected connectances, i.e., $t/n = (r + s)/n$, $Pr(LAS)$ is greater in webs with t links than $Pr(LAS)$ in webs with paired r and s links.

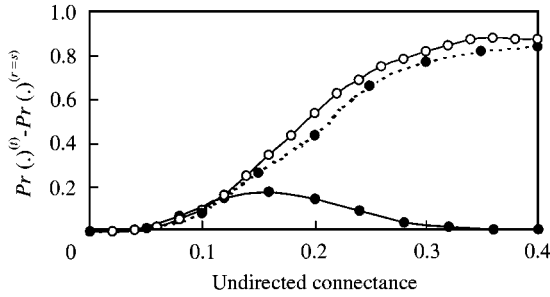


FIG. 7. Differences between effects of coupled positive–negative pairs of links (t) and effects of uncoupled positive–negative pairs of links ($r = s$) on the probability of qualitative global asymptotic stability ($Pr(QGAS)$, $\bullet\text{---}\bullet$), the probability of local asymptotic stability ($Pr(LAS)$, $\circ\text{---}\circ$) and the probability of permanence ($\bullet\text{---}\bullet$) in Lotka–Volterra cascade model with ten species. $Pr(.)^{(0)}$ represents probability of stability as a function of t with $r = s = 0$; $Pr(.)^{(r=s)}$ represents probability of stability as a function of r and s ($r = s$) with $t = 0$. Undirected connectance is measured by t/n or $(r + s)/n$, respectively.

recipient-controlled and donor-controlled links; when regarded as undirected links, consumer–victim links produce a higher probability of LAS than the same number of recipient-controlled and donor-controlled links, given that the number of recipient-controlled links equals the number of donor-controlled links.

For $n = 10$ species, the difference between the effects of t links (i.e., coupled positive–negative pairs of directed links) and the effects of the same number of r and s links (i.e., uncoupled positive–negative pairs of directed links) on the probability of LAS is much greater than the difference of effects on the probability of QGAS when $C_u > 0.12$, and is slightly smaller when $C_u \leq 0.12$ (Fig. 7).

Unlike the probability surface of QGAS, where the recipient-controlled and donor-controlled links have identical effects on the probability of global asymptotic stability, the probability of LAS is asymmetric with respect to r links and s links. To facilitate the comparison, we define the probability of LAS as partial functions of r (with s and t fixed) and s (with r and t fixed), respectively,

$$Pr(LAS)^{(r)} = Pr\{\max(\text{Re}\lambda_i(P)|i = 1, \dots, n) < 0: \\ r \in [0, n - s_c - t_c], s = s_c, t = t_c\}, \quad (2a)$$

$$Pr(LAS)^{(s)} = Pr\{\max(\text{Re}\lambda_i(P)|i = 1, \dots, n) < 0: \\ s \in [0, n - r_c - t_c], r = r_c, t = t_c\}, \quad (2b)$$

where r_c , s_c and t_c are positive constants. We transect the probability surface of LAS [Fig. 1(c)] for $t_c = 0$ along planes parallel to the $r - Pr(LAS)$ plane at $s = c$ (c is a positive constant) and along planes parallel to the $s - Pr(LAS)$ plane at $r = c$, respectively, for several different values of c . The transects in each pair are superimposed and the horizontal axis is transformed from the value of r or s into partial connectance (by dividing by 10) to compare the probability of LAS as a function of the partial connectance of r links (C^r) with the probability of LAS as a function of the partial connectance of s links (C^s) (Fig. 8). The curve $Pr(LAS)^{(r)}$ crosses

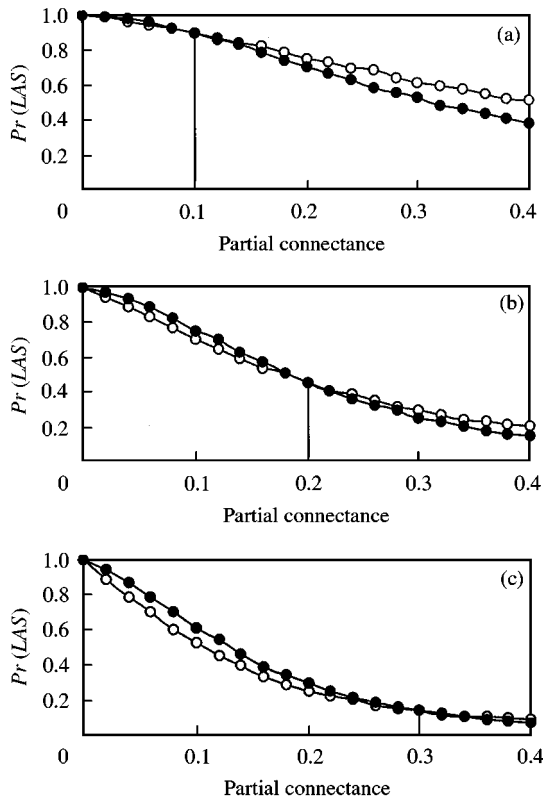


FIG. 8. The probability of local asymptotic stability ($Pr(LAS)$) with respect to the partial undirected connectance of r links (C^r , ●—●) and s links (C^s , ○—○), respectively, with no t links. (a) When varying C^r with $C^s = 0.1$ and varying C^s with $C^r = 0.1$, the two curves cross at 0.1; (b) When varying C^r with $C^s = 0.2$ and varying C^s with $C^r = 0.2$, the two curves cross at 0.2; (c) When varying C^r with $C^s = 0.3$ and varying C^s with $C^r = 0.3$, the two probabilities cross at 0.3.

the curve $Pr(LAS)^{(s)}$ where $C^r = C^s$. Where $C^r < C^s$ for $Pr(LAS)^{(r)}$ and $C^r > C^s$ for $Pr(LAS)^{(s)}$, we find $Pr(LAS)^{(r)} > Pr(LAS)^{(s)}$. Where $C^r > C^s$ for $Pr(LAS)^{(r)}$ and $C^r < C^s$ for $Pr(LAS)^{(s)}$, we find $Pr(LAS)^{(r)} < Pr(LAS)^{(s)}$ (Fig. 8).

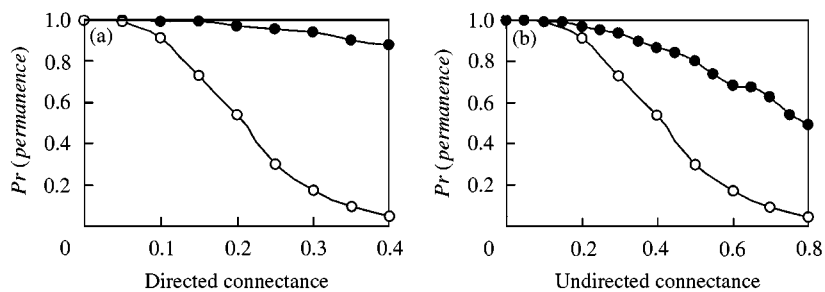


FIG. 9. The probability of permanence of the Lotka–Volterra cascade model in food webs connected by t links (●—●) and by paired r and s links (○—○). (a) Given equal directed connectances, i.e., $t/n = (r + s)/(2n)$, the probability of permanence is greater in webs with t links than the probability of permanence in webs with paired r and s links. (b) Given equal undirected connectances, i.e., $t/n = (r + s)/n$, the probability of permanence is greater in webs with t links than the probability in webs with paired r and s links.

This result leads to our prediction 4: with the same number of t links and the same number of unidirectional links $r + s$, systems with $s > r$ are more likely to have LAS than systems with $r > s$. The biological implication of this property is that if two sets of food webs have the same number of species, the same total number of trophic links ($r + s + t$), and the same number of consumer–victim links (t), the set of webs with more donor-controlled (s) than recipient-controlled (r) links is more likely to be locally asymptotically stable than the set with the reverse relationship of the two types of links.

THE PROBABILITY OF PERMANENCE AND FOOD WEB CONFIGURATION

The probability of permanence in LVCVM food webs with t links ($r = s = 0$) is compared with the probability in webs with paired r and s links ($r = s$ and $t = 0$), based on equal directed connectance [$t/n = (r + s)/(2n)$, Fig. 9(a)] and equal undirected connectance [$t/n = (r + s)/n$, Fig. 9(b)], respectively, for ten species. The probability of permanence with respect to both directed and undirected connectance of t links is greater than the probability with respect to the equivalent connectance of r and s links (Fig. 9).

This result leads to prediction 5: when regarded as coupled pairs of directed links, or as undirected links, consumer–victim links yield a larger probability of permanence than the same number of pairs of recipient-controlled and donor-controlled links, given equal number of recipient-controlled and donor-controlled links.

The difference between the effects of t links (i.e., coupled positive–negative pairs of directed links)

and the effects of the same number of pairs of r and s links (i.e., uncoupled positive–negative pairs of directed links) on the probability of permanence is smaller than that on the probability of LAS but generally greater than that on the probability of QGAS (Fig. 7).

Like the probability of LAS, the probability of permanence shows asymmetric effects of r links and s links. We denote the probability of permanence with respect to r by $PP^{(r)}$ and the probability of permanence with respect to s by $PP^{(s)}$. The values of r and s are transformed into partial connectance C^r and C^s . The probability curves cross where C^r equals C^s . Where C^r is smaller than C^s for $PP^{(r)}$ and C^s is smaller than C^r for $PP^{(s)}$, $PP^{(r)}$ is greater than $PP^{(s)}$ (Fig. 10). Where C^r is greater than C^s for $PP^{(r)}$ and C^s is greater than C^r for $PP^{(s)}$, $PP^{(r)}$ is smaller than $PP^{(s)}$ (Fig. 10).

This result leads to our prediction 6: with the same number of bidirectional links t and unidirectional links $r + s$, systems with $s > r$ are more likely to be permanent than systems with $r > s$. In biological terms, if two sets of food webs have the same number of species, the same total number of trophic links ($r + s + t$), and the same number of consumer–victim links (t), the webs with more donor-controlled (s) than recipient-controlled (r) links are more likely to be permanent than those with more recipient-controlled than donor-controlled links.

Since currently no conditions that are both necessary and sufficient for permanence are known, the proportion of permanent webs undetected by the sufficient condition cannot be accurately determined. Here, we use the probability of systems satisfying the sufficient condition for permanence as a lower bound and the probability of systems satisfying the necessary conditions for permanence as an upper bound to enclose the probability of permanence. The probability that systems persist in numerical simulations is also compared with these two bounds.

For a Lotka–Volterra system of n species with a community matrix P and Jacobian matrix A , necessary conditions for permanence are that $(-1)^n \det A > 0$, $\text{tr} A < 0$, and $(-1)^n \det P > 0$ (Hofbauer & Sigmund 1998).

We determined the persistence of a system numerically by tracing the trajectory starting from random values for 5000 time steps. If the

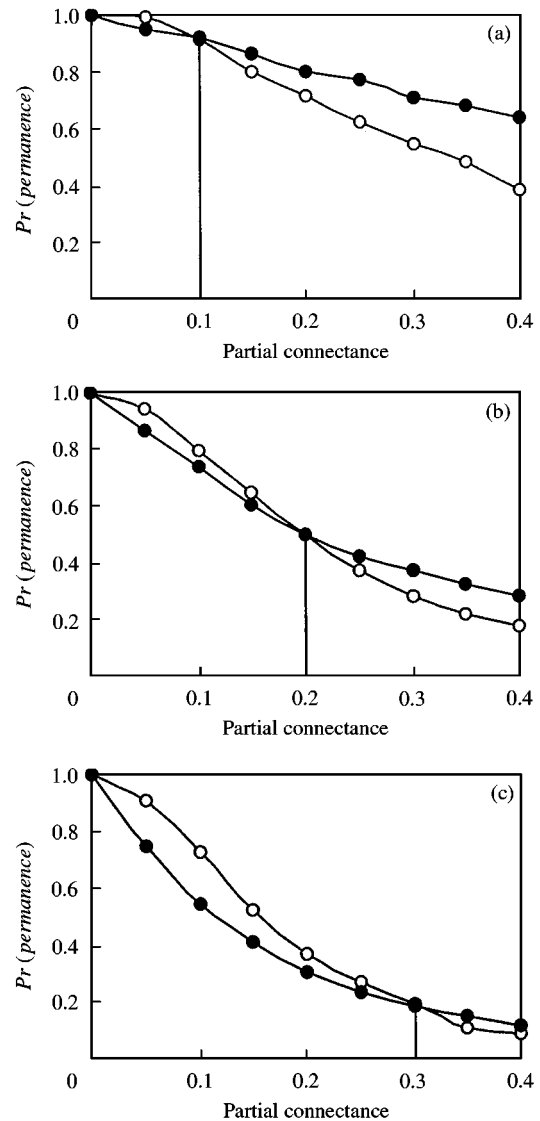


FIG. 10. The probability of permanence in the LVCM with ten species and no t links as a function of the partial undirected connectance of r links (C^r , \circ — \circ) and s links (C^s , \bullet — \bullet), respectively. (a) When varying C^r with $C^s = 0.1$ and varying C^s with $C^r = 0.1$, the two curves cross at 0.1; (b) When varying C^r with $C^s = 0.2$ and varying C^s with $C^r = 0.2$, the two curves cross at 0.2; (c) When varying C^r with $C^s = 0.3$ and varying C^s with $C^r = 0.3$, the two probabilities cross at 0.3.

populations of all species remain greater than 1×10^{-8} during the 5000 time steps, we regard the system as being persistent. For each food web configuration, 1000 sample systems are simulated.

We compared the three probabilities along four lines: (a) the partial connectance of t links was increased with no other links; (b) the partial connectance of r and s links ($r = s$) is varied with

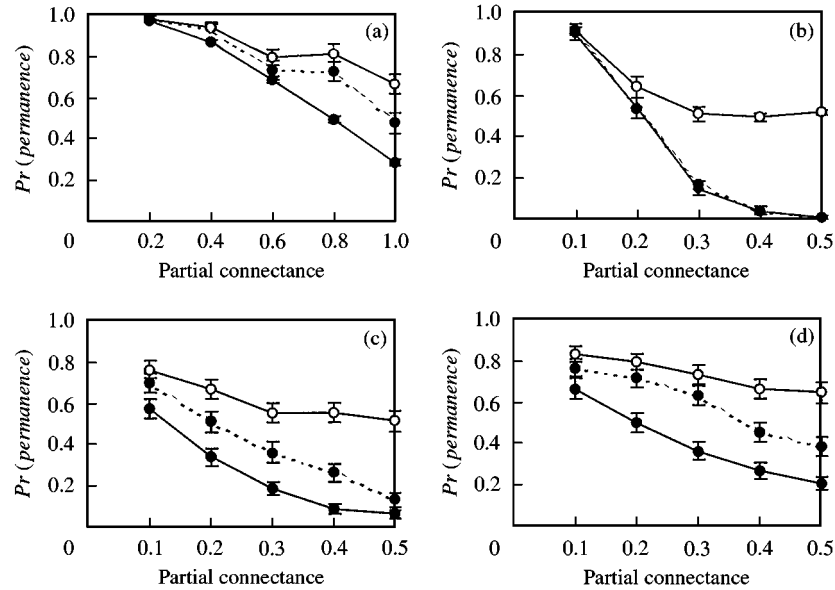


FIG. 11. The probabilities of LVC systems satisfying the sufficient conditions (●—●) for permanence and the necessary conditions (○—○) for permanence and the probability of persistence (●—●) in the LVC with ten species. (a) Webs with varying connectance of t links only. (b) Webs with varying connectance of r and s links only. (c) Webs with varying partial connectance of r links, fixed partial connectance of t links ($C^t = 0.5$) and no s links. (d) Webs with varying partial connectance of s links and fixed partial connectance of t links ($C^t = 0.5$) and no r links.

no t links; (c) the partial connectance of r links is varied with a fixed partial connectance of t ($t/n = 0.5$) and no s links; (d) the partial connectance of s links is varied with a fixed partial connectance of t ($t/n = 0.5$) and no r links.

The probability of persistence falls between the lower and upper bounds set by the sufficient condition and the necessary conditions for webs with only t links [Fig. 11(a)], webs with t and r links [Fig. 11(c)] and webs with t and s links [Fig. 11(d)], while the probability of persistence almost coincides with the lower bound for systems with only r and s links ($r = s$) [Fig. 11(b)].

5. Discussion and Conclusion

This study appears to be the first to explore explicitly the general relationship between complexity and stability of food webs when permanence is used to measure stability. Our result shows that three measures of stability predict qualitatively consistent relationships between complexity and stability of food webs. The probabilities that LVC food webs have QGAS, LAS and permanence all decrease monotonically as food web complexity increases, when complexity is measured by the number of species or by

connectance. However, there are important quantitative differences among the probabilities of the three measures of stability.

Law & Blackford (1992) and Law and Morton (1993) reported that communities with more omnivory links have more prevalent permanent paths and suggested that communities of high connectance are more ready to reassemble themselves. Based on that, they argued that complex communities may be less vulnerable to disturbance than simple ones. Their results do not necessarily have to be considered as being in contradiction with our results as well as results from previous asymptotic stability analysis. The results of Law and colleagues (1992, 1993) emphasize that, within self-assembled communities, complex communities have more alternative permanent states than simple ones. Our results emphasize that within stochastically assembled food webs, complex food webs are less likely to be permanent than simple webs.

This study generates six predictions about the effects of different types of trophic links on the stability measured by the three criteria. Predictions 1, 3 and 5 concern the effects of coupled positive-negative pairs of directed links (t or consumer-victim links) and uncoupled positive-negative

pairs of unidirectional links (r and s , or recipient-controlled and donor-controlled links) on the probability of stability measured by QGAS, LAS and permanence, respectively. Prediction 1 states that, if food webs are considered as directed graphs, coupled positive–negative pairs (t or consumer–victim links) yield a larger probability of QGAS than the same number of uncoupled positive–negative pairs of directed links (r and s , or recipient-controlled and donor-controlled links). On the other hand, if food webs are considered as undirected graphs, consumer–victim links yield a smaller probability of QGAS than the same number of r and s links, assuming $t = r = s$. In contrast, predictions 3 and 5 state that, whether food webs are viewed as directed or undirected graphs, t links yield larger probabilities of LAS and permanence than the equivalent number of paired r and s links.

Predictions 2, 4 and 6 are concerned with the effects of uncoupled negative links (r or recipient-controlled links) and uncoupled positive links (s or donor-controlled links) on the probability of QGAS, LAS and permanence, respectively. Prediction 2 says that with the same number of consumer–victim links and the same number of recipient-controlled plus donor-controlled links, webs with more even proportions of positive (donor-controlled) and negative (recipient-controlled) unidirectional links are less stable than those with less even proportions, regardless of the sign of the imbalance. This prediction implies that food webs with even proportions of donor-controlled and recipient-controlled links are expected to be rare compared with webs with less even proportions of these two types of links. In contrast, predictions 4 and 6 state that food webs with more donor-controlled links have a greater probability of LAS and permanence than do the webs with more recipient-controlled links. This prediction agrees with the observation that donor-controlled interaction is rather common in natural communities (Hawkins, 1992; Hall & Raffaelli, 1993; Polis & Strong, 1996). It is also consistent with the evolutionary trend that many species that serve as food resources of other species have evolved traits to secure reproduction, such as protection of the part of organisms or populations that are important for reproduction, while allowing predators to feed on

the parts that have a trivial contribution to reproduction. There has been hardly any theoretical proof or empirical evidence for the ecological or evolutionary benefits of recipient-controlled interactions. Stability constraints may be a mechanism favoring the donor-controlled interaction, in addition to energetic and demographic mechanisms. Previous theoretical studies showed that food webs rich in donor-controlled interactions require shorter times of return to the equilibrium following a small perturbation (Pimm, 1982; Chen & Cohen, 2001), but have greater transient growth of perturbation (Chen & Cohen, 2001) than webs rich in recipient-controlled interactions.

Combining the above predictions, the food web configurations favored by stability criteria in LVCMS emerge: consumer–victim and donor-controlled links are expected to be the major trophic interactions and recipient-controlled links are expected to be rare.

If food webs are constrained by stability, then which stability measure represents the operative constraint in natural systems? Perhaps the three stability measures operate in different situations. In fluctuating environments, where food webs undergo frequent perturbations of both the population sizes and the coefficients of interactions and reproduction, QGAS is more likely the stability constraint in operation, since LAS and the probability of permanence are structurally unstable and LAS is only locally stable. Here, being structurally unstable means that a small change in the parameters (interaction coefficients) may change qualitatively the dynamic behavior of the system (Hofbauer & Sigmund, 1998). In constant environments, LAS or permanence may be sufficient to maintain food web persistence. Donor-controlled links seem more likely to become established in constant environments than in fluctuating environments, since such links are more likely to appear in web configurations constrained by LAS and permanence. These predictions should be tested empirically.

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