

Transient dynamics and food-web complexity in the Lotka–Volterra cascade model

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How does the long-term behaviour near equilibrium of model food webs correlate with their short-term transient dynamics? Here, simulations of the Lotka–Volterra cascade model of food webs provide the first evidence to answer this question. Transient behaviour is measured by resilience, reactivity, the maximum amplification of a perturbation and the time at which the maximum amplification occurs. Model food webs with a higher probability of local asymptotic stability may be less resilient and may have a larger transient growth of perturbations. Given a fixed connectance, the sizes and durations of transient responses to perturbations increase with the number of species. Given a fixed number of species, as connectance increases, the sizes and durations of transient responses to perturbations may increase or decrease depending on the type of link that is varied. Reactivity is more sensitive to changes in the number of donor-controlled links than to changes in the number of recipient-controlled links, while resilience is more sensitive to changes in the number of recipient-controlled links than to changes in the number of donor-controlled links. Transient behaviour is likely to be one of the important factors affecting the persistence of ecological communities.

Keywords: community persistence; complexity; food webs; local asymptotic stability; Lotka–Volterra cascade model; response to perturbation

1. INTRODUCTION

Stability has been considered a major constraint on ecological communities (May 1972, 1973; Yodzis 1981, 1989; Pimm 1982, 1984; Cohen & Newman 1984, 1985a, 1988; Cohen *et al.* 1985; Paine 1988; Lawton 1989; Pimm *et al.* 1991) but the definition and measurement of ecological stability remain controversial (Lewontin 1969; Holling 1973; Auerbach 1984; Haydon 1994).

Studies of local asymptotic stability conventionally calculate the probability of local asymptotic stability in an ensemble of stochastically generated community matrices of Lotka–Volterra models. The ecological use of local-asymptotic-stability analysis has been challenged for several reasons (Lewontin 1969; Connell & Sousa 1983; DeAngelis & Waterhouse 1987; Paine 1988; Hastings 1988, 1996; Haydon 1994). One reason is that local asymptotic stability provides no information about the short-term transient behaviour of a system. A perturbation may be temporarily amplified, despite local stability (Neubert & Caswell 1997). Frequent perturbations may keep ecological systems far from equilibria (DeAngelis & Waterhouse 1987). Frequently perturbed food webs with locally asymptotically stable equilibria might not persist if their return times are long and perturbations are transiently amplified. Theories of food-web structure based on the asymptotic behaviour near equilibrium need to be re-examined in the light of transient dynamics.

To our knowledge, this study is the first to investigate whether the transient behaviour of food webs at locally stable equilibria and the probability of long-term asymptotic stability have similar relationships with web complexity.

2. MODEL AND METHODS

(a) *The Lotka–Volterra cascade model*

We use the Lotka–Volterra cascade model (LVCM) (Cohen *et al.* 1990b):

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

where x_i is the abundance or biomass of species i , e_i is the intrinsic rate of change of species i and p_{ij} is the interaction coefficient between species i and species j . System (1) has an equilibrium at $x_i = 0, i = 1, \dots, n$ called the trivial equilibrium. The $n \times n$ matrix $P = (p_{ij})_{i,j=1}^n$ is called the community matrix. We assume that system (1) has a positive equilibrium, i.e. that a constant $n \times 1$ vector $Q = (q_i)_{i=1}^n$ exists such that

$$e_i + \sum_{j=1}^n p_{ij} q_j = 0, \quad \text{with } q_i > 0 \text{ for all } i. \quad (2)$$

The LVCM specifies the trophic structure of the community by the cascade model: for each pair of species $i, j = 1, \dots, n$ with $i < j$, species i never eats species j , while species j has probability c/n ($0 < c < n$) of eating species i (Cohen *et al.* 1990a). One of four dynamic effects occurs between each pair of species $i, j = 1, \dots, n$ with $i < j$.

- (i) Species j has a negative effect on species i but species i has no effect on species j (recipient-controlled or r links), i.e. $p_{ij} < 0$ and $p_{ji} = 0$.
- (ii) Species j has no effect on species i but species i has a positive effect on species j (donor-controlled or s links), i.e. $p_{ij} = 0$ and $p_{ji} > 0$.

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- (iii) Species j has a negative effect on species i and species i has a positive effect on species j (consumer–victim or t links), i.e. $p_{ij} < 0$ and $p_{ji} > 0$.
- (iv) Neither species has a dynamic effect on the other or there are no trophic links between species i and species j , i.e. $p_{ij} = 0$ and $p_{ji} = 0$.

A t link is a bidirectional link equivalent to a coupled pair of unidirectional links. Events (i)–(iv) are assumed to occur, independently for each pair of species $i, j = 1, \dots, n$ with $i < j$, with probabilities:

$$\Pr\{p_{ij} < 0 \text{ and } p_{ji} = 0\} = r/n; \quad (3a)$$

$$\Pr\{p_{ij} = 0 \text{ and } p_{ji} > 0\} = s/n; \quad (3b)$$

$$\Pr\{p_{ij} < 0 \text{ and } p_{ji} > 0\} = t/n; \quad (3c)$$

$$\Pr\{p_{ij} = 0 \text{ and } p_{ji} = 0\} = 1 - (r + s + t)/n; \quad (3d)$$

where r , s , and t are non-negative constants with $r + s + t \leq n$ and all species are self-limited, i.e. $\Pr\{p_{ii} < 0\} = 1$ for all i .

(b) Measures of transient dynamics

Monte Carlo simulations of randomly assembled LVCM food webs will be discussed in §2(c). For each sample web, the local asymptotic stability and four characteristics of the transient dynamics are measured.

(i) Local asymptotic stability

An equilibrium is said to be locally asymptotically stable if and only if all eigenvalues of its Jacobian matrix, A , are negative or have a negative real part, i.e. $\text{Re}(\lambda_i(A)) < 0$ for all i . (The Jacobian matrix, A , is defined in equation (12), §2(c).) We define system (1) to be locally asymptotically stable if it has a positive equilibrium that is locally asymptotically stable. If system (1) has a positive equilibrium that is locally asymptotically stable then that positive equilibrium is unique.

(ii) Resilience

Resilience describes how fast the state of a locally asymptotically stable system returns to its (unique) positive equilibrium following a perturbation away from that equilibrium (Pimm & Lawton 1977, 1978; Pimm 1982, 1984; DeAngelis *et al.* 1989). It is calculated as the absolute value of the largest real part of any of the eigenvalues of the Jacobian matrix, A , at equilibrium:

$$\text{resilience} = |\max\{\text{Re}\lambda_i(A); i = 1, \dots, n\}|. \quad (4)$$

The short-term transient growth of a perturbation is characterized using three measures: the reactivity, the maximum amplification and the time at which this maximum amplification occurs (Neubert & Caswell 1997).

(iii) Reactivity

Reactivity is the maximal instantaneous rate at which perturbations (away from the unique positive equilibrium) can be amplified and is defined as

$$\text{reactivity} = \max_{\|y_0\| \neq 0} \left[\left(\frac{1}{\|y_0\|} \frac{d\|y\|}{dt} \right) \Big|_{t=0} \right], \quad (5)$$

where y represents the perturbation away from equilibrium of system (1). The perturbation y is governed by $dy/dt = Ay$. The norm, $\|y\|$, is the Euclidean norm

$$\|y\| = \left[\sum_{i=1}^n y_i^2 \right]^{1/2}. \quad (6)$$

The reactivity is calculated by

$$\text{reactivity} = \max\{\lambda_i((A + [A]^T)/2); i = 1, \dots, n\} \quad (7)$$

where the eigenvalues, λ_i , in equation (7) are all real because $A + [A]^T$ is symmetrical. We define the equilibrium of a system to be reactive if and only if reactivity, computed by equation (7), is strictly positive. We define system (1) to be reactive if and only if the system is locally asymptotically stable and its positive equilibrium is reactive.

(iv) Maximum amplification

The maximum amplification, or the largest possible relative growth of a perturbation, is the maximum over time, t , of the amplification envelope, $\rho(t)$. The amplification envelope at time $t \geq 0$ is the maximum possible growth that any perturbation could have, i.e.

$$\rho(t) = \max_{\|y_0\| \neq 0} \frac{\|y(t)\|}{\|y_0\|}, \quad (8)$$

and is calculated by

$$\rho(t) = \|e^{A \times t}\|, \quad (9) \quad \text{Author: correct to write this as } \|e^{At}\| \text{ or simply } e^{At}?$$

where $\|\cdot\|$ denotes the matrix Euclidean norm. The maximum amplification is then

$$\rho_{\max} = \max_{t \geq 0} \rho(t). \quad (10)$$

(v) The time at which the maximum amplification occurs

The time at which the maximum amplification occurs is determined by

$$T_{\max} = \min\{t \in (0, \infty) | \rho(t) = \rho_{\max}\}. \quad (11)$$

When system (1) is reactive, perturbations from its positive equilibrium are amplified in the short term but decay in the long term. Then ρ_{\max} and T_{\max} represent the largest possible amplification and the earliest time it is achieved, respectively, while resilience and reactivity are the slopes of $\ln[\rho(t)]$ as $t \rightarrow \infty$ and $t \rightarrow 0$, respectively (Neubert & Caswell 1997). Figure 1 illustrates these measures.

(c) Simulations

Numerical simulations are conducted on LVCM food webs with differing numbers of species and differing connectances. The connectance, C , is defined as the fraction of possible links that actually occur in a food web with n species. If bidirectional non-cannibalistic links or pairs of unidirectional non-cannibalistic links are counted by L , then undirected connectance is $C_u = L/[n(n-1)/2]$, and the expected value of C_u is $(r + s + t)/n$. If unidirectional

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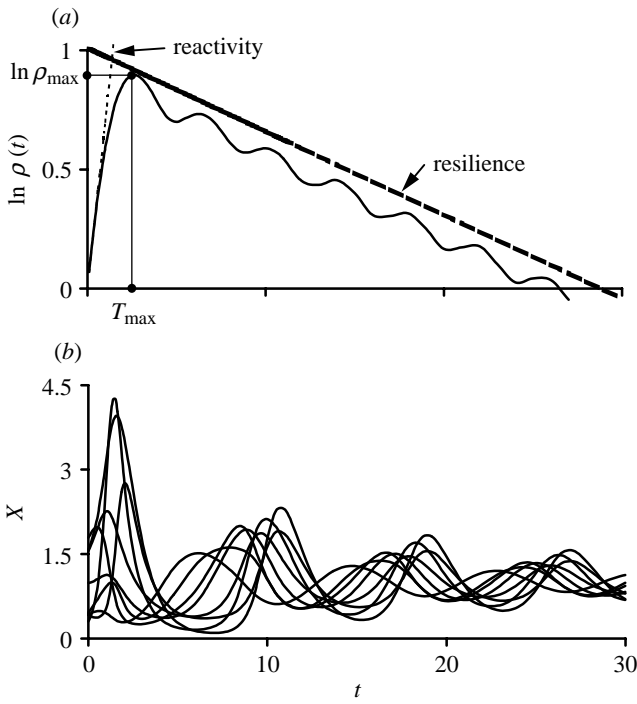


Figure 1. (a) Resilience, reactivity, ρ_{\max} and T_{\max} in relation to the amplification envelope $\rho(t)$ in an eight-species Lotka–Volterra cascade model food web with $r/n = s/n = t/n = 0.1$. Reactivity is the slope of $\ln[\rho(t)]$ as $t \rightarrow 0$; resilience is the slope of $\ln[\rho(t)]$ as $t \rightarrow \infty$; ρ_{\max} and T_{\max} show the position of the maximum of $\rho(t)$. (b) The time trajectory of the same system. Each solid line represents the relative abundance of one species.

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links are considered then directed connectance is $C_d = L/[n(n-1)]$ and the expected value of C_d is $(r+s+2t)/2n$. The probabilities r/n , s/n and t/n represent the partial connectances of r links, s links and t links, respectively. To investigate the effect of variations in connectance, model food webs of ten species were assembled and each probability (r/n , s/n or t/n) was incremented in steps of 0.05 from 0 to an upper bound determined by $r/n + s/n + t/n = 1$.

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To investigate the effect of the number of species, model food webs were assembled and the number of species was incremented in steps of 2, from 2 to 30, for several different combinations of r/n , s/n and t/n . For each combination of r/n , s/n and t/n , the total probability of unidirectional links was 0.4. A bidirectional link (t link) counted as two unidirectional links.

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For each configuration of r/n , s/n or t/n and n , a community matrix $P = (p_{ij})_{i,j=1}^n$ is generated according to the rules of the LVCM. First, a uniformly distributed random number, ψ , is drawn from $(0, 1)$ independently for all pairs of i, j ($i < j$): if $\psi \in [0, r/n]$ then $p_{ij} < 0$ and $p_{ji} = 0$; if $\psi \in (r/n, (r+s)/n]$ then $p_{ij} = 0$ and $p_{ji} > 0$; if $\psi \in ((r+s)/n, (r+s+t)/n]$ then $p_{ij} < 0$ and $p_{ji} > 0$; if $\psi \in ((r+s+t)/n, 1]$ then $p_{ij} = 0$ and $p_{ji} = 0$.

Then each non-zero element of $P = (p_{ij})$ was independently assigned a uniformly distributed random value, with p_{ij} and p_{ii} in $(-1, 0)$ and p_{ji} in $(0, 1)$. We also generated a positive vector of equilibrium, $\mathbf{Q} = (q_i)_{i=1}^n$, with each q_i uniformly distributed in $(0, 1)$. Then a vector

$\mathbf{E} = (e_i)_{i=1}^n$ was chosen so that $e_i + \sum_{j=1}^n p_{ij}q_j = 0$ for all i, j . \mathbf{E} is required for numerical simulations of trajectories. The Jacobian matrix of the LVCM at the equilibrium \mathbf{Q} is then

$$\mathbf{A} = \begin{pmatrix} p_{11}q_1 & p_{12}q_2 & \cdots & p_{1n}q_n \\ p_{21}q_1 & p_{22}q_2 & \cdots & p_{2n}q_n \\ \vdots & \vdots & \vdots & \vdots \\ p_{n1}q_1 & p_{n2}q_2 & \cdots & p_{nn}q_n \end{pmatrix}. \quad (12)$$

If \mathbf{Q} is locally asymptotically stable then so is system (1); if \mathbf{Q} is reactive then so is system (1).

For each configuration of n and r/n , s/n and t/n , 10 000 such stochastic systems were sampled. We estimated the probabilities of locally asymptotically stable systems and reactive systems as well as the average values of resilience, reactivity, ρ_{\max} and T_{\max} for an appropriate set of sample systems. The probability of local asymptotic stability was estimated as the relative frequency of locally asymptotically stable systems across all 10 000 sample food webs. The mean resilience was calculated over the set of locally asymptotically stable systems. The mean values of reactivity, ρ_{\max} and T_{\max} were calculated over reactive systems.

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The random sampling errors of these statistical estimates were represented by the standard deviations of the means. The standard deviation of the probability of local asymptotic stability was bounded above by 0.005, given 10 000 simulations.

3. RESULTS

(a) Local asymptotic stability and resilience

The probability of local asymptotic stability decreases monotonically with increasing numbers of species (figure 2a). With fixed probabilities for the three types of links (r/n , s/n and t/n), the mean resilience of stable systems decreases monotonically as the number of species increases (figure 2b). Systems with a higher probability of t links are significantly more likely to be locally asymptotically stable and have a greater mean value of resilience than systems with a lower probability of t links (figure 2a,b). This pattern is consistent across different numbers of species and for other similar sets of configurations sharing a common total probability of unidirectional links.

With the number of species fixed, the mean resilience may increase or decrease with increasing connectance, depending on the types of links varied. When the probability of t links is increased, with fixed probabilities of r links and s links, the mean resilience increases and then declines as t/n increases (figure 3a,b). The mean resilience also increases when s/n is increased, for small r/n and t/n (figure 3e). In contrast, the probability of local asymptotic stability apparently decreases monotonically with increasing probabilities of any type of link (Chen & Cohen 2001). Resilience may change differently from the probability of local asymptotic stability when connectance increases.

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To compare the effect of one consumer–victim link (t link) with that of an uncoupled pair comprising one recipient-controlled link (r link) and one donor-controlled link (s link) where the r link and the s link involve distinct species, suppose that two sets of food webs

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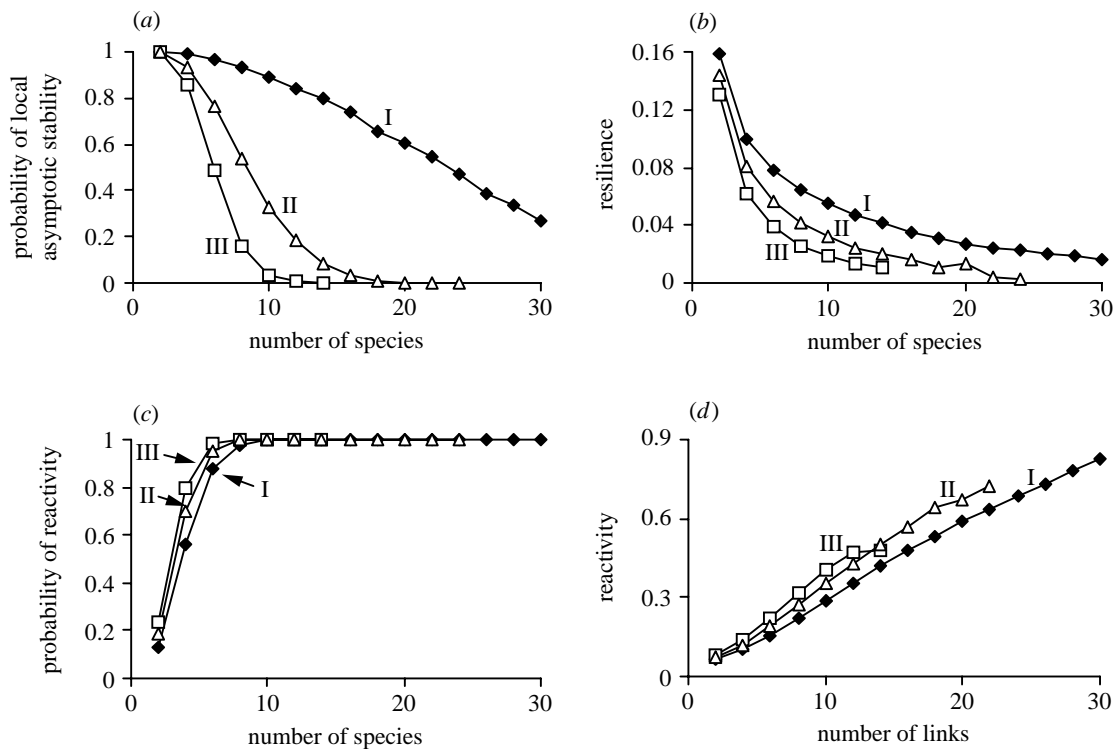


Figure 2. Probabilities of (a) local asymptotic stability and (c) reactivity and the mean (b) resilience and (d) reactivity in relation to the number of species for different combinations of the three parameters r , s and t in Lotka–Volterra cascade model food webs. I, $t/n = 0.4$ and $r/n = s/n = 0$; II, $t/n = r/n = s/n = 0.2$; III, $t/n = 0$, $r/n = s/n = 0.4$. In all three cases $(r/n + s/n + 2t/n)/2 = 0.4$. Each point represents mean ± 1 s.d.; the error bars are not visible for most points since the standard deviations are smaller than the size of the markers on the curves.

have the same number of species and that their community matrices have the same number of negative super-diagonal and positive sub-diagonal elements. In one set of webs, all links are t links, i.e. if $p_{ij} < 0$ then $p_{ji} > 0$, always assuming $i < j$. In the other set of webs, all links are either r links or s links with $r = s$, i.e. if $p_{ij} < 0$ then $p_{ji} = 0$ and if $p_{ij} > 0$ then $p_{ji} = 0$. Model food webs with only t links have a larger mean resilience than those with only r links and s links ($r = s$) (figure 3a).

In two sets of model food webs with the same total numbers of r links plus s links, webs having more s links than r links are, on average, more resilient than webs having more r links than s links (figure 3b,c,d,e,f). The difference in mean resilience between the two sets of webs increases with the difference between the numbers of r links and s links (figure 3c,d,e,f).

(b) Reactivity

With fixed probabilities for each type of link, the probability of reactivity and the mean reactivity of reactive systems increase monotonically with increasing numbers of species (figure 2c,d). With a fixed overall probability of unidirectional links (counting a t link as a pair of unidirectional links), systems with a larger proportion of t links are, on average, less reactive than those with a smaller proportion of t links (figure 2d). This pattern is general for other similar sets of configurations. When there are ten or more species, the probability of reactivity is almost 1.

With a fixed number of species, the mean reactivity usually increases with increasing probability of trophic links (figure 4). However, contrary to this general

pattern, when the probability of s links is large, as the probability of r links increases, the mean reactivity apparently decreases to a minimum and then increases (figure 4f).

Different types of links affect the mean reactivity in different ways. Webs with only t links have a smaller mean reactivity than webs with only r links and s links when $r = s$ (figure 4a). When $r + s + t$ is constant, webs having more s links than r links are, on average, more reactive than webs having more r links than s links (figure 4b,c,d,e,f). The difference between the effects of r links and s links increases with $r - s$ (figure 4c,d,e,f).

Reactivity and resilience respond differently to r links and s links. Reactivity is more sensitive to changes in the number of s links than to changes in the number of r links, while resilience is more sensitive to changes in the number of r links than to changes in the number of s links.

(c) Maximum amplification and the time of maximum amplification

The mean maximum amplification (ρ_{\max}) and the mean time of maximum amplification (T_{\max}) typically increase with the number of species (figure 5). However, for model webs with a high proportion of t links, the mean T_{\max} decreases slightly at first and then increases with increasing number of species (figure 5b). Both ρ_{\max} and T_{\max} are smaller for systems with a larger proportion of t links (figure 5a,b). This pattern is general for other similar sets of configurations.

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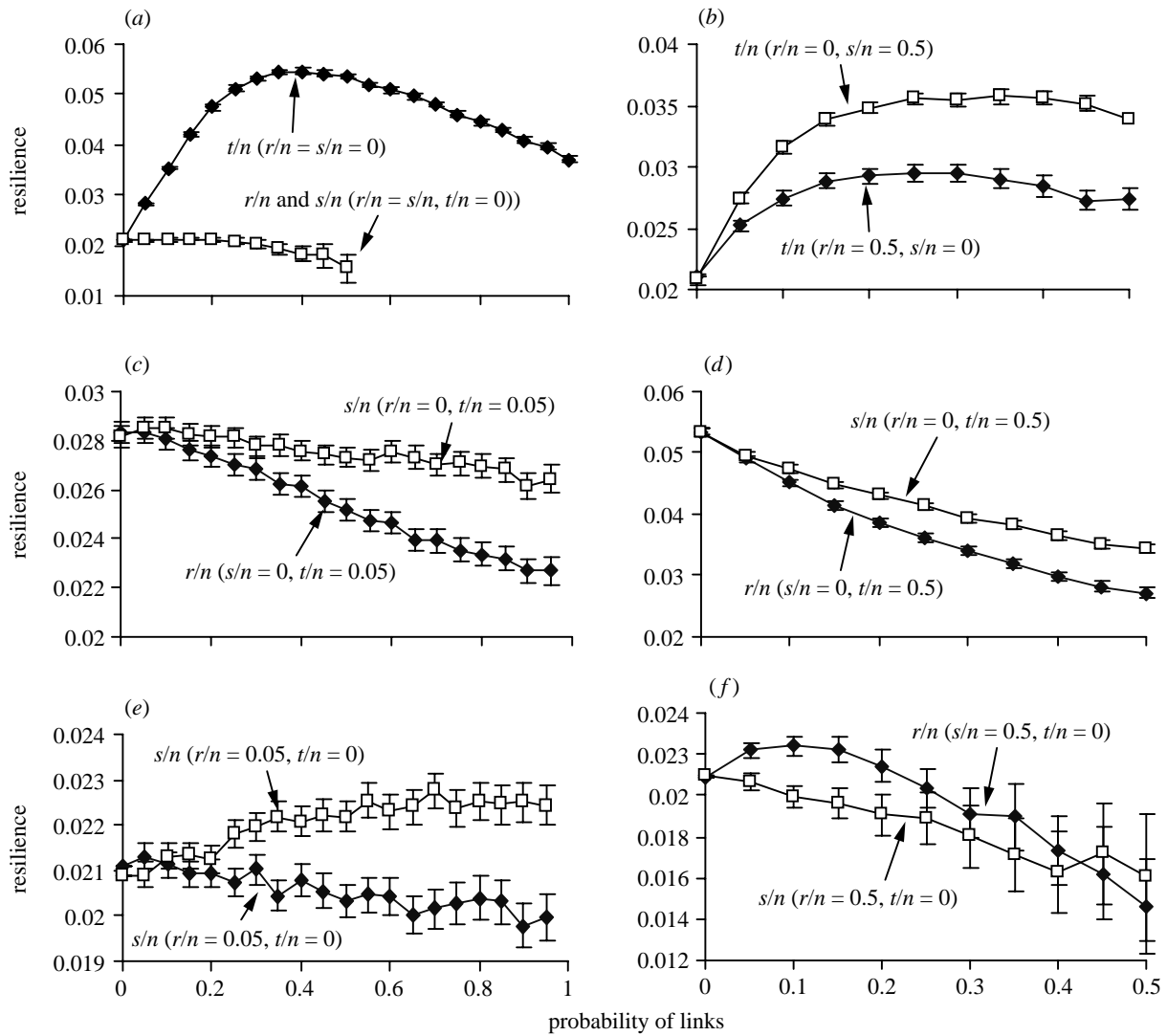


Figure 3. Mean resilience as a function of the probability of different types of links: (a) varying t with $r=s=0$ (black diamonds) and varying r and s ($r=s$) with $t=0$ (open squares); (b) varying t with either r (black diamonds) or s (open squares) fixed at a large value; (c) varying r (black diamonds) or s (open squares) with t fixed at a small value; (d) varying r (black diamonds) and s (open squares) with t fixed at a large value; (e) varying r (black diamonds) and s (open squares) with the other parameters being small; (f) varying r (black diamonds) and s (open squares) with one other parameter being large. The caption on each graph indicates the parameter that is varied and, in parentheses, the values of the other parameters. Each point represents mean \pm 1 s.d.; the error bars are not visible for many points since the standard deviations are smaller than the size of the markers on the curves.

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When $n=10$, the mean values of ρ_{\max} and T_{\max} may increase or decrease in diverse ways as the number of links increases, depending on which type of link is varied and the configuration of the other links (figure 6).

- (i) Average ρ_{\max} and T_{\max} increase monotonically with connectance. This situation is exemplified by increasing t with the value of r being close to that of s (figure 6a,g, black diamonds), increasing r with s being zero or very small and t being large (figure 6d,j, black diamonds) or increasing s with r and t being zero or very small (figure 6c,e,i,k, open squares).
- (ii) Average ρ_{\max} and T_{\max} decrease monotonically as connectance increases. This situation typically occurs when increasing r with s being large and t being small (figure 6f,l, black diamonds) or increasing t with r or s being large (figure 6b,h).

- (iii) Mean ρ_{\max} increases monotonically but mean T_{\max} increases then decreases as connectance increases. Examples of this situation are found when increasing r and s with $r=s$ and $t=0$ (figure 6a,g, open squares) or increasing s with r zero or very small and t large (figure 6d,j, open squares).
- (iv) Mean T_{\max} increases monotonically but mean ρ_{\max} increases then decreases as connectance increases. This situation is exemplified by increasing r with s and t being zero or very small (figure 6c,e,i,k, black diamonds).
- (v) Average ρ_{\max} and T_{\max} do not vary very much or do not show an obvious pattern as connectance increases, as exemplified by increasing s with r large and t zero or very small (figure 6f,l, open squares).

Different combinations of r/n , s/n and t/n also give rise to differences in the relative magnitudes of ρ_{\max} and T_{\max} .

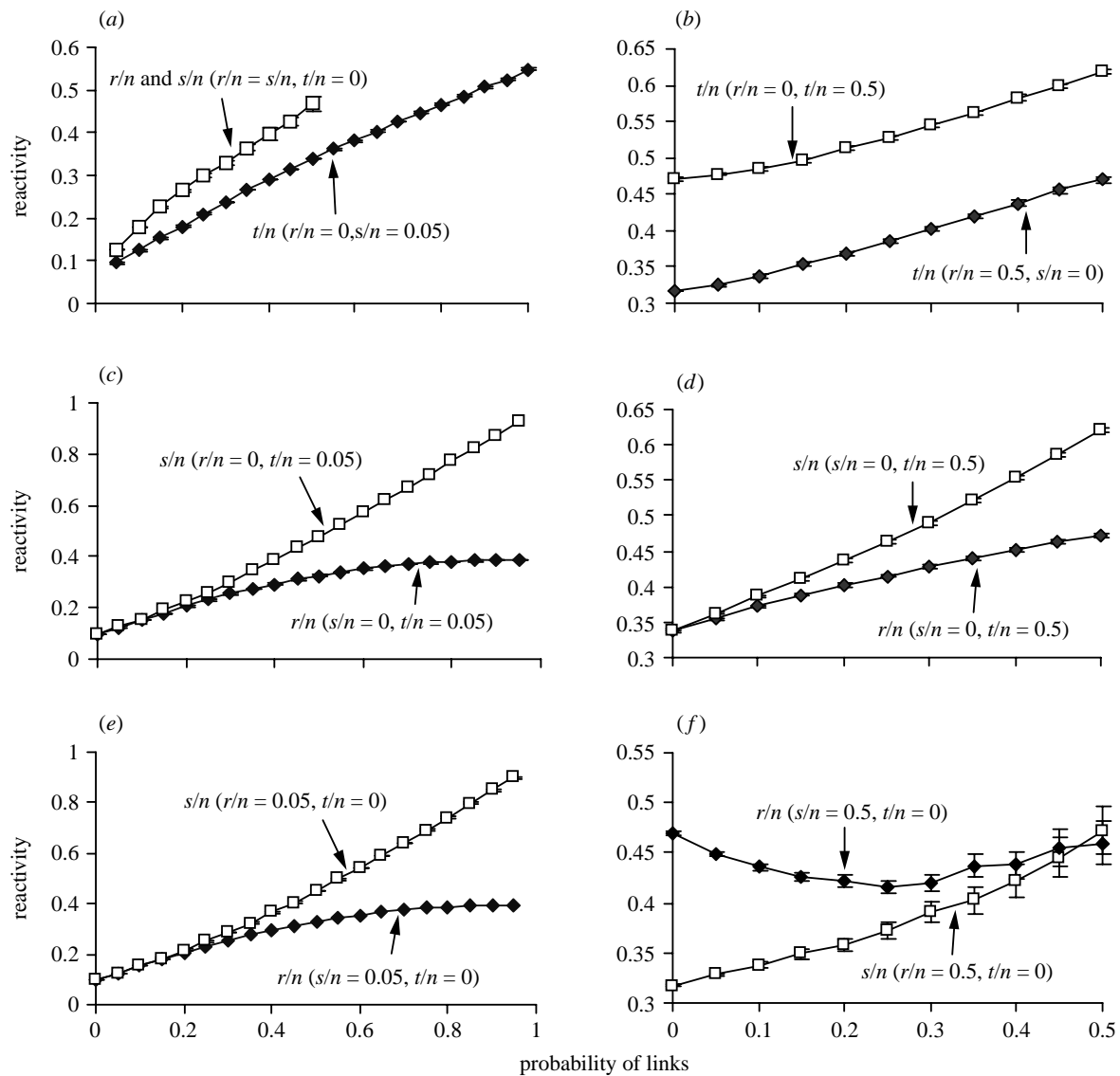


Figure 4. Mean reactivity as a function of the probability of different types of links: (a) varying t (black diamonds) and varying r and s simultaneously ($r = s$) (open squares); (b) varying t with r (black diamonds) and s (open squares) fixed at a large value; (c) varying r (black diamonds) and s (open squares) with t fixed at a small value; (d) varying r (black diamonds) and s (open squares) with t fixed at a large value; (e) varying r (black diamonds) and s (open squares) with the other parameters being small; (f) varying r (black diamonds) and s (open squares) with the other parameters being large. The caption on each graph indicates the parameter that is varied and, in parentheses, the values of the other parameters. Each point represents mean ± 1 s.d. The error bars are not visible for most points since the standard deviations are smaller than the size of the markers on the curves.

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aside from the differences in the qualitative patterns. As with reactivity, mean ρ_{\max} and T_{\max} are smaller for webs dominated by t links than for webs dominated by the same total number of r and s links (figures 5 and 6a,g), indicating that t links contribute less to the transient growth of a perturbation than do r and s links. When the probabilities of t links are fixed, food webs having more s links than r links have, in most cases, larger mean ρ_{\max} but smaller or equivalent mean T_{\max} than webs with more r links than s links (figure 6b,c,e,f,h,i,k,l).

Mean ρ_{\max} can have an accelerated increase and reach very large values (figure 6c,e,i,k, open squares) as the probability of links increases, unlike mean T_{\max} . Mean ρ_{\max} increases convexly when $s/n - r/n$ increases, while it increases concavely or approximately linearly when $r/n - s/n$ increases (figure 6d,j and figure 6c,e,i,k, black diamonds).

4. DISCUSSION AND CONCLUSION

To our knowledge this study is the first to display the diverse behaviours of different measures of long-term and transient behaviour using an integrated model of food-web structure and population dynamics. The conclusions need to be examined using other dynamic models of ecological communities.

The probability of local asymptotic stability declines monotonically as the number of species or connectance increases in the LVCM (Chen & Cohen 2001). By contrast, transient behaviours of LVCM food webs, measured by resilience, reactivity, maximum amplification and the time of maximum amplification, may vary with increasing web complexity in different ways. Average resilience may increase with increasing partial connectance of consumer-victim or donor-controlled links, at least within certain

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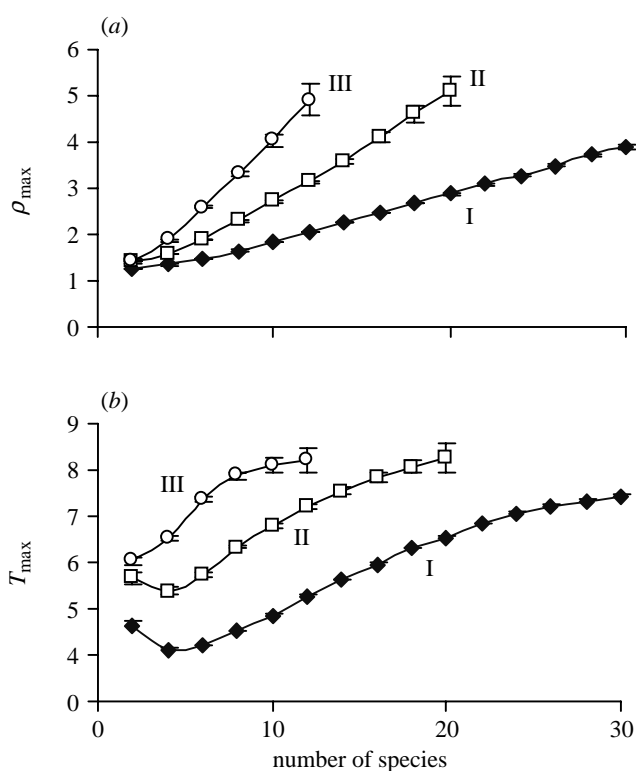


Figure 5. (a) Mean maximum amplification of perturbation (ρ_{\max}) and (b) mean time at which the maximum amplification is first attained (T_{\max}) as a function of the number of species for different combinations of r , s and t in Lotka-Volterra cascade model food webs. I, $t/n=0.4$ and $r/n=s/n=0$; II, $t/n=r/n=s/n=0.2$; III, $t/n=0$ and $r/n=s/n=0.4$. In all three cases, $(r/n + s/n + 2t/n)/2 = 0.4$. Each point represents mean ± 1 s.d. The error bars are not visible for most points since the standard deviations are smaller than the size of the markers on the curves.

ranges of partial connectance. Average reactivity typically increases with complexity but may decrease as the number of recipient-controlled links increases. The maximum amplification of a perturbation and the time at which the maximum amplification occurs may decrease as connectance increases, depending on the partial connectances. Some ensembles of model food webs that are more likely than others to persist in a constant environment may be less likely to persist in an environment with frequent perturbations.

A food-web regularity from both empirical data (Cohen & Newman 1985b; Cohen *et al.* 1990a) and theoretical studies of the local asymptotic stability of dynamic models of ecosystems (May 1972; Cohen & Newman 1984, 1985a, 1988) is the hyperbolic connectance law. This states, empirically and at the frontier of local asymptotic stability, that the product of the number of species (n) and the connectance (C) is approximately constant. If food webs are constrained by the frontier of dynamic stability measured by local asymptotic stability then webs with more species are expected to have, on average, lower connectance than smaller webs. However, this frontier of stability, based on the probability of local asymptotic stability, may not separate persistent from non-persistent food-web configurations, as the persistence of food webs in fluctuating environments may also be constrained by their transient behaviour.

As transient behaviours may vary with food-web complexity in different manners from local asymptotic stability, a frontier of stability that considers transient behaviours may show a C - n relationship that deviates from the hyperbolic connectance law. Environmental variability may contribute to variation in the relationship between C and n (Briand & Cohen 1984).

Other empirical relationships between C and n have been proposed in addition to the hyperbolic connectance law. One alternative is that C is independent of n (Warren 1990); another is that C increases with n (Winemiller 1989, Martinez 1992). While selection of data has been considered a major explanation of these different patterns, it might also be beneficial to examine the transient behaviours and habitat conditions of the food webs that yield these patterns.

Some food-web configurations may be more likely than others to persist in certain habitats, while being less likely to persist in some other habitats. This sensitivity provides a possible mechanism whereby habitat conditions, such as the frequency and amplitude of perturbations, productivity and the rate of nutrient cycling, could strongly influence food-web configurations. A topic for empirical and theoretical study is the selection, by habitat, of food-web configurations. The complexity-stability argument based on local asymptotic stability is probably only a small part of the whole story of community persistence.

Our simulations show that the three different types of links have different effects on both the probability of local asymptotic stability and the transient dynamics. For example, model food webs dominated by consumer-victim interactions are usually more likely to be locally asymptotically stable and are, on average, more resilient, less reactive, have smaller maximum amplifications of perturbation and shorter times at which the maximum amplification initially occurs than webs dominated by recipient-controlled and donor-controlled interactions, provided that the two configurations have equivalent signed directed connectance. Selection for dynamic stability would favour consumer-victim links in complex food webs. LVCM food webs with more donor-controlled links are, on average, more resilient than webs with more recipient-controlled links and are also more reactive, i.e. a perturbation grows at a greater initial rate. Food webs with more donor-controlled links also have a larger amplification of a perturbation than webs with more recipient-controlled links but the maximum amplification is reached in a shorter time.

In general, webs rich in donor-controlled links respond to perturbations by comparatively sharp, quick and large amplifications of the perturbations but the transient behaviours die out quickly. Comparable perturbations are likely to cause milder, slower, more slowly decaying transient behaviours in webs rich in recipient-controlled links.

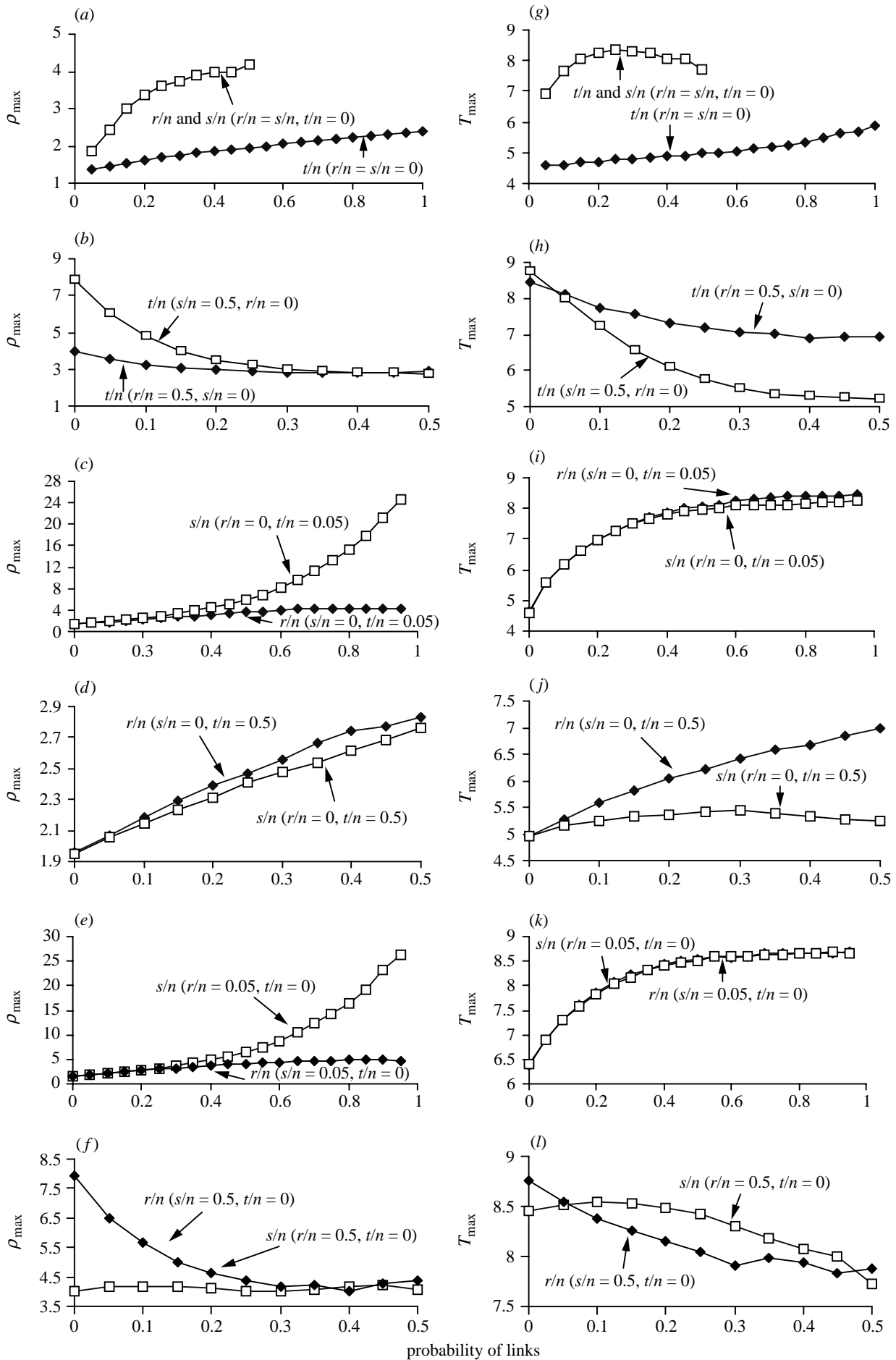
From a mathematical point of view, this study of the transient behaviour of a dynamic system with a linear term plus a non-linear term has striking parallels with recent studies of the transition to turbulence in fluid mechanics (Baggett *et al.* 1995 and citations therein). In both cases, the linear part of the dynamics is non-normal, meaning that its eigenvectors are not mutually orthogonal. The non-linear term involving the community

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matrix in equation (1) is analogous to a non-linear term that represents complex convective effects in fluid-mechanical models. This ecological study and the study of Baggett *et al.* (1995) use some of the same measures of transient behaviour and a similar approach, through numerical simulation, to investigate the dynamic (short- and long-term) consequences of randomly varying parameters. The common mathematical properties shared by ecological and fluid-dynamic non-linear models merit further investigation.

A question related to this study is whether and how often ecosystems rest at their steady states? In ecosystems of small spatial scale, spatial dynamics and time delays usually lead to the dominance of transient dynamics (DeAngelis & Waterhouse 1987; Hastings & Higgins 1994; Hastings 1996). DeAngelis & Waterhouse (1987) argued that the stable equilibrium state should not be viewed as a fundamental property of ecological systems. On a global scale, the population of *Homo sapiens* grew at an accelerating rate until 1965 and shows no signs of reaching any fixed equilibrium (Cohen 1995). A mass extinction of species may be impending or underway and human activities may be a major contributor (Rosenzweig 1995). Global climate change, whether of human or non-human origin, may be imposing a large perturbation on the global ecosystem. It seems unlikely that the global ecosystem is in a steady state. If the global ecosystem and many affected regional ecosystems are in a transient state then perhaps it is time to switch some attention from steady-state to transient dynamics.

This work was supported in part by United States National Science Foundation grants BSR92-07293 and DEB99-81552. J.E.C. thanks Mr and Mrs William T. Golden for hospitality during this work. We thank Michael Neubert and Hal Caswell for helpful improvements to a previous draft of the manuscript and L. N. Trefethen for pointing out the connection between his work (Baggett *et al.* 1995) and ours.

REFERENCES

Auerbach, M. J. 1984 Stability, probability and the topology of food webs. In *Ecological communities: conceptual issues and evidence* (ed. D. R. Strong Jr, D. Simberloff, L. G. Abele & A. B. Thistle), pp. 412–436. Princeton University Press.

Baggett, J. S., Driscoll, T. A. & Trefethen, L. N. 1995 A mostly linear model of transition to turbulence. *Physics of Fluids* **7**, 833–838.

Briand, F. & Cohen, J. E. 1984 Community food webs have scale-invariant structure. *Nature* **307**, 264–266.

Chen, X. & Cohen, J. E. 2001 Global stability, local stability and permanence in model food webs. (In preparation.)

Cohen, J. E. 1995 *How many people can the earth support?* New York: W. W. Norton.

Cohen, J. E. & Newman, C. M. 1984 The stability of large random matrices and their products. *Ann. Probabil.* **12**, 283–310.

Cohen, J. E. & Newman, C. M. 1985a When will a large complex system be stable? *J. Theor. Biol.* **113**, 153–156.

Cohen, J. E. & Newman, C. M. 1985b A stochastic theory of community food webs. I. Models and aggregated data. *Proc. R. Soc. Lond.* **B224**, 421–448.

Cohen, J. E. & Newman, C. M. 1988 Dynamical basis of food web organization. *Ecology* **69**, 1655–1664.

Cohen, J. E., Newman, C. M. & Briand, F. 1985 A stochastic theory of community food webs. II. Individual webs. *Proc. R. Soc. Lond.* **B224**, 421–448.

Cohen, J. E., Briand, F. & Newman, C. M. 1990a *Community food webs: data and theory*. *Biomathematics*, vol. 20. Heidelberg: Springer.

Cohen, J. E., Luczak, T., Newman, C. M. & Zhou, Z.-M. 1990b Stochastic structure and nonlinear dynamics of food webs: qualitative stability in a Lotka–Volterra cascade model. *Proc. R. Soc. Lond.* **B240**, 607–627.

Connell, J. H. & Sousa, W. P. 1983 On the evidence needed to judge ecological stability or persistence. *Am. Nat.* **121**, 789–824.

DeAngelis, D. L. & Waterhouse, J. C. 1987 Equilibrium and nonequilibrium concepts in ecological models. *Ecol. Monogr.* **57**, 1–21.

DeAngelis, D. L., Mulholland, P. J., Palumbo, A. V., Steinman, A. D., Huston, M. A. & Elwood, J. W. 1989 Nutrient dynamics and food web stability. *A. Rev. Ecol. Syst.* **20**, 71–95.

Hastings, A. 1988 Food web theory and stability. *Ecology* **69**, 1665–1668.

Hastings, A. 1996 What equilibrium behavior of Lotka–Volterra models does not tell us about food webs. In *Food webs: integration of patterns and dynamics* (ed. G. A. Polis & K. O. Winemiller), pp. 211–217. Amsterdam: Chapman & Hall.

Hastings, A. & Higgins, K. 1994 Persistence of transients in spatially structured ecological models. *Science* **263**, 1133–1136.

Haydon, D. 1994 Pivotal assumptions determining the relationship between stability and complexity—an analytical synthesis of the stability–complexity debate. *Am. Nat.* **144**, 14–29.

Holling, C. S. 1973 Resilience and stability of ecological systems. *A. Rev. Ecol. Syst.* **4**, 1–23.

Lawton, J. H. 1989 Food webs. In *Ecological concepts: the contribution of ecology to an understanding of the natural world* (ed. J. M. Cherrett), pp. 43–78. Oxford, UK: Blackwell Scientific.

Lewontin, R. C. 1969 The meaning of stability. In *Diversity and stability in ecological systems. Symposium 22. Brookhaven National Laboratory* (ed. G. M. Woodwell & H. H. Smith), pp. 13–24. New York.

Martinez, N. D. 1992 Constant connectance in community food webs. *Am. Nat.* **139**, 1208–1218.

May, R. M. 1972 Will a large complex system be stable? *Nature* **238**, 413–414.

May, R. M. 1973 *Stability and complexity in model ecosystems*. Princeton University Press.

Neubert, M. G. & Caswell, H. 1997 Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology* **78**, 653–665.

Paine, R. T. 1988 Food webs: road maps of interactions or grist for theoretical development? *Ecology* **69**, 1648–1654.

Figure 6. (*Opposite*) Mean maximum amplification of perturbation (ρ_{\max}) and the mean time at which the maximum amplification is first attained (T_{\max}) in relation to different combinations of r , s and t in Lotka–Volterra cascade model food webs: (*a*,*g*) varying t (black diamonds) and varying r and s simultaneously ($r=s$) (open squares); (*b*,*h*) varying t with r (black diamonds) and s (open squares) fixed at a large value; (*c*,*i*) varying r (black diamonds) and s (open squares) with t being small; (*d*,*j*) varying r (black diamonds) and s (open squares) with t being large; (*e*,*k*) varying r (black diamonds) and s (open squares) with the other parameters being small; (*f*,*l*) varying r (black diamonds) and s (open squares) with the other parameters being large. The caption on each graph indicates the parameter that is varied and, in parentheses, the values of the other parameters. Each point represents mean ± 1 s.d. The error bars are not visible for most points since the standard deviations are smaller than the size of the markers on the curves.

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- Pimm, S. L. 1982 *Food webs*. London: Chapman & Hall.
- Pimm, S. L. 1984 The complexity and stability of ecosystems. *Nature* **307**, 321–326.
- Pimm, S. L. & Lawton, J. H. 1977 The number of trophic levels in ecological communities. *Nature* **268**, 329–331.
- Pimm, S. L. & Lawton, J. H. 1978 On feeding on more than one trophic level. *Nature* **275**, 542–544.
- Pimm, S. L., Lawton, J. H. & Cohen, J. E. 1991 Food web patterns and their consequences. *Nature* **350**, 669–674.
- Rosenzweig, M. L. 1995 *Species diversity in space and time*. Cambridge University Press.
- Warren, P. H. 1990 Variation in food web structure: the determinants of connectance. *Am. Nat.* **136**, 689–700.
- Winemiller, K. O. 1989 Must connectance decline with species richness? *Am. Nat.* **134**, 960–968.
- Yodzis, P. 1981 The stability of ecosystems. *Nature* **289**, 674–676.
- Yodzis, P. 1989 *Introduction to theoretical ecology*. New York: Harper & Row.