

Weak interactions, omnivory and emergent food-web properties

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Empirical studies have shown that, in real ecosystems, species–interaction strengths are generally skewed in their distribution towards weak interactions. Some theoretical work also suggests that weak interactions, especially in omnivorous links, are important for the local stability of a community at equilibrium. However, the majority of theoretical studies use uniform distributions of interaction strengths to generate artificial communities for study. We investigate the effects of the underlying interaction-strength distribution upon the return time, permanence and feasibility of simple Lotka–Volterra equilibrium communities. We show that a skew towards weak interactions promotes local and global stability only when omnivory is present. It is found that skewed interaction strengths are an emergent property of stable omnivorous communities, and that this skew towards weak interactions creates a dynamic constraint maintaining omnivory. Omnivory is more likely to occur when omnivorous interactions are skewed towards weak interactions. However, a skew towards weak interactions increases the return time to equilibrium, delays the recovery of ecosystems and hence decreases the stability of a community. When no skew is imposed, the set of stable omnivorous communities shows an emergent distribution of skewed interaction strengths. Our results apply to both local and global concepts of stability and are robust to the definition of a feasible community. These results are discussed in the light of empirical data and other theoretical studies, in conjunction with their broader implications for community assembly.

Keywords: food webs; local stability, permanence; omnivory; interaction strength; extinction

1. INTRODUCTION

The early view of complex ecological systems was that complexity begot stability (MacArthur 1955; Elton 1958). This paradigm was dramatically changed during the mid-1970s (May 1973), when it was reported that features of food webs such as increased food-chain length (Pimm & Lawton 1977) and omnivory (Pimm & Lawton 1978) resulted in decreased resilience (a form of stability, after Pimm 1991). In particular, the finding that asymptotically stable omnivorous webs tended to be statistically rare (Pimm & Lawton 1977, 1978) seeded a well-supported paradigm in the literature: omnivory should be destabilizing and therefore rare in food webs (Cohen 1978; Briand 1983; Cohen *et al.* 1986, 1990; Schoenly *et al.* 1991).

Since the early 1990s, an increasing body of empirical evidence has suggested that omnivory is actually common if not prevalent in empirically documented food webs (Winemiller 1990; Polis 1991; Huxham *et al.* 1995; Memmot *et al.* 2000; Woodward & Hildrew 2001). Contrary to the hypothesis that omnivory is destabilizing, empirical studies have unequivocally found that omnivory has a stabilizing effect on the dynamics of simple food webs (Lawler & Morin 1993; Fagan 1997; Holyoak & Sachdev 1998; Lalonde *et al.* 1999). Coincidentally, theoretical developments have demonstrated that omnivorous links in model food webs are intimately associated with weak species interactions (McCann & Hastings 1997; McCann *et al.* 1998; Neutel *et al.* 2002) and that the specific patterning of species–interaction strengths is critical for food-

web stability (May 1973; Pimm & Lawton 1978; Yodzis 1981; Haydon 2000). At the same time, a substantial body of work has demonstrated that the predator–prey interactions in ‘real’ food webs are strongly skewed towards weak interactions (Paine 1992; Fagan & Hurd 1994; de Ruiter *et al.* 1995; Raffaelli & Hall 1996; Wootton 1997).

Using food-web models to study the skewed distribution of interaction strengths and their specific arrangement within the food web provides insights into the topology and functioning of such ‘real’ complex systems. Understanding the relationships between the observed skew in the distribution of interaction strengths, the stability of these communities and the underlying properties of the food web will enable us better to manage ecosystems in the face of unprecedented human-induced disturbance. Having the ability to identify food-web topologies and the important interactions within these food webs, which promote community persistence, seems imperative. We investigate the role of weak interactions in determining the complexity and stability of model food webs by varying the distribution of interaction strengths. We focus particularly on omnivorous food webs, and show that recent results linking weak interactions with the local stability of a food web (Neutel *et al.* 2002) are generally applicable to both local and global concepts of stability and to feasible food webs.

2. MODEL FOOD WEBS

We take as our starting point the work of Pimm & Lawton (1977, 1978), who studied simple four-species food webs whose dynamics are described by a general Lotka–Volterra system:

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$$\frac{dX_i}{dt} = X_i \left(r_i + \sum_{j=1}^n a_{ij} X_j \right) \quad i = 1, \dots, 4, \quad (2.1)$$

where X_i is the population density, r_i is the intrinsic growth (or decay) rate of the i th species and a_{ij} is an element of the interaction-coefficient matrix, A , describing the *per capita* effect of the j th species on the growth rate of the i th species (the interaction coefficient a_{ij} is positive if it enhances growth, for example prey–predator interactions, and negative if it suppresses growth, for example predator–prey interactions and intraspecific competition). The population densities of all species at equilibrium are given by $\mathbf{X}^* = -A^{-1}\mathbf{r}$, where \mathbf{X}^* is the vector of population densities. The local stability of \mathbf{X}^* is determined by the Jacobian matrix, \mathcal{J} , whose elements are $\mathcal{J}_{ij} = a_{ij} X_i^*$ (the Jacobian matrix is also referred to as the community matrix or the interaction-strength matrix). The elements of the Jacobian matrix, \mathcal{J}_{ij} , should not be confused with the interaction coefficients a_{ij} (Laska & Wootton 1998). To avoid further confusion we let interaction strength mean an element of the Jacobian matrix, \mathcal{J}_{ij} . The interaction-coefficient matrix, A , has elements that we will call interaction coefficients, a_{ij} .

The use of Lotka–Volterra models to simulate ecosystem dynamics is open to debate, primarily owing to the simplistic assumption that all species have a linear (type I) functional response. Other models have moved away from this simple Lotka–Volterra formalism (e.g. Berryman *et al.* 1995; McCann *et al.* 1998), but Lotka–Volterra models, when used with simplistic community-module-type webs (figure 1), can still provide heuristic insights into the functioning of real complex food webs. Despite its simplicity, the Lotka–Volterra system (equation (2.1)) was chosen for several reasons. First, the equilibrium and non-equilibrium dynamics of the system are well understood (Hofbauer & Sigmund 1998); the properties of this system and the patterns that emerge can be used to question our knowledge of the ‘real’ world. Second, the system is simple, allowing insights to be distilled with minimal biological detail being incorporated into the model. Third, its use permits direct comparison with classic (Pimm & Lawton 1977, 1978) and more recent (Law & Morton 1996; Neutel *et al.* 2002) theoretical results. Fourth, the interaction coefficients, a_{ij} , and the interaction strengths, \mathcal{J}_{ij} , of the Lotka–Volterra framework can be estimated for real food webs (de Ruiter *et al.* 1995; Laska & Wootton 1998; Berlow *et al.* 1999; Neutel *et al.* 2002; Emmerson & Raffaelli 2004) in a way that more complicated functional responses cannot. Finally, theory has been developed to calculate robustly both local and global measures of stability. In this context, the Lotka–Volterra framework is one of many tools that contemporary ecologists can use to enhance our understanding of complex real systems. Its use here is meant not to emulate the real world but to question it.

To parameterize the Jacobian matrix, \mathcal{J} , we allow each interaction strength, \mathcal{J}_{ij} , be a random variable with an underlying distribution. To maintain consistency with earlier work (Pimm & Lawton 1977, 1978) we assumed that the average *per capita* effect of a predator upon its prey is 100 times greater than the effect of a prey upon its predator. The mean interaction strength of a predator upon its prey was taken to be -5 , and the mean

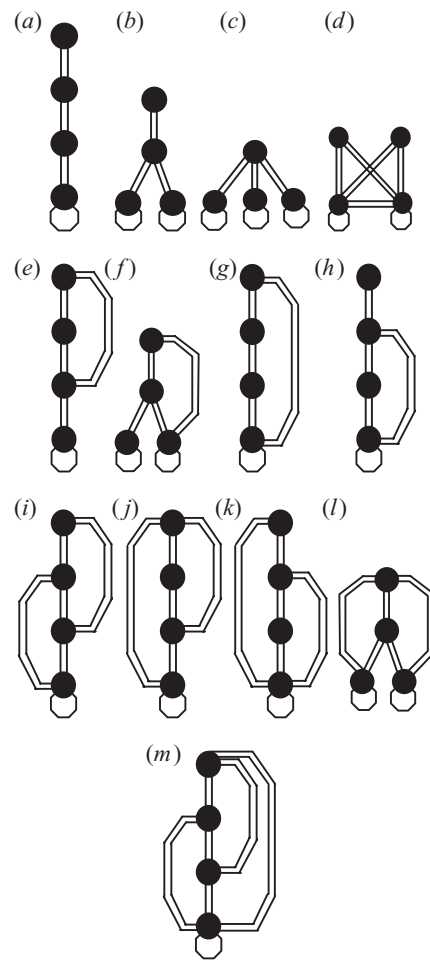


Figure 1. The 13 food webs used in this paper. The food webs in (a–f) are the same as those used by Pimm & Lawton (1977, 1978). The food webs vary in their connectance, number of trophic levels, number of basal species and degree of omnivory.

interaction strength of a prey upon its predator was taken to be 0.05. Each basal species was also given a self-interaction term, \mathcal{J}_{ii} , with a mean of -0.5 . Previous work (Pimm & Lawton 1977, 1978; Yodzis 1981; Pimm 1982) has largely assumed a uniform distribution of interaction strengths, with at least one study using a declining exponential distribution of interaction coefficients (Law & Morton 1996). The consequences of varying the bounds and the mean and variance of the interaction-strength distribution have been explored previously (Pimm & Lawton 1978; Kokkoris *et al.* 2002), although the shape of the interaction-strength distribution, to our knowledge, remains wholly unexplored. We use four different distributions of interaction strength: (i) a uniform distribution for compatibility with previous studies; (ii) an exponentially declining distribution because this closely approximates empirical distributions, which are skewed towards weak interactions (Paine 1992; Fagan & Hurd 1994; Raffaelli & Hall 1996; Wootton 1997); (iii) a linearly declining distribution because this is another distribution skewed towards weak interactions; and (iv) a truncated normal distribution as a non-uniform distribution with no skew towards weak interactions (see Appendix A for a full description of these distributions). For all four distributions, the mean strength of each trophic interaction was

held constant, so that only the higher moments of the distribution were varied.

3. FEASIBILITY AND STABILITY

We use two techniques to explore the stabilities of our model food webs (equation (2.1)): first, we carry out a local stability analysis to investigate the local dynamics of the interior equilibrium point, \mathbf{X}^* , and, second, we use a property known as permanence to investigate the global stability of the system. We also classify each food web as either feasible or infeasible. Our definition of feasibility (see § 3c) extends previous definitions by placing plausible constraints upon the intrinsic growth rates of each species in each food web.

The full procedure used to generate our model communities is as follows. One Jacobian matrix was generated (as described in § 2). We then searched through 40 000 candidate equilibrium communities, \mathbf{X}^* , until a feasible community was found (see § 3c for details). If a feasible community could not be found, then this was noted and a new Jacobian matrix was generated. The interaction-coefficient matrix, A , the Jacobian matrix, \mathcal{J} , and the intrinsic growth rates, \mathbf{r} , of each feasible community were recorded before a local stability analysis was carried out and the permanence of each food web was calculated (after Law & Morton 1996).

(a) Local stability analysis

The local stability of an equilibrium point can be determined by inspection of the eigenvalues of \mathcal{J} . The equilibrium point is locally stable if the largest eigenvalue of \mathcal{J} , λ_{\max} , has a negative real part (May 1973). This stability criterion can be expressed in terms of a return time for each food web, defined as $T_R = -1/\text{Real}(\lambda_{\max})$. A negative return time indicates an unstable equilibrium community, while a positive return time is a measure of the time taken for a community to return to equilibrium following a small perturbation (Pimm & Lawton 1977).

(b) Permanence

Permanence is a measure of the global stability of a system, and establishes whether *all* species in a community are able to persist (i.e. whether their population densities remain positive and finite). Since permanence is a measure of global stability, it provides no information regarding the internal community dynamics. The use of permanence to assess the persistence and coexistence of ecological systems has been discussed extensively elsewhere (Anderson *et al.* 1992; Law & Blackford 1992; Law & Morton 1996; Hofbauer & Sigmund 1998; Law 1999) and we refer the reader to these texts for a thorough treatment of the subject. We tested our model food webs for permanence using linear programming (Jansen 1987).

To check whether a food web is permanent requires that we know the intrinsic growth rates, \mathbf{r} , and interaction coefficients, A , of the community. However, in many studies (e.g. May 1973; Pimm & Lawton 1977, 1978) only the elements of the Jacobian matrix were specified, for reasons discussed in § 3c. It is common for no assumptions to be made regarding the feasible values of interaction coefficients and intrinsic growth rates. We define the equilibrium population densities, X_i^* , of all species, which when







taken together with the Jacobian matrix, \mathcal{J} , is equivalent to specifying the intrinsic growth rates and the interaction-coefficient matrix of the system. To achieve this without straying from the spirit of the earlier work of Pimm & Lawton (1977, 1978) we randomly generated a Jacobian matrix, \mathcal{J} , (as described in § 2) and a vector of equilibrium population densities with a pyramidal structure (Pimm & Lawton 1977), such that predators are less abundant than prey. The density of a species in the k th trophic level was randomly drawn from the interval $[X_{\min}^{(k)}, X_{\max}^{(k)}]$, where $X_{\max}^{(k)}$ is the smallest density in the trophic level immediately below (basal species correspond to $k = 1$ for which $X_{\max}^{(1)}$ was arbitrarily set to 10 000) and $X_{\min}^{(k)}$ was arbitrarily set at 1000, 100, 10 and 1 for $k = 1, 2, 3$ and 4, respectively. This pyramidal structure can be justified from allometric relationships (Peters 1983) by combining predator-prey body-size ratios with the fact that species density scales with body size as $W^{-0.98}$. A factor of 10 between the densities of predators and their prey is typical for a 1 kg predator eating large prey. This procedure ensures that the equilibrium population vector has a pyramidal structure with a moderately uniform distribution of densities. It was then possible to calculate the interaction coefficients, $a_{ij} = \mathcal{J}_{ij}/X_i^*$, and the intrinsic growth rates, $\mathbf{r} = A\mathbf{X}^*$.

(c) Feasibility

Previous studies have defined feasibility as a positive equilibrium population density (i.e. $X_i > 0$) for all species in a community (May 1973; Roberts 1974; Gilpin 1975; Pimm 1982; Kokkoris *et al.* 2002; Jansen & Kokkoris 2003). This definition is convenient because it places no constraints upon the intrinsic growth rates. This allows the Jacobian matrix, \mathcal{J} , to be parameterized without constraint, because a feasible equilibrium community can always be inferred by an appropriate choice of the intrinsic growth rates. It is for this reason that earlier studies concentrated upon parameterization of the Jacobian matrix and avoided the issue of specifying feasible values for the interaction coefficients and intrinsic growth rates. Pimm (1982, p. 66) recognized that realistic constraints on the intrinsic growth rates, r_i , might be difficult to satisfy, implying that $X_i > 0$ is not a sufficiently stringent criterion for a feasible community. Since the calculation of permanence requires that the intrinsic growth rates are explicitly calculated, it is straightforward to extend the usual definition of feasibility by imposing constraints upon the intrinsic growth rates. Biologically, it is plausible that basal species have a positive intrinsic growth rate while those of non-basal species are negative. Basal species here represent primary producers, such as plants, in a community. The growth of plants is determined by the abundance of limiting resources such as nutrients; we have not explicitly included nutrient pools in the food webs represented here and so a basal primary producer's growth is considered positive. The abundances of non-basal species are considered to be functions of the resources in the trophic level below; the intrinsic rate for non-basal species is therefore their natural death rate since a consumer's population cannot grow in the absence of its prey. We therefore defined a feasible food web to be one where all equilibrium densities are positive, all basal species have positive

Table 1. The percentages of communities that were found to be (a) feasible, (b) locally stable, (c) permanent and (d) both locally stable and permanent, for all six of the four-species food webs studied by Pimm & Lawton (1977, 1978), and for four different distributions of interaction strengths.

(The percentages in (a) were calculated from 2000 randomly generated communities; the percentages in (b–d) were calculated from the number of food webs that were feasible.)

						
(a) feasible webs						
truncated normal	97.8	97.5	100.0	100.0	100.0	100.0
uniform	94.6	92.3	100.0	100.0	100.0	100.0
linear	92.2	92.5	100.0	100.0	100.0	100.0
exponential	89.3	88.3	99.9	100.0	100.0	100.0
(b) stable webs						
truncated normal	100.0	4.5	100.0	12.7	100.0	0.1
uniform	100.0	9.5	100.0	22.3	100.0	0.4
linear	100.0	10.5	100.0	25.3	100.0	0.7
exponential	100.0	12.9	100.0	32.0	100.0	1.9
(c) permanent webs						
truncated normal	100.0	11.7	100.0	15.8	100.0	2.1
uniform	100.0	20.3	100.0	26.5	100.0	2.2
linear	100.0	24.1	100.0	28.1	100.0	2.0
exponential	100.0	28.4	100.0	36.0	100.0	3.2
(d) permanent and stable webs						
truncated normal	100.0	4.5	100.0	11.4	100.0	0.1
uniform	100.0	9.5	100.0	21.1	100.0	0.3
linear	100.0	10.5	100.0	23.3	100.0	0.5
exponential	100.0	12.9	100.0	30.4	100.0	1.7

intrinsic growth rates ($r_i > 0$) and all non-basal species have negative intrinsic growth rates ($r_i < 0$).

4. ANTAGONISTIC EFFECTS

The effect of a skew towards weak interactions was investigated using the six simple food webs of earlier studies (figure 1*a–f*; Pimm & Lawton 1977). We created 2000 random communities for each food web with each of the four interaction-strength distributions described in Appendix A. The feasibility, permanence and return time (i.e. the local stability of the equilibrium) of each random community were then calculated. The percentage of feasible communities obtained from 2000 randomly parameterized communities is shown in table 1*a*. The percentages of locally stable (table 1*b*), permanent (table 1*c*) and locally stable and permanent (table 1*d*) food webs are expressed as percentages of the feasible subset of webs.

Initially the distribution of positive return times for the *feasible* communities was created. For illustrative purposes, figure 2 shows these distributions for two of the food webs, one with and one without omnivory, corresponding to figure 1*e* and figure 1*a*, respectively (these distributions are also available for the food webs of figure 1*b–d, f*; see electronic Appendix B, figure 4; available on The Royal Society's Publications Web site). Figure 2 demonstrates our first conclusion, that as the skew towards weak interactions becomes more pronounced the tail of the positive-return-time distribution lengthens. Looking at the non-omnivorous food web (figure 2*a–d*), the percentage of return times exceeding 150 increases

from 31% for a uniform distribution (figure 2*b*) to 55% for an exponentially declining distribution (figure 2*d*). The same trend is evident for the omnivorous food web (figure 2*e–h*). For all six food webs (figure 1*a–f*), we found that the median return time of the locally stable feasible communities increased as the skew towards weak interaction strengths increased (mean interaction strengths were held constant throughout).

Second, given our criteria for a feasible community, the food webs with more trophic levels (figure 1*a,e*) show a decreasing percentage of feasible communities as the skew towards weak interaction strengths increases (table 1*a*). By contrast, food chains with fewer trophic levels (figure 1*b–d,f*) remain feasible irrespective of the interaction-strength distribution. The presence of omnivory in a food web was found to have no effect upon the probability of finding a feasible community.

Third, increasing the skew towards weak interactions in the omnivorous food webs generally increases the percentage of locally stable communities (table 1*b*). Therefore, as the incidence of weak links in omnivorous food webs increases there is a higher statistical probability that a food web will be stable. The same qualitative result holds when permanence is the measure of stability: a greater proportion of webs are found to be permanent as the interaction-strength distribution is increasingly skewed towards weak interactions (table 1*c*). The proportion of locally stable webs does not coincide with the proportion of permanent webs, indicating that there are communities that, although not locally stable, persist on some form of cyclic or chaotic attractor (table 1*d*).

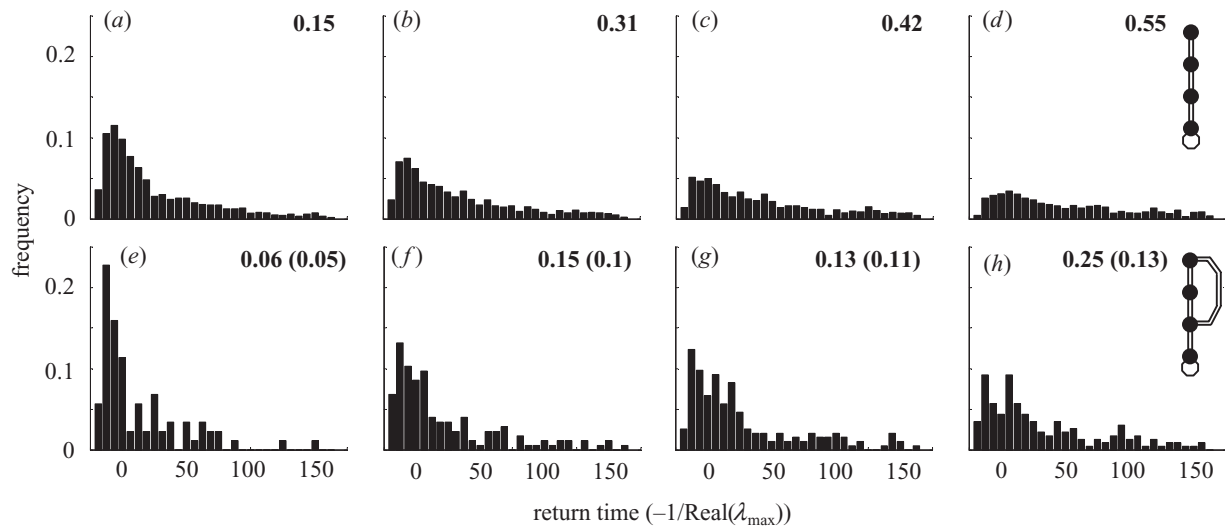


Figure 2. The effect of the interaction-strength distribution on return time for food webs in figure 1*a,e*. Bold numbers on each figure give the proportion of return times that exceed 150 and represent the tail of the return-time distribution. Numbers in parentheses give the proportion of feasible omnivorous food webs that were stable. As the skew is increased towards weak interactions, return times increase. (*a,e*) Truncated normal distribution of interaction strengths, no skew; (*b,f*) uniform distribution of interaction strengths, no skew; (*c,g*) linearly declining distribution of interaction strengths, moderately skewed; (*d,h*) exponentially declining distribution of interaction strengths, highly skewed.

Fourth, irrespective of the underlying interaction-strength distribution, median return times increase with the number of trophic levels (i.e. a skew towards weak interactions does not counteract the destabilizing effect of increasing food-chain length). This supports the conventional view that the number of trophic levels in a food web is inversely related to its local stability.

In common with others before us (Pimm & Lawton 1977, 1978; Pimm 1982), we have used return time as a measure of local stability, because, in the real world, long return times result in an increased susceptibility to perturbations. From our analysis it is clear that using a uniform distribution of interaction strengths to generate model communities underestimates both the return time of an ecological system and the probability of finding a stable omnivorous community. We explored the stability of omnivorous communities further by looking at the two omnivorous food webs shown in figure 1*e,f*. From the communities that were generated using a uniform interaction-strength distribution, we selected those that were both locally stable and feasible. We removed the omnivorous link (spanning more than one trophic level) to create non-omnivorous food webs, and recalculated the return times for these new communities. All of these non-omnivorous communities were stable; however, the median return time of each non-omnivorous food web was double that of its omnivorous counterpart (for the food webs in figure 1*e,f*, median return times are $T_R = 27.09$ and $T_R = 10.38$, respectively, whereas for their non-omnivorous counterparts they are $T_R = 57.03$ and $T_R = 20.88$, respectively). The same pattern emerged when we looked at the proportion of return times greater than 150, with the removal of the omnivorous link causing an increase from *ca.* 11% to 30% and from *ca.* 3% to 15% in the two food webs (figure 1*e,f*, respectively). When a stable omnivorous food web occurs it tends to be more resilient than a non-omnivorous version of the same web. We have considered just one way in which omnivorous

and non-omnivorous food webs might be equivalent (i.e. presence versus absence of the omnivorous link). Subsets of the simple food webs we have examined are also equivalent in the number of links and in their connectance. We have not considered the effects of such equivalency here.

Weak interactions affect the stability of food webs antagonistically. They increase the return time to equilibrium, making a food web more susceptible to future perturbations. By contrast, however, weak interactions also increase the probability that a food web is both locally and globally stable. When omnivorous webs do occur they tend to be more resilient than an equivalent non-omnivorous food web (i.e. when there are more pathways for energy to flow through a food web the community can return to its equilibrium faster).

5. EMERGENT FEATURES

We now concentrate upon omnivorous food webs and look at all topologically distinct four-species omnivorous food-web topologies (figure 1). For each food web, we created 10 000 random communities using a uniform distribution of interaction strengths. We increased the number of random communities to 10 000 to obtain a sufficiently large sample of locally stable and permanent communities. We selected the locally stable subset of feasible communities and the permanent subset of feasible communities. We then examined the emergent distribution of interaction strengths for each individual link in the food web. The results for the permanent food webs of figure 1*f* are shown in figure 3 (see electronic Appendix B for results for the permanent and locally stable subsets of all food webs detailed in figure 1*e-m*). It is clear from figure 3 that, for three of the links (figure 3*f,h,i*), the emergent distributions of interaction strengths are strongly skewed towards weak interactions. These skewed interaction-strength distributions occur in the omnivorous loop; thus, figure 3*f* illustrates the negative *per capita* effect

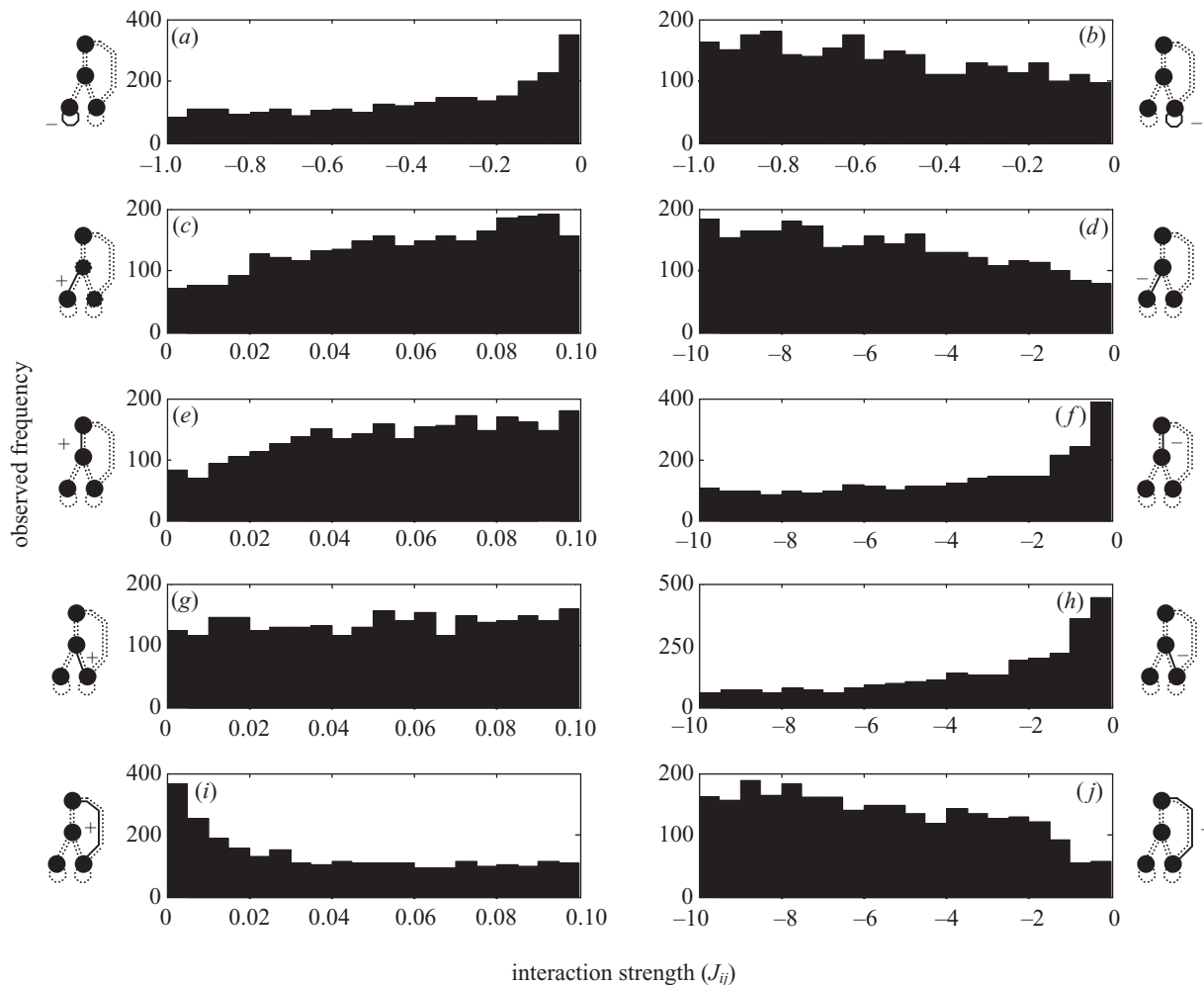


Figure 3. The distribution of interaction strengths for each link in the food web of figure 1*f*. Graphs on the left correspond to positive interactions (with the exception of (a)); graphs on the right correspond to negative interactions. Each panel corresponds to the following interaction strength (a) $\mathcal{J}_{11} = a_{11}X_1^*$; (b) $\mathcal{J}_{22} = a_{22}X_2^*$; (c) $\mathcal{J}_{31} = a_{31}X_3^*$; (d) $\mathcal{J}_{13} = a_{13}X_1^*$; (e) $\mathcal{J}_{43} = a_{43}X_4^*$; (f) $\mathcal{J}_{34} = a_{34}X_3^*$; (g) $\mathcal{J}_{32} = a_{32}X_3^*$; (h) $\mathcal{J}_{23} = a_{23}X_2^*$; (i) $\mathcal{J}_{42} = a_{42}X_4^*$; (j) $\mathcal{J}_{24} = a_{24}X_2^*$. Interactions in the omnivorous loop (\mathcal{J}_{34} – \mathcal{J}_{42} – \mathcal{J}_{23}) are strongly skewed towards weak interaction strengths.

of species 4 on species 3 (\mathcal{J}_{34}). Figure 3*h* shows the negative *per capita* effect of species 3 on species 2 (\mathcal{J}_{23}), and figure 3*i* depicts the positive effect of species 2 on species 4 (\mathcal{J}_{42}). These strongly skewed interaction-strength distributions occur in a counterclockwise direction around the omnivorous loop. For both the permanent and locally stable communities the qualitative pattern of skewed interactions is the same: the emergent weak interactions occur in the omnivorous loops. We consistently find the same patterning of interaction strengths in the omnivorous loops for all nine omnivorous food webs. When more than one omnivorous loop occurs in a food web (figure 1*i–m*), it is the longest loop whose interactions are skewed towards weak interactions. When loops of equivalent length occur (figure 1*l*), the interactions in both loops are skewed towards weak interactions.

For all nine omnivorous food webs studied, we found an emergent skew towards weak interactions in the links of the omnivorous loops when stable communities were selected. The results were the same for both local and global measures of stability. This shows that a stable community is favoured if omnivorous links are weak.

6. DISCUSSION

Our aim in this study was to investigate the effects of changing the skew of the underlying interaction-strength distributions on the stability and feasibility of randomly generated communities. In particular, we are interested in skews towards weak interactions because these reflect ‘real world’ empirical distributions (Paine 1992; Fagan & Hurd 1994; de Ruiter *et al.* 1995; Raffaelli & Hall 1996; Wootton 1997). The association between weak interactions and omnivory (including intraguild predation) is also of particular interest because previous theoretical and conceptual work has suggested links between the two (McCann *et al.* 1998; Polis *et al.* 2000; Neutel *et al.* 2002). This study addresses the issue in two ways: first, four interaction-strength distributions, with differing degrees of skew, are used to generate model communities for analysis; and second, either locally or globally stable communities are selected and the patterning of interaction strengths is analysed. Our results show that a skew towards weak interaction strengths affects stability in two antagonistic ways. First, an abundance of weak interactions increases the

median return time of the community irrespective of the number of trophic levels. The result is a system more prone to the effects of stochastic perturbations and, therefore, less stable than previous studies have suggested (Pimm & Lawton 1977, 1978). Second, an abundance of weak interactions in an *omnivorous* food web increases the probability that a community will have a stable equilibrium structure. The emergent distributions of interaction strengths show strong skew towards weak interactions in the omnivorous links, supporting recent theoretical studies using linear (Neutel *et al.* 2002) and nonlinear (McCann *et al.* 1998) functional responses. In their local stability analysis of 'real' soil food webs, Neutel *et al.* (2002) found weak interaction strengths in long omnivorous loops. They describe a metric (loop weight) for quantifying the magnitude of the interactions in food-web loops. The loop weight is the geometric mean of the absolute values of the interaction strengths in a food-web loop. We calculated the loop weights (see Neutel *et al.* 2002) for each of the omnivorous loops in each of our food-web parameterizations. We found that the longest loops were characterized by small loop weights. Our results confirm Neutel *et al.*'s findings and demonstrate that the same qualitative pattern holds for the globally stable communities we studied here. In fact, all our results hold for both locally and globally stable communities. In summary, a skew in the interaction-strength distribution towards weak interactions will increase the probability of omnivory occurring, while decreasing the stability of any communities that do not contain omnivores.

Local stability analyses have been criticized because they examine a system's behaviour only in close proximity to an equilibrium point. Both the stochastic nature of the environment and the variety of complex dynamics that can be seen in natural ecosystems suggest that communities may rarely be close to equilibrium. Does such criticism of the use of local stability raise doubts about the applicability of previous studies (e.g. May 1973; Pimm & Lawton 1977, 1978; Yodzis 1981; de Ruiter *et al.* 1995; Sterner *et al.* 1997; Neutel *et al.* 2002)? With few exceptions (Brenchley 1979; Thomas & Pomerantz 1981; Lawler & Morin 1993; de Ruiter *et al.* 1995; Neutel *et al.* 2002), there have been almost no attempts to validate the local stability approach empirically. Using permanence, we have shown that our results hold for both local and global concepts of stability. Within the globally stable subset of communities, the same emergent patterns in the specific arrangement of interaction strengths were found as in the locally stable subset of communities. Such a result may depend on the proportion of permanent food webs with unstable interior fixed points. If the subset of permanent and locally unstable food webs is small, then we might expect there to be a correspondence between the results using local and global measures of stability. To put these findings into context, human-induced changes to the biosphere have resulted in large-scale extinction and disturbance. In light of this, it seems naive to assume that an ecosystem's dynamics can be realistically studied using a local stability analysis. However, local stability analyses are mathematically tractable and allow deep insights into the important factors governing a community's dynamics. We suggest that modern computing power allows local and

global stability analyses to be combined so that valuable insights can be distilled from simplistic models.

Another possible weakness of previous studies lies in their definition of a feasible community. Traditionally, a feasible community has been taken to mean one where all equilibrium population densities are positive (Roberts 1974; Gilpin 1975; Thomas & Pomerantz 1981; Pimm 1982; Kokkoris *et al.* 2002; Jansen & Kokkoris 2003), although Pimm (1982) noted that realistic constraints upon intrinsic growth rates might require a more stringent criterion for feasibility. Our criterion for feasibility has been made more stringent by adding the requirement that the values of the intrinsic growth rates must lie within biologically plausible limits. Where our study overlaps with previous work, there is qualitative consistency in the results, indicating that the stabilities of Lotka–Volterra food webs are robust to the definition of feasibility. We argue that, while parameterization of the Jacobian matrix is attractive owing to its simplicity, future studies should explicitly specify the fundamental parameters of a food-web model. In the case of Lotka–Volterra models this implies parameterization of intrinsic growth rates as well as interaction coefficients. In so doing, the biology of these dynamic systems can be incorporated more realistically (Law & Morton 1996; Jonsson & Ebenman 1998).

Recently, Jansen & Kokkoris (2003) have examined how the feasibility and stability of Lotka–Volterra model communities are affected by both the mean and variance of their interaction strengths. They found that the internal patterning of interaction coefficients, a_{ij} , was less important in determining a community's stability and feasibility than were their mean and variance. By contrast, Haydon (2000) argued that the specific patterning of interaction strengths could be 'critical to ecosystem stability'. The variance of the interaction-strength distributions used in this paper increases as their skew towards weak interactions increases. For omnivorous communities it was found that stability increases as the skew towards weak interactions increases, despite the fact that variance is also increasing and contrary to the results of Jansen & Kokkoris (2003). Therefore, our results show that the skew in the interaction-strength distribution is also an important factor determining community stability. Haydon (2000) also demonstrated that the distribution of intraspecific interactions (i.e. a species' self-regulation) is important in understanding the issues of community stability and complexity, and that the effects of intraspecific interactions may override those of interspecific interactions. Our study, like many others before, has not singled out the intraspecific interactions for specific attention, leaving a clear gap for future research.

Real food webs are spatially and temporally dynamic in both their species richness and their topology (Warren 1989). Such changes in food-web structure can occur because of nonlinear functional responses, predator interference, predator switching, variation in prey productivity and changing environmental conditions (Warren 1989; Menge *et al.* 1994, 1997; Polis *et al.* 1996; Spiller & Schoener 1995; Sanford 1999; Navarrete & Castilla 2003). Previous studies have proposed that the stability of a community's dynamics imposes dynamic constraints, which partly determine the assembly of real communities and the shaping of properties such as a food web's top-

ology (Drossel *et al.* 2001; Fox & McGrady-Steed 2002) and the length of food chains (Pimm 1982). Even though our results are derived from static food-web topologies, they indicate that dynamic constraints result in weak omnivorous interactions, and that these weak interactions are most likely to be in a counterclockwise direction around the longest omnivorous loops (see figure 3*f,h,i*). This supports the findings of theoretical studies (McCann *et al.* 1998; Neutel *et al.* 2002), and is in contrast to the work of Sterner *et al.* (1997), who found a lack of theoretical evidence for the effects of dynamic constraints on food-chain length and topology. Furthermore, our results suggest that, once dynamic constraints have shaped the interaction strengths of omnivorous links to be weak, then dynamic constraints continue to maintain omnivory, because removing the omnivorous species causes a reduction in stability. Whether dynamic constraints can shape the distribution of interaction strengths in a community depends upon the mechanisms governing the evolution of community structure; this is an area clearly open to further research. Dynamic constraints could cause a food web to evolve if spatially local variations in food-web structure were allowed to propagate more widely, provided that they promoted community stability. If dynamic constraints do act in such a way, they could explain why empirical studies show a stabilizing effect of omnivory upon a community's dynamics (Lawler & Morin 1993; Fagan 1997; Holyoak & Sachdev 1998; Lalonde *et al.* 1999).

Although the models used in this study are simplistic and their practical application to 'real world' problems is arguable, our emergent patterns of interaction strengths do reproduce the patterns observed in real ecosystems. Specifically, there is a skew towards weak interaction strengths, and our model indicates that this skew promotes stability in both its local and global senses (Paine 1992; Fagan & Hurd 1994; de Ruiter *et al.* 1995; Raffaelli & Hall 1996; Wootton 1997). The model results also single out omnivorous species as being of critical importance. If communities with omnivory evolve to have weak interactions in their omnivorous links (as suggested by our results), then the removal of these omnivorous species will severely reduce the persistence and resilience of the community and ultimately the ecosystem. Exploring the effects of weak interactions and the distribution and structure of interaction strengths in food webs will aid our future understanding of food-web dynamics and the process of community assembly.

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APPENDIX A

We used four different distributions for $f(x;\mu,\sigma)$ with mean μ and variance σ^2 : uniform, linearly declining, exponentially declining and truncated normal. The uniform distribution is defined as

$$0 \text{ if } x < 0,$$

$$f(x;\mu,\sigma) = 1/(2\mu) \text{ if } 0 \leq x \leq 2\mu,$$

$$0 \text{ if } x > 2\mu,$$

with a variance, σ^2 , of $\mu^2/3$. The linearly declining distribution is defined as

$$0 \text{ if } x < 0,$$

$$f(x;\mu,\sigma) = 2/(3\mu) \{1 - x/(3\mu)\} \text{ if } 0 \leq x \leq 3\mu,$$

$$0 \text{ if } x > 3\mu,$$

with a variance, σ^2 , of $\mu^2/2$. The exponentially declining distribution is defined as

$$0 \text{ if } x < 0,$$

$$f(x;\mu,\sigma) = \exp(-x/\mu)/\mu \text{ if } 0 \leq x,$$

with a variance, σ^2 , of μ^2 . Finally, the truncated normal distribution is defined as

$$0 \text{ if } x < 0,$$

$$f(x;\mu,\sigma) = \exp(-(x - \mu)^2/s^2)/N \text{ if } 0 \leq x \leq 2\mu,$$

$$0 \text{ if } x > 2\mu$$

where $N = s\pi^{1/2}\text{erf}(\mu/s)$ and erf is the error function, and s is a parameter of this distribution related to the variance of this distribution by $\sigma^2 = s^2\{0.5 - \mu\exp(-\mu^2/s^2)/N\}$. The parameter σ was chosen so that the variance was equal to that of the uniform distribution, $\sigma^2 = \mu^2/3$. As the skew towards weak interactions gradually increases we move from the uniform and normal distributions, which both have no skew, to the linearly declining distribution and then to the exponentially declining distribution.

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