Topological structure and interaction strengths in model food webs

Christopher Quincea, Paul G. Higgsb and Alan J. McKaneb

aDepartments of Physics and Astronomy, Arizona State University, P.O. Box 871504, Tempe, Arizona 85287-1504, USA
bDepartment of Physics and Astronomy, McMaster University, Hamilton ON, Canada L8S 4M1
cDepartment of Theoretical Physics, University of Manchester, Manchester M13 9PL, UK

Abstract

We report the results of carrying out a large number of simulations on a coevolutionary model of multispecies communities. A wide range of parameter values were investigated which allowed a rather complete picture of the change in behaviour of the model as these parameters were varied to be built up. Our main interest was in the nature of the community food webs constructed via the simulations. We identify the range of parameter values which give rise to realistic food webs and give arguments which allow some of the structure which is found to be understood in an intuitive way. Since the webs are evolved according to the rules of the model, the strengths of the predator-prey links are not determined a priori, and emerge from the process of constructing the web. We measure the distribution of these link strengths, and find that there are a large number of weak links, in agreement with recent suggestions. We also review some of the data on food webs available in the literature, and make some tentative comparisons with our results. The difficulties of making such comparisons and the possible future developments of the model are also briefly discussed.

Keywords: Food webs, coevolutionary model, multispecies communities, weak links, interaction strengths

1
1 Introduction

Food webs, which represent the links between predators and prey in an ecological community, are complex networks which present several problems to the modeller. Firstly, can the range and nature of webs be specified a priori, perhaps using some generic biological principles? Secondly, can a dynamics describing the change in population sizes of species in the web be defined on the network? Thirdly, given that the number of links in a food web of a reasonable size will be of the order of several hundred, is it possible in practice, or even desirable, to give values to all of these link strengths?

The formidable difficulties associated with answering these questions led most early researchers to adopt approaches to the modelling of food webs which either bypassed some of these questions entirely, or implemented them in a very simple way. For example, May (1973) assumed the network to be a random graph, the interactions to be of randomly chosen strength and linearised the dynamics near a fixed point. Other food web modellers ignored the dynamics completely and simply gave rules to construct static graphs (Cohen et al., 1990; Williams and Martinez, 2000). Even in the recent flurry of interest concerning network structure and topology (Albert and Barabási, 2002), most modellers have concentrated on specifying the nature of the network, rather than defining the dynamics on the network. The problem with this approach is that there is no reason why network structures which are appealing or which are found in social or other networks (small world, scale invariance) should apply to food webs. A recent study indeed shows that this is the case (Dunne et al., 2002a).

This suggests a more sophisticated approach to the modelling of food webs should be adopted. A clue as to how we might move forward is that it is clear that the structure of the network depends on the dynamics of the network, and cannot be divorced from it. It is therefore not appropriate to specify the web and then define dynamics — the two are interdependent. For example, a predator-prey link between any two species will disappear if either of the species becomes extinct and this will depend on the nature of the population dynamics that is chosen to govern their interaction. It is also clear that the dynamics on the network will be strongly influenced by the nature of the network itself. This strongly suggests that we cannot separate the population dynamics on the network from the dynamics which changes the network structure, which will occur on much longer time scales.

These comments address the first two of the questions posed at the be-
ginning of this section, but there still remains the difficulty of knowing how to generate the several hundred quantities which specify the parameters in the model dynamics at any given time. The solution to this problem which we favour is to assemble the food web from one (or very few) species, so that the parameters are determined by the dynamics of web assembly. We have already explained that this dynamics is inextricably linked to the population dynamics. Starting with only one species simply amounts to giving an initial condition to the dynamics. In this way we determine those food web structures that can actually be reached rather than simply those that are possible.

A model based on this philosophy was developed by some of us a few years ago and has been under study since then. An original version of the model (Caldarelli et al., 1998) was superseded by a later version with more realistic population dynamics (Drossel et al., 2001), and reviews which discuss the model specifically (Quince et al., 2002) and in a more general context (Drossel and McKane, 2003) are available. Our aim in this paper is to present a more extensive set of results from the model, emphasising aspects that were not stressed in previous investigations. A prime example is the distribution of link strengths, which is a topic which has been discussed extensively in the last year or so (Berlow et al., 2004) and which is an emergent attribute in our model, and consequently a fundamental test of the whole approach.

We begin by outlining the model in Section 2 and then, in order to provide some intuition on how a particular web is built up, we describe the time evolution of a single web in Section 3. The structure of the model food webs which are dynamically constructed through simulation of the model are explored in Section 4 and compared with data in Section 5. The distribution of link strengths in the model is explored in Section 6 and a discussion of our broad conclusions, as well as possible future avenues of investigation, is given in Section 7.

2 The model

In this section we will give an overview of the model, presenting enough detail that subsequent sections of the paper may be understood. Readers should consult Drossel et al. (2001) for further details, especially regarding motivation for various model choices and the specifics of the computer simulation.
The model is unusual in spanning a very large range of time scales, from changes in foraging strategies — which might occur on a time scale of the order of days — to evolutionary time scales. As we have indicated in the Introduction, we believe that phenomena on these different time scales cannot be separated, hence the need to consider them as a coherent whole.

On the shortest time scale the number of species and their populations are fixed, and only the foraging strategy — the fraction of time that an individual of a particular species $i$ spends preying on individuals of another species $j$ — changes. This fraction will be denoted by $f_{ij}$, and will be called the effort that species $i$ puts into preying on species $j$. Clearly $\sum_j f_{ij} = 1$ for all species $i$.

A reasonable foraging strategy would be one in which the amount of effort that a particular predator, $i$, put into preying on each of its prey, indexed by $j$, would be proportional to the gain in resources. Since the rate at which an individual of species $i$ consumes individuals of species $j$ is just $g_{ij}$, the functional response, this amounts to assuming that $f_{ij} \propto g_{ij}$, for a given species $i$ and all its prey species $j$. Using $\sum_j f_{ij} = 1$, gives

$$f_{ij}(t) = \frac{g_{ij}(t)}{\sum_k g_{ik}(t)}.$$  \hspace{1cm} (1)

The justification of the choice (1) is discussed in greater depth by Drossel et al. (2001) where it is shown that in the context of this model this is an evolutionarily stable strategy. It is also interesting that it fixes the efforts in terms of the functional response, which is a far more familiar quantity to ecological modellers, and which will be discussed later in this section.

On a larger time scale, the number of species in the food web is still fixed, but the populations of these species changes, as well as their efforts. This is the regime of conventional population dynamics. In the model it is described by a balance equation for the rate of change of the number of individuals of species $i$ in the food web at time $t$, $N_i(t)$:

$$\frac{dN_i(t)}{dt} = \lambda \sum_j N_i(t)g_{ij}(t) - \sum_j N_j(t)g_{ji}(t) - d_iN_i(t).$$  \hspace{1cm} (2)

Here $\lambda$ is the fraction of prey resource which is turned into predator births and $d_i$ is the constant rate of death of individuals of species $i$, in the absence of interactions with other species. These equations are the natural generalisations of balance equations found in the literature for systems with only a
few species (Maynard Smith, 1974; Roughgarden, 1979), with the first term on the right-hand side representing the growth in numbers of species \( i \) due to predation on other species, the second term the decrease in numbers due to predation by other species, and the last term the death rate of individuals of species \( i \). Where there is no predator-prey relationship between species \( i \) and species \( j \), \( g_{ij} \) is zero.

Finally, on still longer timescales, the number of species may change as well as their populations and efforts. Here we leave the realms of conventional population dynamics, and we need to give the species traits or features which define their behavioural and phenotypic characteristics. This will allow us to set up a scheme in which close variants of existing species are introduced into the community (speciation) and determine how good one species, \( i \), is at preying on another, \( j \) (the score \( S_{ij} \)). We do this by constructing a set of \( K \) distinct features and an antisymmetric \( K \times K \) matrix \( m_{\alpha\beta} \) which gives the score of feature \( \alpha \) against feature \( \beta \). A new matrix is chosen at the start of every simulation run with entries which are Gaussian random variables with zero mean and unit variance. Species are then defined to be sets of \( L \) distinct features. In the simulations we describe in this paper we took \( L = 10 \) and \( K = 500 \), but any two integers which allow for a very large number of distinct species to be created would be acceptable. The score of species \( i \) against species \( j \) is defined in terms of the scores of all the features of species \( i \) against all the features of species \( j \):

\[
S_{ij} = \max \left\{ 0, \frac{1}{L} \sum_{\alpha \in i} \sum_{\beta \in j} m_{\alpha\beta} \right\}.
\]

(3)

Note that \( S_{ij} \geq 0 \) and if \( S_{ij} > 0 \) then \( i \) is adapted to prey on \( j \). In addition, a species \( 0 \), representing the environment, is introduced at the start of a simulation, and is left unchanged throughout that particular run.

The dynamics on the largest, evolutionary, time scale can now be described. Once the population dynamics defined by (2) settles down to a new equilibrium value, a speciation is permitted to occur. This consists of choosing a species in the food web at random to be the parent species. One of its features is then randomly selected and changed randomly to another feature. This resulting child species is then introduced into the food web with a population of \( N^{\text{child}} \) and the parent population reduced by \( N^{\text{child}} \). In simulations reported in this paper we always take \( N^{\text{child}} = 1 \). After the speciation has been carried out, Eq. (2) is then integrated forward and the population dy-
namics are allowed to determine whether the population of the new species, the parent species, and indeed all other species in the web, grow or decline as a result of the change in composition of the web. We set a minimum population level, \( N^{\text{min}} = 1 \). If the population of a species falls below this level at any point in the simulation, this species is assumed to be extinct and is removed from the system.

This describes the essence of the model. It remains to choose the functional response, \( g_{ij}(t) \). Considerable care was taken in making a biologically realistic choice; a detailed account of the logic behind the choice is given in Drossel et al. (2001). To motivate it, let us first describe the form we use, but for a single predator \( i \) feeding on a single prey \( j \):

\[
g_{ij}(t) = \frac{S_{ij}N_j(t)}{bN_j(t) + S_{ij}N_i(t)},
\]

This is known as a ratio-dependent function response (Arditi and Ginsburg, 1996), since \( g_{ij} \) is a only a function of the ratio \( N_i/N_j \). The functional response which we actually use has to apply to a general web, where a given species may have an arbitrary number of predators and prey. We therefore modify (4) by (i) introducing the efforts \( \alpha_{ki} \), and (ii) replacing the term \( S_{ij}N_i(t) \) by a sum of terms over all the predators of \( j \) (denoted by \( k \) and which includes \( i \)). This will involve a function \( \alpha_{ki} \) which describes predator competition and which we take to have the form:

\[
\alpha_{ki} = c + (1 - c)q_{ki}.
\]

Here \( c \) is a constant such that \( 0 \leq c \leq 1 \) and \( q_{ki} \) is the fraction of features of species \( k \) that are also possessed by species \( i \). The result is a generalised ratio-dependent functional response:

\[
g_{ij}(t) = \frac{S_{ij}f_{ij}(t)N_j(t)}{bN_j(t) + \sum_k \alpha_{ki}S_{kj}f_{kj}(t)N_k(t)}.
\]

The choice for the competition function \( \alpha_{ki} \) is motivated by the expectation that species which are different from each other (small \( q_{ki} \)) should be less in competition for resources (i.e. individuals of species \( j \)) than those which are similar.

A flow diagram showing the sequence of steps in a single simulation is shown in Fig. 1. The simulation starts with the choice of species 0 (the
environment) and one other species which will begin by feeding off it (an autotroph). From a practical point of view, the differential equations (2), are solved numerically by discretising time into segments of duration $\Delta T$. At the beginning of one of these periods the population numbers $\{N_i(t)\}$ have just been updated, and therefore new functional responses may be determined from (6). The process of iterating (1) and (6) to produce new efforts corresponding to these new populations take place on the shortest time scale of the model. The iteration of the population dynamics (2) takes place on the intermediate time scale, and the speciation process on the longest time scale.

Finally, we have mentioned several parameters during the description of the model, such as the parameter $b$ in the definition of the functional response (6) and the competition parameter $c$ in (5). The other main parameter of
the model is denoted by $R$, and is the rate of input of resources from the environment into the food web. These parameters, as well as four others which are kept fixed throughout our investigation, are given in Table 1.

## Table 1: The parameters of the model. Only the first three parameters are varied in this paper.

| Symbol | Name                      | Description                                                                 |
|--------|---------------------------|-----------------------------------------------------------------------------|
| $R$    | Resources                 | Rate of input of external resources into food web                           |
| $c$    | Competition constant      | Determines the degree of inter-specific competition                          |
| $b$    | Saturation constant       | Controls the effectiveness of predation                                      |
| $\lambda$ | Conversion efficiency  | Ratio of numerical to functional responses                                   |
| $d$    | Death rate                | Per capita death rate in the absence of interactions                         |
| $N_{\text{min}}$ | Minimum population      | Population below which species are assumed extinct                           |
| $N_{\text{child}}$ | Child population       | Population at which new species are added                                    |

3 Time evolution of an individual simulation

The mechanism summarised in Fig. 1 is capable of generating large complex food webs. This is true for a wide range of parameter space — the boundaries of which we explore in the next section. In Fig. 2 the time evolution, measured in number of attempted speciation events, of the species number is shown for one of these sets of parameter values. For these values of the parameters, the number of species initially increases quite rapidly but with sizable fluctuations. Then after about 10000 iterations it appears that the long time average number of species is approaching a constant value. There is considerable variation about this value representing a continuous overturn of species due to speciation and extinction.

Since speciation is represented as a random event in the model then the sequence of food webs generated during an individual model simulation can be viewed as a realisation of a stochastic process. For each particular choice of initial conditions corresponding to a set of parameter values, the randomly
assigned feature matrix $m_{\alpha \beta}$ and random environment features, there will be a different time dependent probability distribution of food web configurations. The corresponding distribution for any food web statistic, such as the number of species shown in Fig. 2, may then be obtained from these configurations. That the long time average number of species appears to become constant in Fig. 2 suggests that it may be evolving towards a stationary distribution. This has been investigated further by examining extremely long simulations, of the order of $10^6$ speciation events. For these simulations no long term trends in any statistics were found after the initial growth phase. From this we conjecture that the probability distribution of food web structures also evolves towards a time independent stationary distribution.

The simulation shown in Fig. 2 was sampled after 100, 200, 1000 and 10000 speciation events and the food web structure at these times is shown in Fig. 3. The circles in these diagrams correspond to species and the arrows represent predator-prey interactions between species. The arrows point from...
Figure 3: Four food webs sampled at times 100 (top left), 500 (top right), 1000 (bottom left) and 10000 (bottom right) from the simulation described in the caption of Fig. 2.
prey to predator and have thickness that is proportional to the fraction of the predator’s diet constituted by the prey. The vertical arrows originating from the base of the diagrams indicate feeding off the environment. Only those links that constitute greater than 1% of a predator’s diet are shown in the diagram.

The horizontal position of the species in Fig. 3 has no significance except to generate comprehensible diagrams. Species vertical position on the other hand does have meaning, it is proportional to what we will refer to as the trophic height of the species. This is calculated as the weighted average of the lengths of the paths from the species to the environment, with the paths weighted multiplicatively by the predator diet fractions or efforts $f_{ij}$:

$$h_i = 1 + \sum_{j=1}^{S} f_{ij} h_j,$$

$$\Rightarrow h_i = \frac{\sum_{j=1}^{S} (\delta_{ij} - f_{ij})^{-1}}{\sum_{j=1}^{S}} ,$$

where $h_i$ is the trophic height of the $i$th species. The horizontal dashed lines in the food web diagrams have vertical position equal to integer trophic heights. We will also use the term trophic level to indicate the minimum path length from a species to the environment and denote it by $l_i$. A majority of species in the model food webs have a trophic height close to their trophic level. Thus we will use the latter in this paper to investigate food web structures, since it has the advantage of being discrete and being defined for the typically binary empirical food webs. A recent review of the trophic level concept is given by Williams and Martinez (2004). Our definitions of trophic level and trophic height correspond to their shortest and flow based definitions of trophic level respectively.

The diagrams in Fig. 3 give a clear sense of the increase in average community complexity, in terms of species number and the number of predator-prey interactions per species, that occurs during the growth phase of the simulations. It is worth emphasising again that there are considerable fluctuations and that through extinction events the short term trend can be a decrease in complexity. The quantitative statistics of the assembly process are investigated in Quince et al. (2002). The mature food web at time 10000 in Fig. 3 shows some ecologically interesting features. A trophic structure has developed populated by a mixture of predators with many prey (generalists) and
those with few prey (specialists). Most species exploit prey on the level below them but there are some omnivores. There are also ‘functional groups’ of species, a functional group being defined as a subset of species which share the same predators and prey (Walker, 1992). In the next section we will present statistics from these long time structures.

4 The structure of the model food webs

In the previous section it was argued that after a large enough number of speciation events the model generated food web structures from an individual simulation will be drawn from an approximately stationary distribution. It is this stationary distribution of structures that we are interested in here. Our aim is to provide a qualitative understanding of the structures and the processes that generate them. This will be done by presenting, for a range of parameter values, both individual instances of food webs and descriptive statistics from ensembles. A similar analysis has been performed previously (Drossel et al., 2001), but the results here include a wider range of parameter values and have a different emphasis.

The stationary distribution of structures observed in any given simulation will depend not only on the model parameters themselves, but also on the particular realisations of the random feature matrix and environment species used. This was addressed by performing a dual averaging procedure to calculate the statistics in this section. They were first time averaged over the final part of each simulation to obtain approximations to the means of the stationary distributions and then ensemble averaged over multiple runs, each with different realisations for the feature matrices and environment species.

To perform a full investigation of the effect of the model parameters would require simultaneously altering all seven of them (see Table 1). The computational effort involved in each individual simulation coupled with the need for multiple runs at each set of parameter values means that this is beyond the scope of this study. Instead we will restrict our attention to the main three parameters ($R$, $c$ and $b$) and ask how the food webs change as we alter each one of these parameters independently of the other two. The other four parameters will be kept constant in this section, and in fact throughout this paper, with the values $\lambda = 0.1$, $N^{\text{min}} = 1.0$, $N^{\text{child}} = 1.0$ and $d = 1.0$. 

12
4.1 Change in food-web structure with $R$

We begin by considering the effect of altering the parameter $R$, the rate of resources input into the food webs. The data set for this study consisted of 20 independent simulations at each of 19 different values of $R$. The actual values used were $R = 10^{3+x}$, with $x = 0.25n$ and $n = 0, \ldots, 10$, and $R = m \times 10^4$, with $m = 2, \ldots, 9$. An additional 60 runs with $R = 100000$ were generated, making a total of 80 for this particular value. The other two major parameters were kept constant with $b = 0.005$ and $c = 0.5$. The runs were independent in the sense that different sets of pseudo-random numbers were used in their generation. They therefore had different feature matrices, $m_{\alpha\beta}$, different environment species, and different speciation events throughout. All runs lasted for 120000 speciation events, except for $R = 316200$, where the model was run for 220000 speciation events until the web ceased to grow on average. The statistics presented here were calculated by time averaging over the last 20000 iterations of each run and then ensemble averaging over all runs.
runs at a particular set of parameter values.

In Fig. 4 we show the mean number of species as a function of \( R \) for these simulations, from which it can be seen that as \( R \) is increased the number of species in the ecological communities also increases. This is due to \( R \) scaling the population sizes and hence allowing more species to exist with populations above the critical value \( (N^{\text{min}}) \). In fact, the characteristic ratio \( R/\lambda N^{\text{min}} \) should control this effect.

The parameter \( R \) does not only impact on the species diversity of the food webs, it has considerable effect on the food web structure. This is illustrated graphically in Fig. 5 using the same conventions as Fig. 3, where four food webs with four different values of \( R \), such that \( R \) increases from left to right and from top to bottom in the figure, are displayed.

In Fig. 6A the number of species occupying each trophic level averaged over multiple simulations at different \( R \) values is shown. At a given value of \( R \) the distributions are hump shaped indicating that the largest occupation numbers occur for intermediate trophic levels. As \( R \) increases the number of species occupying all levels increases, but at varying rates, so that the peak of the distribution shifts to higher levels. The same hump shaped distribution of species between trophic levels and its dependence on \( R \), or equivalent parameter, has been found both in the earlier version of the model (Caldarelli et al., 1998) and in a mean-field approximation to a Lotka-Volterra evolving food web model (Lässig et al., 2001).

To the right of this figure the total population of each level \( (N) \) averaged over the same simulations is shown (Fig. 6B). The total population does not show a peak as for the occupation numbers. Instead it declines approximately geometrically with level at a particular \( R \) value and on each level the total population is roughly proportional to \( R \). The reason for this decline is that setting \( \lambda \) to be smaller than one ensures that predator populations will in general be smaller than their prey populations.

An intriguing feature of the four food webs shown in Fig. 5 is that the species on higher trophic levels appear to be less specialised and exploit more prey, than those on the lower levels. In addition, the species on lower trophic levels have more predators on average than those on the higher levels. These patterns are also affected by \( R \), so that as \( R \) increases the species on a trophic level become more specialised and have more predators on average. That these patterns are general is confirmed by the statistics presented in Fig. 7 where four different quantities have been averaged over all the species on a given trophic level and these quantities were, as usual, then both time
Figure 5: Four example food webs generated by the model. These food webs are the final states, after 120000 speciation events, from four of the simulations used to investigate the effect of altering $R$. The simulations had $R$ values of $10^{3.5}$ (top left), $10^4$ (top right), $10^{4.5}$ (bottom left) and $10^5$ (bottom right). All other parameters were kept constant as described in the text.
Figure 6: The mean number of species (A) and total population (B) on each trophic level for simulations spanning eleven logarithmically scaled values of $R$. The actual simulations used were the subset of the simulations used to investigate the effect of altering $R$ described in the text with $R = 10^{3+x}$, $x = 0.25n$ and $n = 0, 1, \ldots, 10$. The $R$ values of the lines can be determined by noting that species number on each level and total population always increases with $R$. The error bars in both graphs show standard deviations.

averaged and ensemble averaged. The upper right hand graph (Fig. 8B) and the lower right hand graph (Fig. 8D) give the average number of predators ($N^{\text{pred}}$) and the average number of prey ($N^{\text{prey}}$) per species for each trophic level as a function of $R$ respectively. In calculating the number of predators and prey all trophic links constituting greater than 1% of a predators diet were counted and for the purposes of calculating the prey number the environment was treated as just another species. Thus it appears that predator number does indeed decrease with trophic level, and increase with $R$, whilst conversely prey number increases with trophic level and decreases with $R$.

These observations can be used to understand the observed patterns in trophic level occupation by hypothesising that each trophic level exists on a continuum lying between two regimes, its position on the continuum being determined by the total population of the level below. We will refer to the regime at the bottom end of this continuum as ‘prey population limited’.
Figure 7: The effect of $R$ on four quantities as a function of trophic level. A: the number of species on each trophic level. B: the number of predators averaged over all species on the same trophic level. C: the mean score averaged similarly. D: the number of prey again averaged over trophic level. The details of the simulations are contained in the text.

This regime is characterised by generalist species with very little prey overlap between competing species. The species diversity of the trophic level for this regime is limited by the total population of the level below. The other end of the continuum, when the prey population on the level below is very high, we will designate the ‘niche limited’ regime. Here species are specialised to feed off only one prey and many species exploit the same prey. In this regime the species diversity of the trophic level is limited by the total number of prey in the level below and the number of species that can exploit the same prey. A diagram illustrating the two regimes is shown in Fig. 8.

The total population of a level decreases with trophic level (see Fig. 6B). Thus as we go up the levels we pass from the niche limited to the prey population limited regimes. For trophic levels near the niche limited regime, the number of available niches, and hence species diversity, increases with trophic level. This is because the number of species in the level below increases from just one, the environment, as trophic level increases. For trophic levels in the
prey population limited regime the species diversity will decrease for higher trophic levels, since the population of the level below decreases. This then explains the humped shaped distributions of Fig. 6A. This argument owes a great deal to the ideas presented in Lässig et al. (2001) and Bastolla et al. (2002).

The hypothesis also explains the changes in trophic level occupation with $R$ which are more easily understood from Fig. 7A, where $R$ is plotted on the $x-$axis, than Fig. 6A. Initially at low $R$ values all trophic levels are prey population limited and their species diversity increases with $R$. The species diversity of the first trophic level then becomes niche limited, this occurs at very small $R$ values. Increasing $R$ further does not result in more level 1 species, since the maximum number of species that can exploit a single resource has been reached. The species diversity of the other three levels continues to increase with $R$, until at very high $R$ values, level 2 becomes niche limited and its occupation saturates to a constant value. This value is much higher than that for level 1, since there are more prey available to level 2.

The above ideas are consistent with the observed changes in prey number with trophic level and $R$ (Fig. 7A), but they do not explain why species specialisation should increase with the population of their prey. It seems likely that this occurs within the model because a predator lineage that
predates only a few prey can evolve to be a better adapted predator than one that exploits many. This will be true because the $m_{\alpha\beta}$ determining the effectiveness of one feature with respect to another are independently distributed. Thus it is much less likely that changing one of a predator’s features for another, as occurs in a speciation event, will simultaneously improve all the scores of a predator with many prey, rather than improve the score of a predator with a single prey. Specialisation allows improved evolutionary adaptation.

As the total population of the level below increases, then it becomes possible for predators with fewer prey to exist and still maintain their populations above the critical value. If highly specialised predators can exist then they will replace generalists because they are better adapted. This is why the transition from niche limited to population limited regimes occurs. If this argument is valid then species should become better adapted predators as trophic level decreases and $R$ increases. We investigate this by defining the mean score of species $i$ by

$$\bar{S}_i = \sum_{j=0}^{S} f_{ij} S_{ij}. \quad (8)$$

This quantity is shown averaged over all the species on each trophic level for different $R$ values in Fig. 7C. As expected, the average score on a trophic level mirrors the changes in predator specificity (Fig. 7D).

### 4.2 Change in food-web structure with $c$

We will now consider the effect of altering the competition constant $c$, which controls the strength of direct inter-specific competition in the model by parameterising the equation for the degree of interference competition, $\alpha_{ij}$, between two species that share the same resource (see Eq. (3)). Increasing $c$ at a given feature overlap, $q_{ij}$, increases $\alpha_{ij}$, corresponding to greater competition. Given the importance of competition in the above arguments explaining the trophic level structure of the food webs, we might expect that $c$ should have a significant effect on the food web structure. We shall see that this is indeed the case.

The data set for this part of our study was obtained by performing twenty independent runs of the model for $c = 0.1, 0.2, \ldots, 0.4$ and ten runs for $c = 0.5, 0.6, \ldots, 1.0$ with $R = 1 \times 10^4$. In addition ten runs were performed at eight values of $c$: $c = 0.3, 0.4, \ldots, 1.0$, for both $R = 5 \times 10^4$ and $R = 1 \times 10^5$. 

19
Figure 9: The effect of the competition constant on species number (A) and links per species $L/S$ (B) for three different values of $R$. The details of these simulations are contained in the text. The error bars show standard deviations.

The other parameters were kept constant with $b = 0.03$. The simulations were run for 200000 speciation events, by which time the community properties had become time independent. The statistics presented here were obtained by the usual procedure of time averaging over the last 20000 iterations of each run and then ensemble averaging over the ten runs at each set of parameter values.

In Fig. 9 the species diversity $S$ and links per species $L/S$ are shown as a function of $c$ and $R$. The links per species is simply the number of predator-prey interactions in the food web ($L$) divided by the total species number ($S$). In calculating $L$ only links which constituted greater than 1% of a predator’s diet were counted. Both statistics increase rapidly once $c$ is smaller than some critical value. This indicates that there is some threshold competition level above which complex food webs cannot be evolved, but below which complexity in terms of species number and interactions increases rapidly. This critical value is around $c = 0.7$, and does not seem to depend strongly on $R$, although with just three different $R$ values spanning one order of magnitude it is difficult to be certain.

The increased species number and links per species resulting from de-
creased interference competition arises from a number of intertwined processes. Smaller $c$ values allow a greater number of species to exploit the same prey, which increases $L/S$ and also $S$, because each prey species can now support more predators which themselves provide food for other species. In addition, decreasing $c$ should decrease the size of the denominator in $L/S$, resulting in increased feeding rates and allowing more species to exist with equilibrium populations above $N_{\text{min}}$.

The reason for the critical value in $c$ seems to be that above this point the probability of more than one species being able to exploit the same prey is very small. Thus the food webs are restricted to food chains, or at most one or two species on each trophic level. This has been checked by visual inspection of webs evolved at high $c$ values. The length of the food chains is determined by $\lambda$ and $R$, and is for the values used here at most four. Thus the food chains possess few species and few trophic links.

In explaining the trophic level structure of the model food webs and the effect of $R$ on that structure, we proposed that each trophic level can be placed on a continuum between prey population limited and niche limited regimes. We will now further explore these ideas by investigating the effect of $c$ on the trophic level structure of the food webs. In Fig. 10 we present four statistics averaged over all the species on the same trophic level as a function of $c$. It was mentioned above that reducing $c$ increases the number of species that can exploit the same prey. This is partially confirmed by Fig. 10B, which shows average predator number increasing with decreasing $c$ values for the lower two levels, but not the top level. The latter however is exploited by only a few omnivorous predators. From Fig. 10B we see that the average number of prey species per predator increases for trophic levels 2 and 3, but not for trophic level 1, where species are specialised to feed off the environment for all $c$ values. This high specificity suggests that trophic level 1 is niche limited. The average prey numbers for levels 2 and 3 imply that the generalist species on level 3 are prey population limited, whereas those on level 2 lie somewhere between the two extreme regimes.

These observations explain the changes in trophic level occupation with decreased $c$ shown in Fig. 10A. The reduced level of inter-specific competition allows more species to be specialised to feed off the environment so the occupation of level 1 increases. These provide more potential prey for the level 2 species and each level 1 species can support more predators. These two effects will compound each other, explaining the rapid increase in the occupation of trophic level 2. In contrast, the number of level 3 species re-
Figure 10: The effect of the competition constant, $c$, on four quantities as a function of trophic level. A: the number of species on each trophic level. B: the number of predators of each species averaged over species on the same trophic level. C: the mean score averaged similarly. D: the number of prey again averaged over trophic level. These statistics are from the simulations with $R = 1 \times 10^4$ performed to investigate the effect of altering $c$ described in the text.

Mains roughly constant, as the diversity of this level is limited by the total population of, rather than the number of niches in, the level below.

The bottom left graph of Fig. 10 shows the mean score as defined by Eq. (8) for each of the trophic levels as a function of $c$. This quantity has a hump shaped appearance for all three trophic levels. The increase in mean score for small $c$ values is probably because increasing $c$ reduces the disadvantage of high feature overlap values between groups of competing species, see Eq. (5). This allows groups of competitors to evolve towards possessing the same set of optimum features for exploiting their mutual prey. The decrease in mean score as $c$ is further increased beyond the critical value is less explicable. It is probably related to the collapse in community size.
4.3 Change in food-web structure with $b$

The last parameter we will consider is the saturation constant $b$, which controls the strength of predator-prey interactions within the webs. This can be shown by rearranging the general form of the functional response such that it is parameterised by $S_{ij}/b$. Thus $b$ scales the interaction scores. The effect of altering $b$ was determined by running ten independent simulations of the model at each of eleven values of $b$: $b = 0.00, 0.01, \ldots, 0.10$. This was repeated for 7 different values of $R$: $R = 10^4, 10^{4.25}, \ldots, 10^{5.5}$. In addition for $R = 10^{5.75}$ ten simulations were performed at $b = 0.02, 0.03, \ldots, 0.10$ and for $R = 10^6$ the values $b = 0.04, 0.05, \ldots, 0.10$ were used. For $R = 10^{5.75}$ and $R = 10^6$ it was not possible to implement the full range of $b$ values, as for small $b$ and large $R$ the webs become prohibitively large. This gives a total of 930 separate simulations. The other parameters were kept constant with $c = 0.5$. The simulations lasted for 120000 speciation events. The statistics were first time averaged over the last 20000 iterations of each run, and then ensemble averaged over the ten runs at each set of parameter values.

In Fig. 11 the number of species is shown for all parameter values. We can see from this that for any particular rate of resource input, $R$, the community size decreases with increasing $b$, until at some critical value of $b$ the webs collapse to just a few species. The webs remain small as $b$ is increased beyond this point. Increasing $R$ and keeping $b$ constant leads to increased size, as was seen in Fig. 11. However the critical value of $b$ above which large webs cannot be assembled is only weakly dependent on $R$. It increases from around $b = 0.04$ to $b = 0.06$, as $R$ increases by two orders of magnitude.

The reason for the critical value is not clear. Certainly larger $b$ values will reduce the magnitude of the predator functional responses, perhaps making it difficult for a diverse collection of species to exist with equilibrium populations above $N_{\text{min}}$. However it is hard to see why this should cause such sudden declines in species number with $b$, especially as some species do exist above the critical value.

In this section we have shown that the parameters $R$, $b$ and $c$ each have significant effects on the model food web structures. The parameter $R$ scales the food web size and impacts on the trophic level structure of the food webs. For the parameters $b$ and $c$ critical values exist above which large communities cannot be evolved. These critical values will depend on the other model parameters in ways not fully investigated here. However it was shown that they are relatively insensitive to $R$. In addition, we proposed a
Figure 11: The effect of the saturation constant, $b$, on species number $S$, for different values of $R$. The statistics are ensemble averages over ten runs at each set of parameter values. The error bars show the standard deviations for these ensembles. The details of the simulations and averaging procedure are contained in the text.

framework of niche limited and prey population limited regimes that could explain the changes in trophic level occupation with $c$ and $R$. In the next section we discuss the relevance of these results to real food webs.

5 Comparison to empirical food webs

The food webs constructed from simulations of the model have been compared to empirical food webs in earlier publications (Caldarelli et al., 1998; Drossel et al., 2001). The emphasis in these earlier papers was on comparing the percentage of species which were basal (having no prey), intermediate (having both prey and predators) and top (having no predators) and the percentage of predator-prey links which connected species of this type. Agreement was generally good, with the exception of the number of links per species which tended to be lower in model webs than in real ones. However,
there are considerable problems with the direct comparison of model and empirical webs in this way, and it is not even clear that comparisons of this type are really meaningful. One problem is that real webs differ considerably in structure. It is not clear if this is because of the different nature of the community (marine, desert,...), differences in methodology, inadequate sampling, or a whole host of other reasons. The amount of time and effort required to get reliable data is formidable, and so the accuracy of much of the data is unknown. Some of these questions are discussed in a recent review of food webs (Drossel and McKane, 2003; see also references therein). Another problem rests with the interpretation of the modelling process. In the current state of development of the model, it is unclear on what scale the predictions are expected to hold. On the one hand the model communities are quite small suggesting a local or regional scale, but on the other there is no immigration, a situation which may best correspond to a continental scale where diversity, for instance, is controlled by speciation and extinction (Rosenzweig, 1995). However, bearing these caveats in mind, it is nevertheless interesting to make a tentative comparison between the predictions of the model and empirical webs.

The three parameters $R$, $c$ and $b$ each have significant effects on model food web structure but of these three parameters only $R$ can be identified with any property of real ecosystems: it being reasonable to associate $R$ with the rate of input of limiting external resources such as light or nutrients. If this interpretation of $R$ is correct, then we would expect it to correlate with primary productivity, and in fact the relationship is almost exactly linear. Therefore we can compare the trends observed when altering $R$ in the model food webs with the trends observed in empirical food webs that span a range of primary productivities. There are several studies of the effect of productivity on species diversity and these can be compared with Figures 4 and 6A, which show the effect of $R$ on the species diversity of the complete food web and the individual trophic levels respectively.

The species diversity of the individual trophic levels in the model are monotonically increasing saturating functions of $R$ (Fig. 6A). The degree of saturation increases as the trophic level decreases so that level 1 or producer diversity is practically independent of $R$ for all but the smallest values. For animal studies of regional species, diversity within a trophic group generally show unimodal i.e. hump-shaped dependence on productivity, so that diversity peaks at an intermediate productivity level (Mittelbach et al., 2001). Thus the model obtains the correct behaviour for low productivities, which is
probably because the model incorporates the same energetic considerations as are used to construct the most widely accepted explanation for the increasing phase in the real diversity: the “species-energy” hypothesis (Wright, 1983), but fails to predict the decrease in diversity at high productivities. This may indicate that the model lacks some important components but it could equally well be due to equating trophic levels with trophic groups. In addition, some studies have concluded that on a continental scale a monotonic relationship between diversity and productivity may be the dominant pattern (Waide et al., 1999; Chase and Leibold, 2002).

For plants the empirical studies paint a similar picture with hump shaped patterns predominating on regional scales but with some evidence for monotonic relationships on larger scales (Waide et al., 1999; Mittelbach et al., 2001; Chase and Leibold, 2002). Neither possibility corresponds to the effectively constant number of level 1 species observed in Fig. 4A. There are no empirical studies, at least known to the authors, comparable to Fig. 4 where the total diversity is considered. Such a study might give the model behaviour, a monotonic relationship between total diversity and productivity. This remains to be seen.

There are other predictions from the previous section, regarding model food web trophic structure, that are independent of the model parameters. We shall focus on two of these: the hump shaped distribution of species between the trophic levels and the increase in predator specialisation as trophic level decreases. These patterns were explained in the model ecosystems using the ideas of niche limited and prey population limited regimes. If such ideas are applicable to real webs we would expect to find the same patterns in the empirical data. In Table 2, the number of species occupying each trophic level, calculated as the minimum path length from the species to the environment, and the number of prey averaged over all species on the same trophic level, counting the environment as a prey species, are shown together with links per species and total number of species of the whole food web for fourteen of the largest and most highly resolved food webs in the current literature. The statistics were calculated using taxonomic rather than trophic species since although using the former may reduce methodological bias (Briand and Cohen, 1984), the latter are the functional units in the food webs. These webs span a range of sizes and habitats, the details of which are contained in the individual references or summarised in Dunne et al. (2002b).

Of these fourteen ecosystems, ten have a distribution of species between levels that peaks at an intermediate trophic level number, indicated by an
| Ecosystem Name       | Number of species | Links per species | Trophic Level | Reference |
|----------------------|-------------------|-------------------|---------------|-----------|
|                      |                   |                   | Mean number of prey |          |
|                      |                   |                   | 1   2   3   4 |           |
| Bridge Brook Lake†   | 75                | 7.37              | 39  34  2 —   | Havens, 1992 |
|                      |                   |                   | 1.0 15.2 18.0 — |           |
| Scotch Broom*        | 154               | 2.40              | 1   24  117 12 | Memmott et al., 2000 |
|                      |                   |                   | 1.0 2.5 2.5 1.8 |           |
| Canton Creek†        | 108               | 6.56              | 56  52 — —   | Townsend et al., 1998 |
|                      |                   |                   | 1.0 13.6 — — |           |
| Chesapeake Bay*†     | 33                | 2.18              | 5   15  13 — | Baird & Ulanowicz, 1989 |
|                      |                   |                   | 1.0 2.5 2.6 — |           |
| Coachella Valley*†   | 30                | 9.67              | 3   22  5 —  | Polis, 1991 |
|                      |                   |                   | 1.0 10.7 10.8 — |           |
| El Verde Rainforest* | 156               | 9.68              | 28  98 28 2  | Waide & Reagan, 1996 |
|                      |                   |                   | 1.0 13.5 6.6 1.0 |           |
| Grassland †          | 75                | 1.51              | 8   15  52 — | Martinez et al., 1999 |
|                      |                   |                   | 1.0 1.1 1.9 — |           |
| Little Rock Lake*†   | 181               | 13.12             | 63  80 38 —  | Martinez, 1991 |
|                      |                   |                   | 1.0 17.9 24.8 — |           |
| Skipwith Pond*†      | 35                | 10.86             | 1   18 16 —  | Warren, 1989 |
|                      |                   |                   | 1.0 1.8 21.7 — |           |
| St. Marks Seagrass*† | 48                | 4.60              | 6   31 11 —  | Christian & Luczkovich, 1999 |
|                      |                   |                   | 1.0 5.0 5.9 — |           |
| St. Martin Island*   | 44                | 4.95              | 6   29 6 3  | Goldwasser & Roughgarden, 1993 |
|                      |                   |                   | 1.0 5.0 11.7 1.3 |           |
| Stony Stream         | 112               | 7.43              | 63  46 3 —  | Townsend et al., 1998 |
|                      |                   |                   | 1.0 17.9 2.7 — |           |
| Ythan Estuary 2*     | 92                | 4.58              | 5   44 42 1 | Hall & Raffaelli, 1991 |
|                      |                   |                   | 1.0 3.1 6.7 4.0 |           |
| Ythan Estuary 1*     | 134               | 4.46              | 5   44 81 4  | Huxham et al., 1996 |
|                      |                   |                   | 1.0 3.1 5.6 2.0 |           |

Table 2: The number of species, links per species, distribution of species between trophic levels and mean prey number as a function of trophic level for fourteen food webs. The details of this data set are summarised in Dunne et al. (2002b). The ecosystems with hump shaped level distributions are marked by an asterisk (*) and those with decreased predator specialisation with trophic level by a dagger (†).
asterisk (*) in Table 2. This is more than might be expected by chance, assuming that any level is equally likely to be the modal one. However from this we cannot conclude that the trophic level structure of real food webs is controlled by an interplay between number of available niches on the lower levels and resource availability on the higher levels, as was proposed for the model food webs. This is because many other hypotheses are likely to be consistent with this data, for instance, it is easy to show that similar hump-shaped trophic level distributions are obtained if ecosystems are generated with links apportioned randomly. However this result is reassuring, and this feeling is reinforced by the number of trophic levels possessed by the food webs in Table 2, there being only one two level ecosystem, all others having either three or four levels. This is also consistent with model ecosystems where, except in the case of very low $R$ values, there are always at least three levels and for larger $R$ generally four. This can be seen from Fig. 6A.

The status of the second proposed pattern, the increase in predator specialisation with decreased trophic level, is not so clear. It holds for eight of the fourteen webs, those marked with a dagger (†) in Table 2, but for two of these eight webs, Chesapeake Bay and Coachella Valley, the difference between the mean prey number on the second and third levels is very small. Given that the mean prey number for the first trophic level is always going to be 1.0, guaranteeing that a two a level food web will display the pattern, we conclude that the current state of the data is such that a meaningful comparison is not warranted.

Finally, the number of links per species $L/S$, given in the third column of Table 2. For the model webs this quantity depends on the parameters used. For the parameters $R = 1 \times 10^5$, $c = 0.5$, $b = 0.005$, the long time average number of links per species is 1.69. This value increases as $c$ decreases, as can be seen from Fig. 9B, but it rarely approaches the sorts of values observed in Table 2. This confirms the earlier findings that the model food webs are link poor compared to real food webs.

The problems we have encountered in this section when making comparisons between model and empirical webs have been typical. A major difficulty is that a property of model webs may be seen in a number of empirical webs, perhaps even a large majority of them, but it is not clear if those in which the property is absent are different in some way, or if it is simply that the data is not good enough. For this reason, it may prove more productive to seek out properties of real food webs which are more universal, and so allow more meaningful comparisons with model webs. We now move on to the
investigation of a property which may be of this type: the distribution of link strengths in food webs.

6 Interaction strengths in model food webs

The majority of the food web statistics examined in the previous sections take no account of the strength of the predator-prey interactions in the model generated communities. They describe properties of binary food webs for which a link is either present or absent. This approach was adopted for reasons of simplicity and to facilitate comparison with the empirical data, where for most well resolved food webs the strengths of the interactions are not known. For those natural communities for which interaction strengths have been quantified, significant variation in link importance has been observed and a putative general pattern of “a few strong interactions embedded in a majority of negligible effects” proposed (Paine, 1992; Fagan and Hurd, 1994; Raffaelli and Hall, 1996; Wootton, 1997), although this emerging consensus has not remained unchallenged (Sala and Graham, 2002). It was soon realised that the variation of interaction strengths within ecosystems could have important implications for their functioning. In particular, it has been shown that using interactions drawn from realistic distributions increases the probability that a random model food web will be stable (Yodzis, 1981). This idea that the observed pattern of interaction strengths could be important for community stability was refined by suggestions that the pattern of variation in interaction strengths between trophic levels (de Ruiter et al., 1995), the preponderance of weak interactions (McCann et al., 1998) and the presence of weak omnivorous interactions in long loops (Neutel et al., 2002) could all be important factors in determining ecosystem stability. In light of these ideas and observations we will now investigate the distribution of link strengths generated by the model.

We will begin by considering the distribution of the efforts, $f_{ij}$, in the model food webs. These quantities, defined by (1), give the fraction of an individual predator’s diet obtained from a particular prey. Thus they do not represent interaction strengths but rather diet contributions. Just because a predator consumes only one particular prey does not necessarily imply that the effect of the predator on that prey will be high. In fact it has been shown in real food webs that the percentage of a particular prey in a predator’s diet does not correlate strongly with interaction strength (Wootton, 1997).
Figure 12: The distribution of efforts or predator diet fractions $f_{ij}$ averaged over 400 model communities evolved for 120000 iterations with the parameters $R = 1 \times 10^5$, $b = 0.005$ and $c = 0.5$. The inset shows the same data but with both axes logarithmically scaled and logarithmically spaced bins. The power law fit shown for the inset has an exponent of $-0.74 \pm 0.01$.

However since our criterion for including a link in the previous section was that $f_{ij}$ should be greater than 0.01, and because $f_{ij}$ is a quantity with an unambiguous meaning relevant to real food webs, then investigating the distribution of $f_{ij}$ is a worthwhile exercise.

In Fig. 12 the probability distribution of the efforts is shown averaged over the final communities from four hundred independent runs, with the same parameters, of the model. The probability distribution is calculated for all predator-prey links with $f_{ij} > 10^{-6}$. This minimum cut off was applied because this is the smallest value that $f_{ij}$ is allowed to take if $S_{ij} > 0$ (Drossel et al., 2001). Thus we have only included efforts whose values were determined by iterating (1) and (6), rather than by the limitations of our algorithm.

From the main graph of Fig. 12 it is clear that $P(f_{ij})$ is heavily biased towards the limits of its possible range, $f_{ij} = 1$ and $f_{ij} = 0$. The probability that a randomly chosen link has an effort in between these two limits is low.
This effect is actually more dramatic than it appears, since the vertical axis of this graph has been scaled logarithmically. There is also a slightly greater weighting towards small $f_{ij}$ values: 60% of links have $f_{ij} \leq 0.5$. The inset graph of Fig. 12 shows $P(f_{ij})$ plotted with both axes scaled logarithmically and using bin intervals that are also logarithmically spaced. This reveals that the probability distribution of $f_{ij}$, for small $f_{ij}$, is well described by a power law with an exponent of $-0.74$.

It seems that predation patterns in the model are highly uneven with most species possessing one main prey, but including very small amounts of other species in their diets. The fraction of species that predate several species evenly, resulting in intermediate $f_{ij}$ values, must be low. A similar shaped distribution of efforts to this, albeit with a greater proportion of small values, has been observed in a food web model with adapting but not evolving foragers (Kondoh, 2003). This pattern can also be compared to a detailed study of a detritus based stream food web, where the dietary importance of links to a consumer were quantified with a measure similar to $f_{ij}$ (Tavares-Cromar and Williams, 1996). Links were characterised as weak, moderate, strong and very strong depending on the fraction of the predators diet represented by the link. The percentage of links in these categories were 42-52%, 17-25%, 5-13% and 21-25% respectively, indicating a significant bias towards weak links and some bias towards very strong links as well. However it is difficult to reconstruct the shape of the true distribution from just four categories whose boundaries are inevitably arbitrary.

In Fig. 12 we have shown $P(f_{ij})$ at only one set of parameter values. However this pattern is remarkably insensitive to the choice of parameters. The probability distribution of $f_{ij}$ was calculated for a large range of $b$, $c$ and $R$ values using the webs generated in the previous section, and the same bias to $f_{ij} = 0$ and $f_{ij} = 1$ was found in all instances where the communities were reasonably large. In particular, the power law distribution for small $f_{ij}$ was found with the same exponent, $0.725 \pm 0.025$, for all values of the rate of resource input, $R$, and the saturation constant, $b$, that produced food webs with more than a few species. The distribution was found to depend slightly on $c$. As the competition constant is reduced there is an increased probability of finding predator-prey links with intermediate $f_{ij}$ values. This is what we would expect from the findings of the previous section: decreased $c$ results in reduced competition, allowing predators to exploit a greater range of prey species.

As mentioned above, the effort $f_{ij}$ associated with a predator-prey in-
teraction may not be a good measure of its strength. The interaction score $S_{ij}$ is a better candidate since it parameterises the predator functional response (6). However this quantity has the drawback of being relevant only to our particular choice of functional response. In addition, since interference competition is incorporated into (6), competition is a direct interaction in the model the strengths of which it would be useful to quantify with the same measure as used for the predator-prey interactions. For these reasons we shall use as our definition of interaction strength, the Jacobian or “community matrix” $J$ (May, 1973). This is an $S \times S$ matrix with elements $j_{ij}$ defined by:

$$j_{ij} = \left( \frac{\partial H_i(N_1(t), N_2(t), \ldots, N_S(t))}{\partial N_j(t)} \right)^*,$$

where $H_i \equiv dN_i/dt$ is the net growth rate of species $i$ (2). This is a function of the population densities of all species that directly interact with $i$. The asterisk indicates that the partial derivatives are to be calculated at an equilibrium point. The latter is defined as a set of population densities that give zero growth rates, i.e. $H_i(N_1^*, N_2^*, \ldots, N_S^*) = 0$ for all $i$. This restriction to an equilibrium point means that the elements of $J$ are the coefficients of the linearization of the population dynamics about this point, and the perturbations from equilibrium, $x_i(t) = N_i(t) - N_i^*$, obey

$$\frac{dx_i(t)}{dt} = \sum_{j=0}^{S} j_{ij} x_j(t),$$

to first order. Therefore the community matrix determines the local stability of the equilibrium point. If all its eigenvalues have negative real parts, the system will return asymptotically to the equilibrium after any infinitesimal small perturbation of the population densities.

The method for calculating the Jacobian matrix of a model food web involves two steps. Firstly, location of an equilibrium point: this was simple as almost always the population dynamics integrated to a stable equilibrium suitable for the calculation of the Jacobian. On the rare occasions when such an equilibrium was not found, reducing the size of the integration time step resolved the problem. Secondly, calculation of the partial derivatives: this was more complicated as it is not possible to derive analytic expressions for the partial derivatives by differentiating (6). This is because the $f_{ij}$, which we do not have an explicit expression for, will also depend on the population densities. This problem was circumvented by numerically calculating the
Figure 13: The distribution of the elements of the Jacobian matrix $j_{ij}$ for the effect of a prey species on its predator (A), the effect of a predator on its prey (B) and the effect of competitors on each other (C). The latter is subdivided into inter-specific, omnivorous and intra-specific interactions. These results were obtained by averaging over 400 communities evolved for 120000 iterations with the parameters $R = 1 \times 10^5$, $b = 0.005$ and $c = 0.5$.

partial derivatives using Ridders’ method (Ridders, 1982; Press et al., 1988). This involves calculating the change in species growth rates resulting from increasingly small perturbations of one of the population densities, the other densities remaining unchanged, and then extrapolating from these values to estimate the result of a infinitesimal perturbation corresponding to the partial derivative. During the calculation of the adjusted growth rates the efforts were allowed to change from their values at the population equilibrium such as to always satisfy (1), thus generating Jacobian elements for species that are adaptively changing their foraging efforts.

The Jacobian matrices were calculated numerically for the four hundred food webs used to generate Fig. 12. The distribution of all non-zero $j_{ij}$
values was found to be strongly skewed towards weak interactions, which is perhaps unsurprising given the distribution of $f_{ij}$ values discussed above. In order to better understand the structure of the Jacobian matrices we then examined the distribution of $j_{ij}$ values associated with specific direct interactions. Firstly, we examined the effect of a prey species on a predator for all predator-prey interactions where the prey formed greater than 1% of the predator’s diet and the predator and prey were not also competitors. This is shown in Fig. 13A. It shows a broad distribution of values between 0 and 0.1, with a peak lying just below the upper limit of this range. That the lower limit of this distribution is zero derives from the fact that the direct effect of a prey on a predator is always positive. The upper limit can be understood as follows. We would expect that the impact of a prey on a predator will be greatest when the prey is the only species in the predator’s diet. In this case indexing the predator as $i$ and the prey as $j$, we have using (4)

$$j_{ij} = \lambda N^*_i \left( \frac{\partial g_{ij}(t)}{\partial N_j(t)} \right)^* = \lambda N^*_i \frac{S^2_{ij}N^*_i}{(bN^*_j + S_{ij}N^*_i)^2}. \quad (11)$$

For a given predator population density this will be maximised in the limit of low effective equilibrium prey population density in the ratio-dependent functional response, $bN^*_j \ll S_{ij}N^*_i$, which gives $j_{ij} = \lambda$ and $\lambda = 0.1$ for this simulation. The peak indicates that a significant number of predator-prey interactions are close to this prey limited regime. In Fig. 13B the corresponding distribution of Jacobian matrix elements for the effect of predators on prey is shown. This distribution is peaked around zero, but with a significant probability of values with a magnitude large compared to those for the effect of prey on predators. These values have both positive and negative sign. This last fact is quite striking and indicates that in many instances the direct effect of a predator on its prey is positive. It arises from the interference terms in (4). This means that mutualistic interactions, at least at equilibrium, occur within the model with $j_{ij} > 0$ and $j_{ji} > 0$. For the four hundred food webs considered here roughly one third of all predator-prey interactions are mutualistic.

The bottom graph in Fig. 12 (labelled C) gives the distribution of Jacobian matrix elements for interactions between competitors. These have been subdivided into three types denoted inter-specific, omnivorous and intra-specific. The first category refers to all competitive interactions between different species that are not also predator-prey pairs. A competitive inter-
action is considered to occur if the two predators both obtain more than 1% of their diet from the same prey species. These interactions are almost always negative. It is not apparent from the graph, but very occasionally a species has a positive effect on its competitor, probably as a result of adaptive foraging; they have a broad distribution that has local maxima at both zero and an intermediate interaction strength value. The second category, omnivorous, refers to all competitive interactions between different species that are also predator-prey pairs. This is a slight misnomer, as actually this definition encompasses only a subset of the omnivorous interactions in the webs. They were considered separately in order not to confuse the results for strictly competitive interactions. The last category, intra-specific, refers to interactions within a species, corresponding to the diagonal elements of the Jacobian matrix. These values are also always negative but on average have a larger magnitude than the inter-specific competitive interactions. These negative diagonal elements play an important role in generating locally stable equilibrium points (May, 1973).

In Fig. 14A we show the Jacobian matrix elements for the effects of a prey on a predator, as in Fig. 13A, but now with the interactions subdivided by the trophic level of the predator species. Similarly Fig. 14B shows the distribution of Jacobian matrix elements for the effects of predators on prey subdivided by the prey trophic level, and Fig. 14C the elements between competitors on the same level. The results are quite striking. As predator trophic level increases, the distribution of \( j_{ij} \) values shift towards the upper limit of \( \lambda = 0.1 \), and the effect of prey species on their predators increases. Conversely as prey trophic level increases the distribution of the effect of predator on prey becomes more strongly peaked at zero, corresponding to a decrease in the average magnitude of the interaction strength. The situation is less clear-cut for competitive interactions, which become somewhat stronger from levels 1 to 2, and then show an increase in weak interactions for level 3. These changes in interaction strength must derive from the decrease in population size with trophic level shown in Fig. 6B, but understanding exactly how is difficult. Semi-quantitatively, for the effects of prey on predators, we see that the right-hand side of (11) will be become larger until it saturates at a value \( \lambda \), as the prey population becomes small.

These results indicate that species populations are controlled by predators and competitive interactions on the lower trophic levels, but are limited by prey population size on the upper levels. This fits with the theory of niche limited and prey population limited regimes advanced in Section 4. The same
Figure 14: The distribution of the elements of the Jacobian matrix $j_{ij}$ for the effect of a prey species on its predator (A), the effect of a predator on its prey (B), the effect of one competitor on another (C). The results are subdivided by the trophic level of the predator and prey respectively. These results were obtained by averaging over 400 communities evolved for 120000 iterations with the parameters $R = 1 \times 10^5$, $b = 0.005$ and $c = 0.5$.

Patterns of increasing effects of prey on predators and decreasing impacts of predators on prey with trophic level has been found in real food webs (de Ruiter et al., 1995). They propose that this pattern stabilises food webs structures by ensuring that long loops must contain weak links hence reducing their negative impact on local stability (Neutel et al., 2002). It is possible that the same effect operates here to stabilise the model communities.

To conclude this section we will discuss whether the distribution of interaction strengths observed in the model food webs fit the proposed empirical pattern of many weak and few strong interactions referred to above. The elements of the Jacobian matrix, $j_{ij}$, measure the direct effect of an individual of species $j$ on the total population of species $i$ (Laska and Wootton,
In empirical studies, per-capita interaction strengths are more often quoted. These are readily obtained in our case by defining the per-capita interaction strength matrix $A$ with elements $a_{ij} = j_{ij}/N^*_i$. The distribution of elements in this matrix averaged over the four hundred communities considered throughout this section is shown in Fig. 15. Only those elements associated with a predator-prey interaction where the prey forms greater than 1% of the predator’s diet, or a competitive interaction where the shared prey comprises greater than 1% of both competitors diet, were used to calculate this distribution. This was done to avoid any implicit bias towards weak interactions. This distribution is clearly heavily skewed towards zero and thus fits the most commonly observed empirical pattern.

7 Discussion

In this paper we have reported the results of performing a very large number of simulations on a model of a coevolving multispecies community in order to generate food webs. The results obtained were considerably more extensive.
than those reported in earlier publications. They were also complementary: in Drossel et al. (2001) the emphasis was on comparing model webs with empirical webs by looking at the number of top, intermediate and basal species and the links between them. The aim was to find values of $R$, $c$ and $b$ which gave agreement with particular empirical webs. It was found that, while values of these parameters could indeed be found which gave good agreement between the model and particular empirical webs, the data was not sufficiently consistent to warrant such detailed fitting. The aim in this study has had a different focus: to see how the model webs change their nature as the parameters $R$, $c$ and $b$ are varied. We will not repeat the conclusions of Section 4, except to draw attention to critical values of $c$ and $b$ above which the growth of complex webs does not seem possible. Another change in focus was the classification of species in terms of the level they occupied, rather than whether they were basal, intermediate or top species. Several trends were identified, but once again comparisons with data was problematical. We also listed other quantities (see Table 1) as parameters of the model, but which we did not vary. Of course, exactly what constitute “parameters of the model” is not well-defined, but in any case it would be interesting to carry out an investigation, not as detailed as the one reported here, in which $N^{\text{min}}$ and $N^{\text{child}}$ are changed from their present value of 1. We hope to carry out such a study in the near future.

In order to facilitate the comparison of model and empirical webs it would be useful to identify a property, trend or attribute which was shared by all empirical webs. One possibility is the existence of many weak links, with perhaps the distribution of weak link strengths resembling a power law. In Section 6 we showed that such a distribution was present in our model. This is a highly nontrivial result, since these distributions are an emergent property of the system, and not put in by hand as in some other work. It is a strong indication that weak links are the natural outcome of long-term community evolution coupled to population dynamics. The main difficulty here lies with the definition of link strengths, of which there are a large number, both theoretically and empirically (Berlow et al., 2004). Fortunately, there are indications that the “many weak links” result holds independently of the precise definition of link strength.

The collection of empirical food web data is an extremely difficult, time consuming and labour intensive task. The data is improving, but it still remains difficult to know whether differences in structure between food webs are due to real effects, differences in methodology or inadequate sampling.
We have mentioned one way forward — the identification of novel effects which seem to be present in all webs. Another approach is to develop the model further by including additional structure which may give rise to different kinds of webs which mirror those found empirically. A prime candidate is the degree of isolation of a community. We have already commented on possible differences between the structures of communities on a continental scale and more local ones in Section 5. We plan to explore this aspect in more detail in the future.

In summary, the method of constructing food webs dynamically from the model studied in this paper seems to give food webs which are similar to empirical webs. This is particularly true for link strength distributions, but less so for the number of links per species. The difficulty in extracting universal attributes from food web data suggests that a way forward may be the further development of the model so as to produce a greater diversity of food webs.

**Acknowledgements:** We wish to thank Jennifer Dunne, Mark Huxham and Phillip Warren for supplying food web data. CQ wishes to thank the EPSRC (UK) for financial support during the early part of this work.
References

Albert, R., Barabási, A.-L., 2002. Statistical mechanics of complex networks. Rev. Mod. Phys. 74, 47-97.
Arditi, R., Michalski, J., 1996. Nonlinear food web models and their responses to increased basal productivity. In: Polis, G. A., Winemiller, K. O. (Eds.), Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, pp. 122-133.
Baird, D., Ulanowicz, R. E., 1989. The seasonal dynamics of the Chesapeake bay ecosystem. Ecol. Monogr. 59, 329-364.
Bastolla, U., Lässig, M., Manrubia, S. C., Valleriani, A., 2002. Dynamics and topology of species networks. In: Lässig, M., Valleriani, A. (Eds.), Biological Evolution and Statistical Physics. Springer-Verlag, Berlin, pp. 299-311.
Berlow, E. L., Neutel, A.-M., Cohen, J. E., de Ruiter, P. C., Ebeman, B., Emmerson, M., Fox, J. W., Jansen, V. A. A., Jones, J. I., Jonsson, T., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., Petchey, O., Raffaelli, D. G., 2004. Interaction strengths in food webs: issues and opportunities. J. Anim. Ecol. in press.
Briand, F., Cohen, J. E., 1984. Community food webs have scale-invariant structure. Nature 307, 264-267.
Caldarelli, G., Higgs, P. G., McKane, A. J., 1998. Modelling coevolution in multispaces communities. J. Theor. Biol. 193, 345-358.
Chase, J. M., Leibold, M. A., 2002. Spatial scale dictates the productivity-biodiversity relationship. Nature 416, 427-430.
Christian, R. R., Luczkovich, J. J., 1999. Organizing and understanding a winter’s seagrass foodweb network through effective trophic levels. Ecol. Model. 117, 99-124.
Cohen, J. E., Briand, F., Newman, C. M., 1990. Community food webs, Biomathematics Vol. 20. Springer-Verlag, Berlin.
de Ruiter, P. C., Neutel, A-M., Moore, J. C., 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269, 1257-1260.
Drossel, B., Higgs, P. G., McKane, A. J., 2001. The influence of predator-prey population dynamics on the long-term evolution of food web structure. J. Theor. Biol. 208, 91-107.
Drossel, B., McKane, A. J., 2003. Modelling Food Webs. In: Bornholdt, S., Schuster, H. G. (Eds.), Handbook of graphs and networks. Wiley-VCH, Berlin, pp. 218-247.

40
Dunne, J. A., Williams, R. J., Martinez, N. D., 2002a. Food-web structure and network theory: The role of connectance and size. Proc. Natl. Acad. Sci. USA 99, 12917-12922.

Dunne, J. A., Williams, R. J., Martinez, N. D., 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol. Lett. 5, 558-567.

Fagan, W. F., Hurd, L. E., 1994. Hatch density variation of a generalist arthropod predator: population consequences and community impact. Ecology 75, 2022-2032.

Goldwasser, L., Roughgarden, J., 1993. Construction and analysis of a large Caribbean food web. Ecology 74, 1216-1233.

Hall, S. J., Raffaelli, D., 1991. Food-web patterns: lessons from a species-rich web. J. Anim. Ecol. 60, 823-842.

Havens, K., 1992. Scale and structure in natural food webs. Science 257, 1107-1109.

Huxham, M., Beaney, S., Raffaelli, D., 1996. Do parasites reduce the chances of triangulation in a real food web? Oikos 76, 284-300.

Kondoh, M., 2003. Foraging adaptation and the relationship between food web complexity and stability. Science 299, 1388-1391.

Laska, M. S., Wootton, J. T., 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology 79, 461-476.

Lässig, M., Bastolla, U., Manrubia, S. C., Valeriani, A., 2001. Shape of ecological networks. Phys. Rev. Lett. 86, 4418-4421.

Martinez, N. D., 1991. Artifacts or attributes: effects of resolution on the Little Rock Lake food web. Ecol. Monogr. 61, 367-392.

Martinez, N. D., Hawkins, B. A., Dawah, H. A., Feifarek, B. P., 1999. Effects of sampling effort on characterization of food-web structure. Ecology 80, 1044-1055.

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

Maynard Smith, J., 1974. Models in ecology. Cambridge University Press, Cambridge.

McCann, K., Hastings, A., Huxel, G. R., 1998. Weak trophic interactions and the balance of nature. Nature 395, 794-798.

Memmott, J., Martinez, N. D., Cohen, J. E., 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. J. Anim. Ecol. 69, 1-15.
Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Willig, M. R., Dodson, S. I., Gough, L., 2001. What is the observed relationship between species richness and productivity? Ecology 82, 2381-2396.

Neutel, A-M., Heesterbeek, J. A. P., de Ruiter, P. C., 2002. Stability in real food webs: Weak links in long loops. Science 296, 1120-1123.

Paine, R. T., 1992. Food web analysis through field measurement of per-capita interaction strength. Nature 355, 73-75.

Polis, G. A., 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. Am. Nat. 138, 123-155.

Press, W. H., Teukolsky, S. A., Vetterling, W. T., Flannery, B. P., 1988. Numerical recipes in C: the art of scientific computing. Cambridge University Press, Cambridge, pp. 186-189.

Quince, C., Higgs, P. G., McKane, A. J., 2002. Food web structure and the evolution of ecological communities. In: Lässig, M., Valeriani, A. (Eds.), Biological Evolution and Statistical Physics. Springer-Verlag, Berlin, pp. 281-298.

Raffaelli, D. G., Hall, S. J., 1996. Assessing the relative importance of trophic links in food webs. In: Polis, G. A., Winemiller, K. O. (Eds.), Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, pp. 185-191.

Ridders, C. J. F., 1982. Technical note: accurate computation of $F'(x)$ and $F'(x)F''(x)$. Adv. Eng. Softw. 4, 75-76.

Rosenzweig, M. L., 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Roughgarden, J., 1979. Theory of population genetics and evolutionary ecology: an introduction. MacMillan, New York.

Sala, E., Graham, M. H., 2002. Community-wide distribution of predator-prey interaction strength in kelp forests. Proc. Natl. Acad. Sci. USA 99, 3678-3683.

Tavares-Cromar, A. F., Williams, D. D., 1996. The importance of temporal resolution in food web analysis: evidence from a detritus-based stream. Ecol. Monogr. 66, 91-113.

Townsend, C. R., Thompson, R. M., McIntosh, A. R., Kilroy, C., Edwards, E., Scarsbrook, M. R., 1998. Disturbance, resource supply, and food-web architecture in streams. Ecol. Lett 1, 200-209.

Waide, R. B., Reagan, D. P., 1996. The food web of a tropical rain forest. University of Chicago Press, Chicago.
Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P., Parmenter, R., 1999. The relationship between productivity and species richness. Annu. Rev. Ecol. Syst. 30, 257-300.

Walker, B. H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6, 18-23.

Warren, P. H., 1989. Spatial and temporal variation in the structure of a fresh-water food web. Oikos 55, 299-311.

Williams, R. J., Martinez, N. D., 2000. Simple rules yield complex food webs. Nature 404, 180-183.

Williams, R. J., Martinez, N. D., 2004. Trophic levels in complex food webs: Theory and data. Am. Nat. in press.

Wootton, J. T., 1997. Estimates and tests of per capita interaction strength: Diet, abundance, and impact of intertidally foraging birds. Ecol. Monogr. 67, 45-64.

Wright, D. H., 1983. Species-energy theory: an extension of species-area theory. Oikos, 41, 496-506.

Yodzis, P., 1981. The stability of real ecosystems. Nature 289, 674-676.