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Evolving complex food webs

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Abstract. We describe the properties of a model which links the ecology of food web structure with the evolutionary dynamics of speciation and extinction events; the model describes the dynamics of ecological communities on an evolutionary timescale. Species are defined as sets of characteristic features, and these features are used to determine interaction scores between species. A realistic population dynamics, which incorporates these scores, is used to determine the changes in population sizes on ecological time scales and so determine mean population sizes. We display typical examples of food webs constructed using the model and comment on the good agreement which is found between the model predictions and data on real webs.

PACS. 87.23.Kg Dynamics of evolution – 87.23.Cc Population dynamics and ecological pattern formation – 89.75.Fb Structures and organization in complex systems

1 Introduction

Food webs are the networks of feeding relationships which occur between species in an ecological community. Early ecological studies were descriptive and comprised largely of the natural history of a given habitat. However, at the end of the nineteenth century, matrices of feeding relationships in a given community were being constructed, with rows representing predators and columns representing prey. These soon gave way to diagrammatic representations of food webs, an example of which is shown in Figure 1.

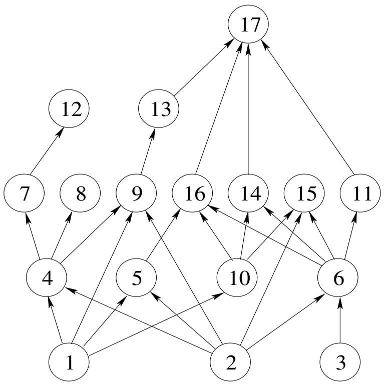

Fig. 1. Narragansett Bay food web (After Kremer and Nixon, 1978. *A coastal marine ecosystem*, Springer-Verlag, Berlin.)

These graphs consist of vertices which represent species in the food web, with a directed link — that is, a line with an arrow attached — from vertex A to vertex B, if species A is eaten by species B. Notice that the direction of the arrows signifies the flow of resources. This is a minimal description; it says nothing about the strengths of the different links — whether, for example, a particular species which preys on two species derives 99% of its resources from one, and only 1% from the other. Such information has been started to be collected in recent years, but it takes a formidable amount of field work to come up with such detail.

Much of the theoretical work on predator-prey relationships has concentrated on the population dynamics of a few species (typically two) or on the elucidation of various effects that might be expected to occur in food webs, without incorporating them into a model of a multispecies dynamics, as can be seen from a perusal of the standard textbooks on mathematical ecology [1,2]. The relative rarity of theoretical studies of entire food webs is understandable: these are extremely complex entities, which require extensive computer modelling if any degree of realism is to be achieved. In fact, comprehensive computer models of specific food webs, with perhaps hundreds of model parameters, are not usually a goal of ecologists. The aim is more a model which describes the generic structure of ecological systems, focusing on universal attributes, rather than on specific details of any given food web. The modelling procedure used is more akin to that seen in the physical sciences, and theoretical physicists have the potential to significantly advance this area of ecology [3].

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The earliest work on the dynamics of multispecies communities dates from the 1970's and circumvents the need for computer modelling by making the simplest assumption about the interactions between species: that they are essentially random [4]. Although this is obviously unrealistic for evolved communities, it did provide a number of stimulating results and showed the need for quantitative analysis of predator-prey systems. The empirical aspects of the subject were also developing, and during the 1980's, many of the published foods webs were collected together and various regularities were noticed for the first time. During roughly the same period ecologists introduced simple static models in which species were simply represented as vertices in a graph and directed links between them were drawn according to some rule. We refer the reader to a review of empirical and theoretical studies of food webs [5] for a more detailed discussion of the modelling of food webs over the last twenty or thirty years.

Food webs provide a number of challenges for the modeller. Foremost among these is that fact that, while the focus is very often on the population dynamics of the species in a given web, it is the dynamics responsible for the actual construction of the web that is in a sense more fundamental. However these two types of dynamics are intrinsically interlinked, despite the fact that the time scale appropriate for the description of the population dynamics is typically very much less than that appropriate for food web construction. It follows that both types of dynamics have to be studied in unison in order to understand the formation of the web. This is the basis of our approach. In the past phenomena on these two times scales were considered separately: questions regarding the nature of predator-prey interactions and population dynamics were considered on the shorter ecological time-scale, comparable to the lifetime of individual organisms, whereas questions regarding the modification of the food web structure through the introduction of new species by speciation processes were considered on an evolutionary time scale orders of magnitude longer than the lifetime of an organism. In the model we discuss here, the dynamics of web construction will be affected by the population dynamics, and vice versa.

In this model we introduce new species purely through speciation events. We will start from a single species, together with the environment, and every evolutionary time step add a new species to the model. The new species may survive, cause extinctions or go extinct itself. Whether the population of a particular species grow or decline after a new addition to the web, is decided by using the equations describing the population dynamics. The model is a macroevolutionary model: no reference will be made to genetics. Of course, speciation ultimately has a genetic origin, but we are imagining that we observe our ecosystem on a very coarse time scale, so that species may appear within a single time step in our model. We may call this a speciation "event", but it is in fact modelling the very complex and (in real time) perhaps lengthy process of speciation. We will also need to specify how species interact with each other; our main assumption will be that the dominant factors will be competition between species for shared resources, and predator-prey interactions.

The plan of the article is as follows. In Section 2 we introduce some basic definitions concerning food webs and list the main quantities used to characterise different webs. The modelling approach which we adopt is described in Section 3 and Section 4 contains a summary of some the main predictions it makes. We end in Section 5 with a discussion of the relationship of the model to others in this area, and comment briefly on possible future work. The presentation here is designed to emphasise the essential points and to give a overview of the general idea behind our approach. For those who read this article and wish to find out more, we refer them to the original papers on the subject [6–8] and to the review on the modelling of food webs already mentioned [5].

2 Food webs

In this section we will define the most important terms that are used in the quantitative description of food webs. Generally data is given not in terms of species in the biological sense, but in terms of *trophic species*; two species are said to belong to the same trophic species if they share the same set of predator and prey species. Therefore trophic species form the nodes in a food web and they are said to be linked if one of these species preys on the other. The links are directed: an arrow shows the direction of the flow of resources from prey to predator. Those species (in what follows we will frequently refer to trophic species simply as species) which have no prey are termed *basal* species (denoted by B), those that have no predators *top* species (T) and all others with both predators and prey are called *intermediate* species (I). Several quantities are frequently used by ecologists to characterise a food web. They include the percentage of B, I and T species, the proportional of links between top and basal species (TB) (and similarly the proportion of TI, II and IB links), the ratio of predator to prey species (given by $(B+I)/(T+I)$) and the total number of links per species.

Ecosystems are reliant on the input of resources from the external, non-living environment (e.g. minerals, sunlight). The concept of *trophic levels*, or simply levels, is frequently used in the literature. The idea is that basal species are on the lowest, or first level, with top species being on the higher levels. But the exact definition of a level is a matter of convention: for example, species which feed directly from the environment may also have basal species as prey. Are these level 1 or level 2 species? Here we will define the level of a species as the length of the shortest food chain from the external environment to that species. Other definitions are possible. For example, all the possible routes for the species to the environment could be listed and the most common (the mode) could be designated as the trophic level [9]. However, since the majority of resources obtained by a species are likely to come through the shortest route, transfer of resources through each link of the food chain being relatively inefficient [9, 10], we believe that our definition is more natural. In a recent paper [11] we have investigated the extent of differences between this definition, and one which uses the weighted average of the lengths of the paths from the species to the environment, which we called the *trophic height*. The paths are weighted multiplicatively by the predator diet fractions (introduced later in the article). We find that a large majority of species in the model food webs have a trophic height very close to their trophic level [11], giving further credence to the usefulness of the simple definition of trophic level which we have adopted. Our definitions of trophic level and trophic height correspond to what are denoted respectively as the shortest and flow based definitions of trophic level in a recent review of the trophic level concept [12].

The problems of getting reliable data on real food webs are formidable; we cannot even begin to discuss this complex matter here (see Ref. [5] for an extensive set of references). Some broad trends are observable and deviations from the norm can be understood in some cases. Of course, there is no claim that the results should be universal. Here our aim is simply to argue that a considerable amount of quantitative data exist for food webs and that this puts stringent constraints on any model of species interaction of the type that we are proposing here.

3 The model

Our model is a stochastic one: random speciation together with competition for resources leading to complex adaptive dynamics. We begin with a definition of what we mean by a species. We might define a species by its phenotypic and behavioural characteristics — the keywords in a description which could be found in a good encyclopedia. Two of these keywords might, for instance, appear in the following descriptive sentence: a *nocturnal* creature which is *able to run fast*. These two keywords would appear in a list of possible *features* as numbers 47 and 297, say. So, in this case, this particular creature would have among its list of features numbers 47 and 297. More generally, we construct the species of the model by picking L features out of a pool of K possible features. There is no attempt to assign biologically realistic attributes to these features: they are just integers which run from 1 to K. In our work we frequently take $L = 10$ and $K = 500$ for illustrative purposes.

Since presumably the success of a species against a competitor is ultimately dependent on how good its features are against those of the competitor, we derive the predator-prey relationship between species from the "score" of one feature against another. These numbers, denoted by $m_{\alpha\beta}$, reflect how useful one feature, α, is against any other feature, β. The $K \times K$ matrix $m_{\alpha\beta}$ is antisymmetric and is chosen at the beginning of a simulation run and does not change during that particular run. The score S_{ij} of one species i against another species j is then defined as

$$S_{ij} = \max\left\{0, \frac{1}{L}\sum_{\alpha\in i}\sum_{\beta\in j} m_{\alpha\beta}\right\}, \qquad (1)$$

where the index α runs over all the features of species i and β runs over all the features of species j. Thus the species score against each other is essentially the pairwise sum of the relevant features score against each other. The definition (1) ensures that $S_{ij} \geq 0$. If $S_{ij} > 0$ then i is adapted to prey on j. The external environment is represented as an additional species 0 which is assigned a set of L features randomly at the beginning of a run and which do not change during that run.

This describes the constituents of the model. We now need an algorithm which defines the dynamics of the set of species. As this article is designed as a brief introduction to the model, we will simply outline the essential ideas. The time development of the model is divided into three different regimes:

1. A short time regime where the number of species in the system and the population of these species is constant. After the most recent change in population numbers which has occurred, predators may wish to change their foraging strategies to take into account the fact that, for instance, one of their prey species has become more plentiful. They do this by modifying their relative preference for a particular prey, which we denote by f_{ij}. These are fractions which give the amount of "effort" (or available searching time) that i puts into preying on the particular species j. Clearly $\sum_j f_{ij} = 1$, where the sum is over all prey species of i. In previous models which included predator preferences [13], these efforts were constants, but we believe that adaptive foraging is an important ingredient in models of food webs, and we will shortly describe how this is introduced into the present model.

2. An intermediate time regime where the external resources, R, are distributed among the species as a function of their scores. These resources are then tied up in the ecosystem as potential "food" in the form of prey for predator species. Eventually, the set of species settles down into a steady state, with the resources allocated according to the population dynamics equations. Three parameters, in addition to R, are introduced into the model at this stage. One is the ecological efficiency λ, which tells us what fraction of the resources invested in a species can be passed on to predators. It is clear that such a factor is required: for example, in real communities energy consumed by a warm-blooded animal in order to maintain body temperature will not be passed on to predators. During this period all species with less than one unit of resource are eliminated (rendered extinct).

3. The period in regime 2 is simply a time step in evolutionary time, and so after the system has reached a steady state as described above, a speciation event takes place where a new child species is created by taking one of the existing species at random and changing one of its randomly chosen features to another feature. The child species is then introduced into the ecosystem with its parent and the whole process repeated.

At this stage we should stress again that the topology of the web — the nature of the new species which are successfully introduced and those which are removed due to their failure to sustain more than one individual in the system — depends crucially on the nature of the population dynamics which is adopted. In our view it is not correct to postulate a particular web topology and introduce a dynamical system on this structure. A feedback mechanism between the processes of web construction/destruction and the dynamics on the web is an important part of the modelling process.

Most of the discussion in the literature on the formulation of equations which describes the population dynamics of a set of species concerns two, or possibly three species. There is very little discussion which is concerned with population dynamics equations which might describe a community of an arbitrary number of species, still less equations which allow for changes in foraging strategy which change according to the fortunes of the different species. Since the nature of the population dynamics is central to the structure of the food web produced, as well as to the determination of the populations of the species in the community, we have devoted a considerable amount of time to the development of the appropriate form of population dynamics equations.

We began with a general balance equation for the population number of species i, denoted by N_i, which is at least standard for two species [1,14]:

$$\frac{dN_i(t)}{dt} = \lambda \sum_j N_i(t) g_{ij}(t) - \sum_j N_j(t) g_{ji}(t) - d_i N_i(t). \quad (2)$$

Here $g_{ij}(t)$ is the functional response, that is, the rate at which an individual of species i feeds on species j. It depends on the population sizes, and its analytical form will be specified below. The first term on the right-hand side represents the growth in numbers of species i due to predation on other species j, the second term the decrease in numbers due to predation by other species j, and the last term is the death rate of individuals of species i, in the absence of interactions with other species. Where there is no predator-prey relationship between species i and species j, g_{ij} is zero. There are two minor variants on (2): the basal species may be treated differently from the other species, and given a positive growth term to represent feeding off the environment, or the environment may be included as a "species 0" and these growth terms represented by functional responses g_{i0}. Here we use the second variant, since we do not wish treat basal species differently from other species.

Apart from the constant death rates, d_i, and the ecological efficiency, λ, the model is completely specified once the functional responses have been chosen. Let us recall some of the more well-known forms that have been proposed for the case of one predator and one prey — denoted here as P for predator and V for victim. The earliest, and simplest, assumption is that the functional response is linearly dependent on the number of prey available: $g(P, V) = aV$. That is, the consumption of a predator goes up linearly with the density of prey in the system. This is the assumption behind, for example, Lotka-Volterra models. However, it is clearly incorrect for large V; the predator needs time to "handle" the prey (capture, consume, ...) and this will reduce the rate of consumption when prey are abundant. Allowing for these large V corrections [15] leads to the Holling form for the functional response: $g(P, V) = a_1 V/[1 + a_2 V]$. Further corrections may be introduced due to competition between predators for prey: $g(P, V) = a_1/[1+a_2 V + a_3 P]$ — the Beddington form [16]. In recent years there has been a reaction against the modelling of predator-prey interactions in terms of simple predator-prey collisions — the "mass-action" approach — and a move towards a modelling of predator-prey interactions on a longer time scale. One of the consequences of this reassessment of the basis on which the functional response is modelled is the suggestion that $g(P, V)$ should take the form $g(V, P) = a_1 V/[a_2 V + a_3 P]$. This is the so-called ratio-dependent functional response [17]. This may seem to be a very slight modification of the Beddington form, but its introduction has caused some discussion [18]. We have chosen a special form of the ratio-dependent functional response (by taking $a_3 = a_1$), but this was more reduce the number of parameters in the model, rather than anything else. We have just completed a study of the model using the other forms of functional response mentioned above (as well as others) [19]. However, our aim here is to describe the essentials of the model, and so going back to our previous notation — for a single predator i feeding on a single prey j — we choose

$$g_{ij}(t) = \frac{S_{ij} N_j(t)}{b N_j(t) + S_{ij} N_i(t)}. \quad (3)$$

This form of the functional response is fine if there is just one predator and one prey species, but what happens if there are other species preying on j as well? Let us denote the predator species by k. Then we might expect that in addition to the term $a_3 P$ in the denominator of the Beddington and ratio-dependence response, there would be terms representing competition from all individuals which are predators of j: $S_{ij} N_i(t)$ in (3) would be replaced by $\sum_k S_{kj} N_k(t)$, where the sum includes a term $k = i$. This is the form we adopted, except that we include an extra competition term in the interaction. The reason for this is that we wish to build in the fact that species which are similar to each other will be in much stronger competition with each other than those which have nothing in common. We therefore define

$$\alpha_{ki} = c + (1 - c) q_{ki} \quad (0 \le c \le 1), \quad (4)$$

where q_{ki} is the *overlap* between the two species k and i, defined as the fraction of features which they have in common. Thus if the species are identical, $k = i$, $\alpha_{ii} = c + (1 - c) = 1$. If they have no features in common $\alpha_{ki} = c$. The competition c is one of the parameters of the model. These considerations lead to a functional response of the form

$$g_{ij}(t) = \frac{S_{ij} N_j(t)}{b N_j(t) + \sum_k \alpha_{ki} S_{kj} N_k(t)}. \quad (5)$$

Finally, what happens if a particular species i has several prey j? It is at this point that we introduce adaptive

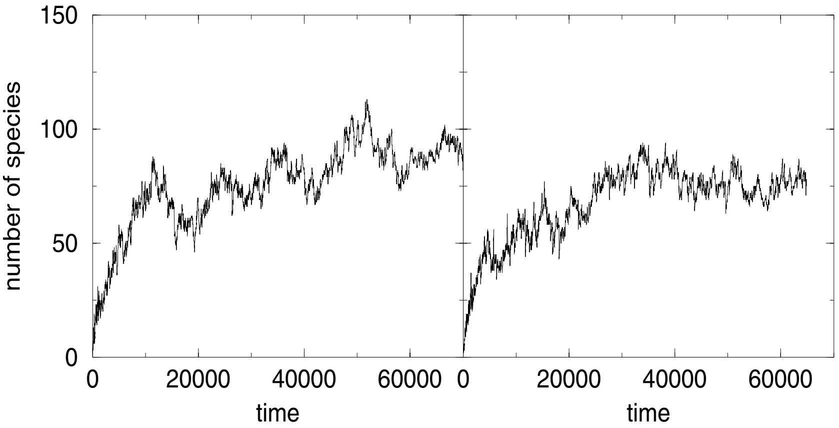

Fig. 2. Number of species as a function of time for two different sets of random numbers.

foraging: one might expect that predators assign more effort to those prey from which they obtain more food per unit effort, so that a stationary point is reached only when a predator obtains the same amount of food per unit effort from each prey. We would therefore expect that

$$f_{ij} = Ag_{ij}, \tag{6}$$

for all j with i fixed. Here A is a constant, which can be determined using $\sum_j f_{ij} = 1$. This yields

$$f_{ij}(t) = \frac{g_{ij}(t)}{\sum_k g_{ik}(t)}. \tag{7}$$

This condition is such that no individual can increase its energy intake by putting more effort into a different prey, and is an evolutionarily stable strategy [7]. Putting the efforts into the functional response (5) we obtain

$$g_{ij}(t) = \frac{S_{ij} f_{ij}(t) N_j(t)}{bN_j(t) + \sum_k \alpha_{ki} S_{kj} f_{kj}(t) N_k(t)}. \tag{8}$$

The f_{ij} are obtained from by solving (7) and (8) self-consistently.

This summarises the model. In the next section we shall briefly describe how the simulations were carried out, and then indicate the nature of the webs obtained from these simulations.

4 Results

Many simulations of the model have now been performed. Each one had (a) different random matrices for the scores of features against each other, and (b) different random feature sets for the environment. Each run was for 100,000 evolutionary time steps, except when very large webs were created, when the model was run for 200,000 time steps. The main parameters of the model are: R (total resources), c (the competition parameter, $0 \le c \le 1$), λ (the ecological efficiency which we took to be equal to 0.1) and b (the saturation level of the functional response).

In addition to exploring the space of these parameters to see how the structure of the webs changed, it was necessary to collect data from many different webs constructed with the same set of parameter values and to average over the results. While simulations with the same set of parameter values, but different random numbers, give rise to similar webs, different realisations will still be noticeably different, as illustrated in Figure 2.

In simulations of the model, the population sizes with a fixed number of species quickly reach a fixed point of the population dynamics. Large food webs can be built that consist of several hundreds of species. Their size varies with the parameters of the model, principally R, the amount of resources available, as shown in Figure 3. No stable species configuration is reached, but instead a dynamic equilibrium consisting of ongoing species creation and extinction is eventually established. No more than a few species become extinct at the same time, and the size distribution of extinction events has a sharp exponential cutoff. The evolutionary dynamics of the model, combined with the population dynamics, thus create large stable webs, which have ongoing changes due to species overturn, but do not show strong responses to small perturbations.

The results from the model are not far from the values observed in real food webs in most cases. It would be possible to choose parameters so that the results match a particular set of real food webs far more closely, however, given the uncertainties in present food web data we have not tried to do this. In fact, since the model seems to capture the essential features of real food webs, it might be useful in the investigation of several controversies concerning real food webs. Here we will simply give a flavour of some of the results which we have obtained; we refer the reader to the original papers for more details. In Tables 1 and 2 results are shown for a range of values of the parameters. Apart from the number of links per species, which seems a little low compared to most empirical data, these values are those commonly found in real webs.

Two examples of webs that have been constructed using the model are shown in Figures 4 and 5. We have chosen to show rather small webs for the sake of clarity. The radius of the open circles in Figures 4 and 5

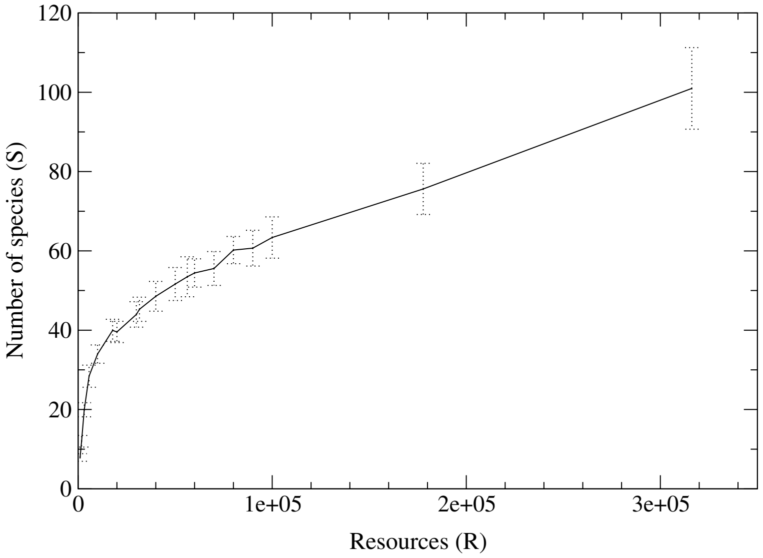

Fig. 3. The effect of resources (R) on the mean web size (S).

Table 1. Results of simulations of the model with $c = 0.5$ and $b = 5 \times 10^{-3}$ for three values of the resource R.

$c = 0.5$ $b = 0.005$ $\lambda = 0.1$			
	$R = 10^4$	$R = 10^5$	$R = 10^{5.54}$
no. species	33	57	82
links per species	1.76	1.91	1.91
average level	1.95	2.35	2.65
av. max level	3.0	3.9	4.0
B species (%)	18	9	5
I species (%)	80	89	89
T species (%)	2	2	6

Table 2. Results of simulations of the model with $R = 10^5$ and $b = 5 \times 10^{-3}$ for three values of the competition c.

$R = 10^5$ $b = 0.005$ $\lambda = 0.1$			
	$c = 0.8$	$c = 0.6$	$c = 0.4$
no. species	27	55	79
links per species	1.68	1.70	2.33
average level	2.15	2.28	2.38
av. max level	4.0	3.91	3.69
B species (%)	12	9	8
I species (%)	86	90	90
T species (%)	2	1	2

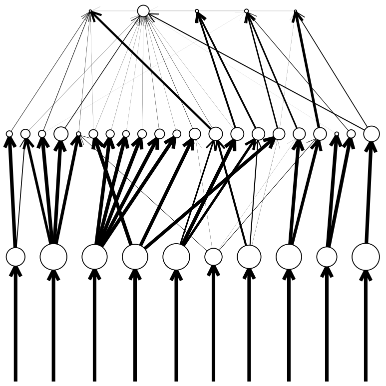

Fig. 4. A typical web generated from the model. This is a snapshot of the structure of a mature web, where originations and extinctions balance on average.

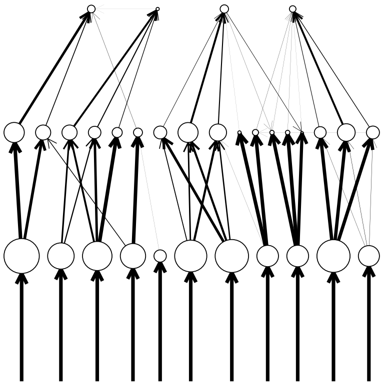

Fig. 5. A typical web generated from the model. The positions of species in the webs are not preassigned: they emerge from the dynamics of the model.

are proportional to the logarithm of population sizes of the species in the system. The thickness of the links represent the fraction of the effort that the predator is putting into preying on the species it is linked to. Weak links are not shown.

The order in which a particular web is constructed can be illustrated by looking at the time evolution of a single ecosystem. An example is shown in Figure 6, where dashed lines occur at times 100, 500, 1000 and 10000. If the food web is sampled at these times the structures shown in Figure 7 are found.

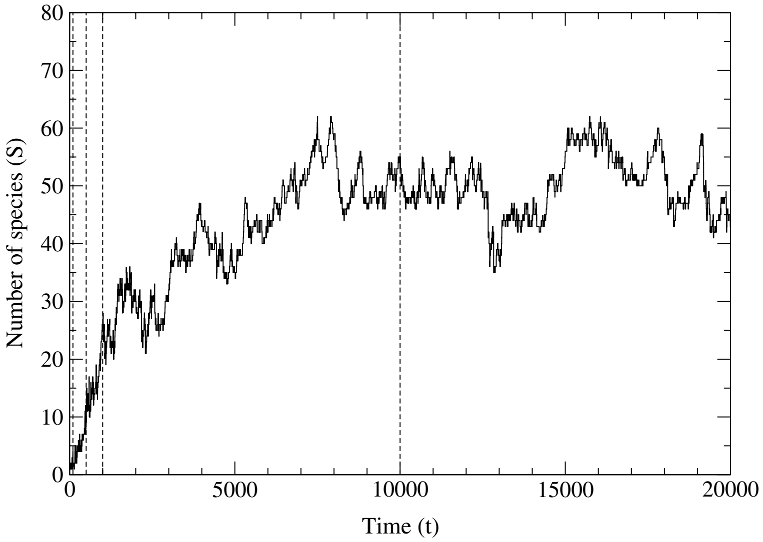

Fig. 6. The time evolution of a single system with $R = 10^5, b = 0.005$ and $c = 0.5$. The dashed lines represent the times at which the food web was sampled to produce the partially constructed webs shown in Figure 7.

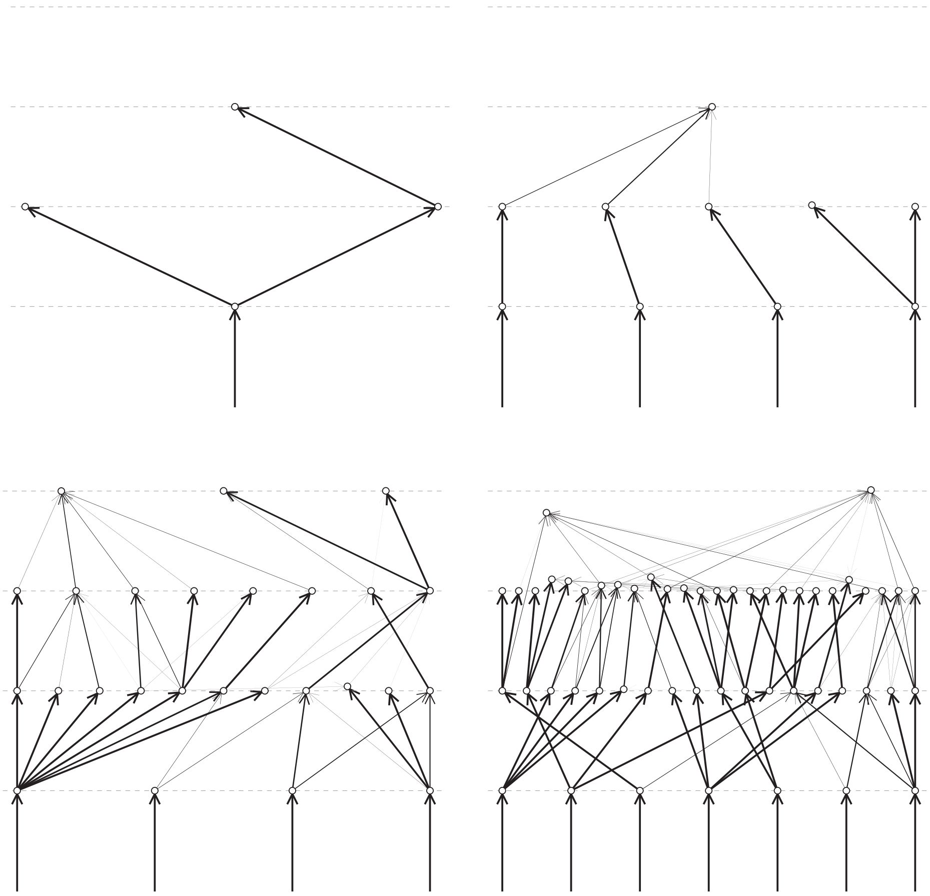

Fig. 7. Food webs produced in the simulation shown in Figure 6, sampled at times 100, 500, 1000 and 10000.

5 Discussion

In this article we have reviewed a model which allows food webs to be constructed *dynamically*. The model is relatively rich, yet we would contend that it contains only those elements which are believed to be important and relevant in determining the structure of food webs. Of course, one of the strengths of the modelling procedure is that the assertion that a particular element is important or not can be tested. In order to be able to "grow" a food web we need to recognise that there are two types of dynamics. The first type gives rise to new species in the web (by speciation) and eliminates them from the web (extinction). The second type is conventional population dynamics, which describes the interaction between individuals when the number of species present in the community is fixed. One of the key points on which the model is based is the fact that these two types of dynamics are coupled: population dynamics should not be defined on a static web — the web itself changes in response to the growth or decline of species numbers, which are determined by the population dynamics.

There are three time scales in the model. On the longest time scale, new species are introduced. They are variants of randomly chosen species already in the system. On the intermediate time scale, the number of species is fixed, and the dynamics is that of conventional population dynamics. On the shortest time scale, the populations of each species are fixed, but the foraging strategies may change, so that species may alter their feeding habits to take advantage of recent changes in population sizes. Although the model covers a very large range of time scales, the results it produces are intuitively appealing and in broad agreement with food web data from real ecosystems.

There are very few similar studies to which our work can be compared. About a decade ago there were a number of evolutionary toy models which were introduced, largely by theoretical physicists (see for example [20], or [21] for a review). However, the purpose of these models was not so much to reproduce realistic web structures, as to study the large-scale dynamics of species extinctions. We would expect that the extreme simplicity of these models, lacking as they do important ingredients that are present in real ecosystems, would give results which are not reliable. Mention should also be made of a model of interacting molecular species which has a population dynamics defined on a network which evolves topologically [22]. Theoretical ecologists have also studied assembly models [23], which are capable of generating intermediate-size webs with a predetermined number of trophic layers. However there are several drawbacks to these models, not least is the fact that species are drawn from a species pool which consist of species which have not co-evolved and are given a pre-determined role in the web. Perhaps the model which is closest to ours is a model which uses Lotka-Volterra dynamics [24]. However, computer simulations of this model [25] seem to indicate that only one tropic layer of species eventually survives.

Although the model is producing satisfactory results, we are continually looking for modifications and elaborations which can improve it. For example, in the original paper describing the approach [6], the population dynamics was rather simple. One consequence was that it became progressively more and more difficult for new species to enter the system and survive, so that eventually a final state was reached which no species could invade. The second version of the model [7], which is the one that has been reviewed here, has a much more realistic population dynamics and instead predicts a state of dynamic equilibrium with a continuous overturn of species with originations and extinctions balancing on average. Thus while the structure of the mature web may not appear to change too much over very long time scales most, if not all, of the species will have become extinct and been replaced by other similar ones. Presently we are modifying the nature of some of the specific assumptions which lie at the heart of the model. We believe that the essential predictions of the model will not be altered by changing these details. In other words, we believe that the model is robust, and the essential nature of the predictions will not be changed by perturbations of the specifics of the model.

The other papers in this volume show the great interest which is being shown in the study of networks and their properties. We hope that researchers in the general theory of networks will benefit from a study of the approach we have adopted in the modelling of food webs and that it will also contribute to the generalisation and elucidation of the theory of food webs.

I would like to thank Chris Quince for providing many of the figures used in this paper.

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