



Modelling Coevolution in Multispecies Communities

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We introduce the Webworld model, which links together the ecological modelling of food web structure with the evolutionary modelling of speciation and extinction events. The model describes dynamics of ecological communities on an evolutionary time-scale. Species are defined as sets of characteristic features, and these features are used to determine interaction scores between species. A simple rule is used to transfer resources from the external environment through the food web to each of the species, and to determine mean population sizes. A time step in the model represents a speciation event. A new species is added with features similar to those of one of the existing species and a new food web structure is then calculated. The new species may (i) add stably to the web, (ii) become extinct immediately because it is poorly adapted, or (iii) cause one or more other species to become extinct due to competition for resources.

We measure various properties of the model webs and compare these with data on real food webs. These properties include the proportions of basal, intermediate and top species, the number of links per species and the number of trophic levels. We also study the evolutionary dynamics of the model ecosystem by following the fluctuations in the total number of species in the web. Extinction avalanches occur when novel organisms arise which are significantly better adapted than existing ones. We discuss these results in relation to the observed extinction events in the fossil record, and to the theory of self-organized criticality.

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1. Introduction

Our aim in this paper is to introduce a model for the evolution of many interacting species in an ecosystem. A great deal of information has been assembled on the properties of food webs for naturally occurring ecosystems (Cohen, 1989; Martinez, 1991; Polis, 1991; Hall & Raffaelli, 1991; Goldwasser & Roughgarden, 1993), and a variety of models describing the structure of food webs have been studied (Pimm, 1982; Briand & Cohen, 1984; Cohen *et al.*, 1990; Cohen, 1990; Pimm *et al.*, 1991; Morin & Lawler, 1995). Most of these models concentrate on static properties of the webs, such as the proportions of species at each of the trophic levels, and the lengths of food chains. There have also been models for the assembly of food webs by gradual addition of species (Luh & Pimm, 1993;

Morton & Law, 1997). One essential property of real food webs is that they have evolved. Species diversity will accumulate over time as new species arise due to speciation. Species may also become extinct due to competition from better adapted species. Here we study a model which has the evolutionary dynamics of speciation and extinction built into it. We will analyse the properties of the food webs which arise in the model and compare these with ecological data.

The variation in the diversity of species seen in the fossil record is well documented (Sepkoski, 1993). Attention has focused on the large-scale extinction events in which very large fractions of the existing species apparently become extinct almost simultaneously on a geological time-scale. Some of these large scale extinctions may be caused by catastrophic external events, or by major climate changes.

However it has been shown (Sneppen *et al.*, 1995; Solé *et al.*, 1997) that both the distribution of sizes of extinction events and the distribution of lifetimes of species in the fossil record are very broad and approximate to power-laws. It has been argued that the large fluctuations in species diversity which are seen may result from the internal dynamics of the ecosystem. A newly-evolved species may cause extinction of its immediate competitors. The extinction of one species may lead to the extinction of other species which prey upon it, and these extinctions may lead to further extinctions, and so on. Hence there is the possibility of avalanches of extinction events spreading through an ecosystem. A link has been made between macroevolutionary dynamics and the theory of self-organized criticality (SOC). This theory was originally formulated in the language of sandpiles (Bak *et al.*, 1988) and has since been applied to many other dynamical systems including earthquakes and forest fires. In the sandpile model one grain of sand is added at a time onto a pile of sand. This may either add stably to the pile, or may cause an avalanche of one or more grains to tumble from the pile. The evolutionary analogy is clear: evolution leads to new species being added slowly to an ecosystem, and these may sometimes add stably to the system or may sometimes cause extinction events.

There is now a huge variety of evolutionary models inspired by the idea of SOC (Bak & Sneppen, 1993; Paczuski *et al.*, 1996; Kramer *et al.*, 1996; Solé & Bascompte, 1996; Solé *et al.*, 1996; Roberts & Newman, 1996). These models are deliberately extremely simple, and they focus on the dynamical properties of extinction avalanches and species lifetimes. They do not tell us anything about ecosystem structure, because the couplings between species are introduced either at random or in an *ad hoc* manner (e.g. species are arranged on a line and neighbours interact). In our view it is essential to have a realistic model of ecosystem structure in order to study the way extinction events will propagate through a food web. By linking the ecological modelling of food web structure with the evolutionary modelling of speciation and extinction events we believe that the Webworld model described in this paper makes a significant advance in both fields.

At this stage it is useful to introduce some notation used in the description of food webs. If one species preys on another then they are said to be *linked*. *Basal species* are those with predators but with no prey and *top species* are those with prey but with no predators. *Intermediate species* have both predators and prey. We will refer to the percentages of basal, intermediate and top species as B , I , and T . Two species are said

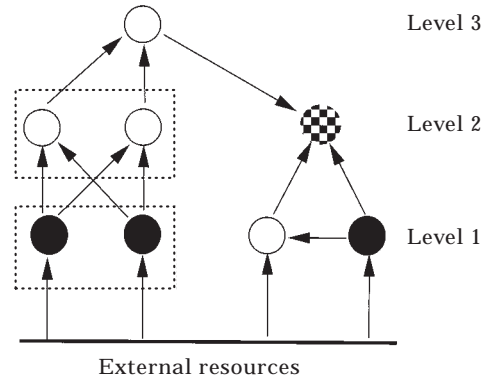


FIG. 1. An illustrative example of a food web. Arrows indicate the direction of flow of resources. Input of external resources is specifically indicated. Basal species are black, intermediate species are white, and top species are patterned. Boxed species form part of the same trophic species. The trophic level of a species is the length of the shortest food chain from the external resources to that species.

to belong to the same *trophic species* if they share the same set of prey and the same set of predators (see Fig. 1). It is customary to group the original species in a web into trophic species and to analyse the properties of the trophic species web. This goes some way toward standardizing webs obtained by different researchers using different criteria for inclusion of species and different degrees of resolution. The statistics presented in this paper will be for trophic species webs. One food web statistic which we quote for the model webs is the ratio of prey to predator species, defined as $(B + I)/(T + I)$. Another characteristic property of webs is the average number of links per species, defined simply as the total number of links divided by the total number of species. It is also useful to classify the links according to the type of species which they connect, i.e. we can measure the proportion of links between top and basal (TB), top and intermediate (TI), intermediate and intermediate (II) and intermediate and basal (IB) species.

Ecosystems are reliant on the input of resources from the external, non-living environment. Within the model the environment is treated explicitly as a node in the food web. Species which are linked to the environment node are primary producers, i.e. they may survive in the absence of any other species. It follows that basal species (those having no prey) must be primary producers, otherwise they would have no means of survival. However, not all primary producers are basal species, since a primary producer may also be a predator of other species.

We will use the following definition of *trophic levels*. All species linked to the environment node (i.e. primary producers) are defined as level 1 species. All

species which have at least one level 1 prey are defined as level 2 species. All species with at least one level 2 prey are defined as level 3, and so on. Hence, the level of a species is the length of the shortest food chain from the external environment to that species. We could also have chosen to characterize species by the length of the longest chain linking them to the environment, or the average length of all the possible chains, however these quantities are time consuming to calculate for large webs, and also special rules are required to deal with the possibility of loops in the web. The definition we use is rapid to calculate, and is unambiguous, even when loops are present in the web. Also the majority of resources obtained by a species are likely to come via the shortest route, since transfer of resources at each link of the food chain is relatively inefficient. Therefore, it seems that the definition of trophic level that we use is meaningful from an ecological point of view.

2. Definition of the Webworld Model

2.1. FEATURES AND SPECIES

A species is defined in terms of a set of L characteristic features. Such features may be either morphological or behavioral characteristics possessed by all the individuals of that species, e.g. sharp teeth, binocular vision, webbed feet, being nocturnal, forming social groups etc. The L features for each species are picked from a total number of K possible features. In the simulations presented here $L = 10$ and $K = 500$. The species are labelled by integers $n, n' = 1, 2, \dots$

The predator-prey relationships between species are determined by the features possessed by those species. The matrix, m , is a $K \times K$ matrix of scores representing the usefulness of any feature i of one species for predation against any feature j of another species. We suppose that m is anti-symmetric, and that the elements are assigned randomly, such that $m_{i,j}$ is a random Gaussian variable with mean zero and variance 1 if $i > j$, $m_{j,i} = -m_{i,j}$ and the diagonal elements $m_{i,i}$ are zero. This matrix of the scores is chosen at the beginning of a simulation run and does not change during the run. The score $S_{n,n'}$ of one species n against another species n' is then defined as

$$S_{n,n'} = \max \left\{ 0, \frac{1}{L} \sum_{i \in n} \sum_{j \in n'} m_{i,j} \right\} \quad (1)$$

where i runs over all the features of species n and j runs over all the features of species n' . The max operator ensures that all scores are positive or zero. A positive score indicates that n is adapted to be a

predator of n' , and a zero score indicates that there is no interaction. The factor of $1/L$ has been chosen so that the scores have a root mean square value of order 1.

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 does not change. If $S_{n,0} > 0$ the species n may be a primary producer, provided it is not out-competed (see below).

2.2. TRANSFER OF RESOURCES

A total amount, R , of external resources is distributed amongst the primary producers, as a function of the scores $S_{n,0}$, according to the rules for competition described below. These resources determine the population size of the primary producers. The population of species n is denoted $N(n)$. For simplicity, we measure resources and population size in the same units, so that $N(n)$ is equal to the amount of resources obtained by species n . Predator species obtain resources from their prey. We assume that a fraction $\lambda N(n)$ of the resources of a given species n is available to be passed on to predators of n . Thus λ is a parameter of the model which determines the relative sizes of predator and prey populations.

2.3. COMPETITION FOR RESOURCES

The resources obtained from species n are distributed between the predators of n in the following way. (The same rules are used for the case $n = 0$, where the resources are the external resources R , and the “predators” are the primary producers). The better adapted the predator, the more resources it gets. We therefore define the *main predator* of n as the one with the best score against n :

$$S_n^M = \max \{ S_{n',n} \} \text{ where } n' \text{ is a predator of } n \quad (2)$$

The predators of n will obtain a share of the available resources proportional to the quantity:

$$F_{n',n} = \max \left\{ 0, \left(1 - \frac{S_n^M - S_{n',n}}{\delta} \right) \right\} \quad (3)$$

where δ is a parameter of the model which determines the strength of competition. The smaller δ the stronger the competition. We also define $F_{n',n}$ to be zero if $S_{n',n} = 0$, so that only species for which $S_{n',n} > S_n^M - \delta$, and $S_{n',n} > 0$ successfully obtain any resources from n . The actual fraction of resources obtained is found by normalizing the $F_{n',n}$:

$$\gamma_{n',n} = \frac{F_{n',n}}{\sum_m F_{m,n}} \quad (4)$$

2.4. POPULATION SIZES

We will calculate the population sizes of the species by iteration of a set of equations representing transfer of resources between the species. Each iteration represents a small time period of order one generation time. If $N(n, t)$ is the population of species n at iteration t then we may write

$$N(n, t + 1) = \gamma_{n,0}R + \sum_{n'} \gamma_{n,n'}\lambda N(n', t) + \gamma_{n,n}\lambda N(n, t). \quad (5)$$

The first term represents external resources obtained by n , which may be zero if $\gamma_{n,0} = 0$. The second term represents resources obtained from prey (n' runs over all the prey of n). The third term represents resources lost to predators. Here we have defined

$$\gamma_{n,n} \begin{cases} -1, & \text{if } n \text{ has at least one predator species} \\ 0, & \text{if } n \text{ has no predators.} \end{cases} \quad (6)$$

After several iterations the population sizes will converge to stationary values. We suppose that the stationary population sizes determined by this method represent mean population sizes over many generations. The iteration procedure can be viewed as an algorithm which determines the solution of the following set of linear equations for the stationary values:

$$N(n) = \sum_{n'} \gamma_{n,n'}\lambda N(n'). \quad (7)$$

Here n' runs over all the species, including n and 0, and for convenience we have defined $N(0) = R/\lambda$.

There have been many studies of population dynamics at short time-scales using either difference equations like (5), or differential equations like the Lotka–Volterra equations, or generalizations of them (Vida *et al.*, 1990; Berryman *et al.*, 1995; Arditi & Michalski, 1996; Zheng *et al.*, 1997). Many of these equations have interesting dynamical behaviour, such as periodic solutions or chaos which may be relevant to real ecological population dynamics. In fact we are not interested in the population dynamics at the scale of a few generations. We are only interested in evolutionary time. We have deliberately chosen difference equations which are as simple as possible, and which have only one stationary state. These equations converge rapidly, and always reach the same stationary state irrespective of the initial conditions. It is a property of our equations that the amount of resources passed from a prey to a predator species is proportional to the prey population size

only. This situation is usually called donor control (Zheng *et al.*, 1997). We will be interested in the way the population sizes change as the ecosystem evolves. Before describing the long time-scale evolutionary dynamics of our model it is useful to consider the following simple example which illustrates competition between species and transfer of resources between levels.

Suppose there are two primary producers, 1 and 2, having scores $S_{1,0} = 1.0$ and $S_{2,0} = 0.95$. In addition, species 3 is a predator of species 1, i.e. $S_{3,1} > 0$. Let the competition parameter δ be 0.1. From the above rules $\gamma_{1,0} = 2/3$ and $\gamma_{2,0} = 1/3$, and since 3 is the sole predator of 1, $\gamma_{3,1} = 1$. The iterative equations are therefore

$$N(1, t + 1) = 2R/3 - \lambda N(1, t)$$

$$N(2, t + 1) = R/3N(3, t + 1) = \lambda N(1, t) \quad (8)$$

and the stationary states are $N(1) = 2R/3(1 + \lambda)$, $N(2) = R/3$, and $N(3) = 2\lambda R/3(1 + \lambda)$. Notice that the sum of the populations is equal to R . It is a property of the model that the sum of the populations at the stationary state is always equal to the amount of external resources put in.

Given the lists of features representing any set of species it is possible to calculate the scores $S_{n,n'}$ and hence the steady-state population sizes. We suppose that there is a minimum population size necessary for survival of the species, and we set this limit to 1. Any species for which $N(n) < 1$ becomes extinct and is deleted from the list of species. The resulting ecosystem is then stable, and properties of the web can be measured.

For the purposes of defining the food web structure, a link is assumed to be present between n and n' if n successfully obtains resources from n' , i.e. if $\gamma_{n,n'} > 0$. Cannibalism has been excluded from the model ($S_{n,n}$ is defined to be zero for all n). Also, since the m_{ij} matrix is anti-symmetric, then for any pair of species it is impossible for both $S_{n,n'}$ and $S_{n',n}$ to be non-zero, i.e. there are no reciprocal pairs of links. Loops of three or more species can occur in the model, however.

2.5. EVOLUTIONARY DYNAMICS

Evolutionary time in the model proceeds in timesteps such that one speciation event occurs in every timestep. At each step an existing species is chosen to undergo speciation with a probability proportional to its population size. A new species is created by copying the list of features of the parent species, randomly picking one of these features, and replacing it by another randomly chosen feature from

the complete list of possible features. The new species thus differs by only one feature from the old one. The stationary population sizes of all the species are now recalculated, taking account of the presence of the new species. There are several possible outcomes: (i) the new species may add to the web in a stable fashion, so that the total number of species increases by one; (ii) the new species may be poorly adapted, and may become extinct immediately; (iii) the new species may survive, and cause one or more other species to become extinct. A new species will often be in direct competition with the parent species, therefore a special case of outcome (iii) is that the new species simply replaces its parent in the ecosystem.

Having eliminated any species which become extinct due to the new addition, the web is once again in a stable state. This is the end of one complete timestep. This process is repeated many times and the properties of the webs are recorded at the end of each step and subsequently averaged. When choosing the new feature for each new species a restriction is made that no feature may appear more than once in the list of features possessed by any one species. Also, when the new feature list is created, we check that it is not identical to the feature list of any other species, and that it is not simply a permutation of any other list. This prevents the occurrence of multiple copies of identical species.

The only remaining thing to be specified is the initial state of the web. One possibility is to consider an "origin of life" scenario, where the web begins with exactly one primary producer species. Another possibility is to begin with a small number of randomly chosen species. We carried out runs where the initial state was composed of 1, 10 and 20 different species, and found very little difference between these. All the results presented here were started with a set of 10 random species. Since the features of these species are chosen at random, the species are not well adapted to survive together, hence there is a tendency for several extinctions to occur immediately on the first timestep.

3. Properties of the Model

In this section we discuss some of the important properties of the model which are relevant to understanding the numerical results in the next section. The model contains three parameters, R , λ and δ , and these will affect the shapes of the food webs in various ways.

We would intuitively expect that increasing the amount of resources available should increase the diversity of the ecosystem. In the model the sum of the

population sizes is equal to R , and since every species must have a population of at least one, there can never be more than R species. In fact the mean number of species observed is always much less than R because resources are not distributed evenly between species. Species at lower levels have much larger populations. The ratio of population sizes between predator and prey is controlled by λ . Together R and λ determine the maximum possible number of trophic levels in the system.

Consider a web consisting of a single food chain of k species. The stationary population sizes obtained from the model for each level j except the top level are $N(j) = \lambda^{j-1}R/(1 + \lambda)^j$, and the population of the top level is $N(k) = \lambda^{k-1}R/(1 + \lambda)^k$. A chain of length k can only be supported if $N(k) > 1$. This gives the condition

$$k < 1 + \frac{\log(R)}{\log((1 + \lambda)/\lambda)} \quad (9)$$

and, since k is an integer, the maximum level is actually the largest integer below this limit. Thus the maximum food chain length only increases logarithmically with R . Although this limit has been calculated assuming the web is a single chain, we believe that this is a strict limit to the number of levels for any possible web generated by the model. This is because adding extra links and more species to the web always decreases the fraction of resources reaching the top level in comparison to the single chain calculation.

The number of levels observed in the model food webs is strongly sensitive to λ . We have chosen to set $\lambda = 0.1$ in all the simulations reported here. This gives realistic numbers of trophic levels in the model food webs and is also consistent with measured values of predator-prey population ratios, and estimates of the ecological efficiency (Pimm, 1982).

The value of the parameter δ affects the properties of the web considerably. In order to choose a sensible value of δ we note that the scores $S_{n,r}$ are all of order 1, and that when a single feature is changed, the score changes by an amount of order $1/L$. In other words, species competing for the same resources should have scores which differ by an amount of order $1/L$. We should therefore set δ to be roughly of this size. If we make $\delta \gg 1/L$, even very uncompetitive species will be allocated some resources. Hence the number of predator species per prey species will be large, and this will lead to a highly connected web with a large number of links per species. As $\delta \rightarrow 0$, only the main predator will be allocated resources, and so in the limit the web will become a single food chain. For

most of the results given in this paper δ is in the range 0.05–0.2, which is comparable with $1/L = 0.1$.

It is useful to mention several features which have deliberately been excluded from the model. Firstly, there is no variation between individuals of a given species, and there is no genetics. Species are simply represented by a list of phenotypic features, which represent average properties for all members of that species. A model which included both many species and many individuals per species, each with its own genotype and/or phenotype would require enormous computational resources. Secondly, even though speciation is an essential part of the model, we do not attempt to consider the mechanism by which speciation occurs. We simply suppose that species have an inherent tendency to diversify. Speciation involves the establishment of reproductive isolation by some means or another, and we cannot deal with this in the absence of a genetic description of the species. When a new species is created it differs by only one feature from the parent species. However, this is intended to represent a major change to the phenotype, which would probably involve changes in more than one gene sequence, and possibly some considerable alteration to the developmental biology of the organism. Thus changing a single feature does not represent a single mutation, but is the result of many changes at the genetic level. In addition we make no distinction between sexual and asexual methods of reproduction, and the model is intended to apply equally well to either case.

4. Results—Structure of Model Food Webs

The figures presented in the tables of results represent averages taken over many webs. For each set of parameters several independent simulation runs were performed using different randomly generated m

TABLE 1
Results of a simulation of the model with $\lambda = 0.1$ and $R = 10^3$ for four values of the competition parameter δ

	$R = 10^3$			
	$\delta = 0.05$	$\delta = 0.1$	$\delta = 0.15$	$\delta = 0.2$
No. species	40	80	290	320
No. links	55	150	800	1250
Links per species	1.4	1.9	2.7	3.8
Average level	1.7	1.4	1.2	1.1
Max level	3.0	3.0	3.0	3.0
<i>B</i> species (%)	40	56	74	78
<i>I</i> species (%)	59	44	26	22
<i>T</i> species (%)	1	0	0	0
<i>IB</i> links (%)	53	73	83	88
<i>II</i> links (%)	43	27	17	12
<i>TI</i> links (%)	4	0	0	0
Prey/predators	1.6	2.2	3.8	4.6

matrices and different random feature sets for the environment (species 0). Each run was for 250000 timesteps, with the exception of the runs with $R = 10^{10}$, which were for 500000 timesteps. In each case, average quantities were measured during the second half of the run. The different runs for each parameter set were then averaged. Fluctuations in the number of species and the number of links between different runs with the same parameter values were surprisingly large, with standard deviations being up to 50% of the mean. Since these quantities increase in relation to one another, the fluctuations in the number of links per species are much smaller (typically ± 0.2). Standard deviations in the percentages of *B* and *I* species are typically 7–10%. We have omitted error estimates from the tables for clarity. We are principally interested in the main trends in the web properties as the parameters are varied, rather than in precise values. We have checked that these trends are significant. The quoted figures in the tables apply to webs of trophic species.

TABLE 2
Results of a simulation of the model with $\lambda = 0.1$, $R = 10^6$ or 10^{10} and various values of δ

	$\delta = 0.05$	$R = 10^6$			$R = 10^{10}$ $\delta = 0.05$
		$\delta = 0.1$	$\delta = 0.15$	$\delta = 0.2$	
No. species	150	200	410	810	220
No. links	240	510	1420	5930	350
Links per species	1.6	2.5	3.5	7.3	1.6
Average level	2.5	2.4	2.3	1.8	3.2
Max level	5.2	5.2	5.3	5.5	7.2
<i>B</i> species (%)	10	25	32	60	3
<i>I</i> species (%)	90	75	68	40	97
<i>T</i> species (%)	0	0	0	0	0
<i>IB</i> links (%)	22	47	51	70	10
<i>II</i> links (%)	78	53	49	30	90
<i>TI</i> links (%)	0	0	0	0	0
Prey/predators	1.1	1.3	1.5	2.5	1.0

Tables 1 and 2 show results for $R = 10^3$, 10^6 and 10^{10} , for δ in the range 0.05–0.2. In all cases $\lambda = 0.1$. There is a clear tendency for the mean number of species to increase with R , for fixed values of δ and λ . However, it should be noted that the number of species is very much less than the theoretical maximum of R . In fact the number of species only increases very slowly with R : a change in R by seven orders of magnitude only causes a five-fold increase in the number of species. In contrast, the number of species increases rapidly with δ at fixed R . Also, changing δ has a large effect on the total number of links. The number of links increases more rapidly than the number of species, so that the number of links per species increases significantly with δ . The number of links per species increases slightly with R for fixed δ .

These results imply that competition is a significant factor in determining the number of species and the number of links in the web. The competition parameter δ determines the cut-off in the function $F_{n,n'}$ in eqn (3), and hence controls the number of predator species which can successfully obtain resources from each prey. It is therefore to be expected that the number of links per species will increase with δ . Also, when the competition is weaker, it is easier for a species to find at least one prey for which it is sufficiently well adapted to be a predator, therefore the total number of species should also increase with δ , as is observed. The importance of δ in controlling species numbers also provides an explanation of why the number of species only increases very slowly with R . The number of level 1 species is limited by competition for external resources. Increasing R at fixed δ tends to increase the populations of all level 1 species proportionately, rather than increasing the number of level 1 species. The same is also true of intermediate levels. However at the higher trophic levels species numbers are limited by the criterion of the minimum population size necessary for viability ($N(n) > 1$). The principal effect of increasing R is therefore to increase the maximum number of trophic levels possible in the web, and to allow a few high level species to survive, without changing the number of low level species very much. We have already shown that the maximum number of levels increases logarithmically with R , and this therefore suggests that the total number of species should increase as $\log R$, which is consistent with our results. Figure 2 shows a histogram of the mean number of species at each level, and the way that this depends on R . This confirms the fact that increasing R leads principally to an increase in species at higher trophic levels.

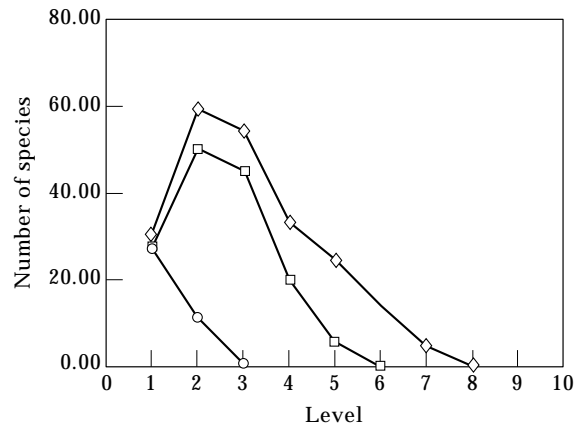


Fig. 2. The mean number of species on each level with $\lambda = 0.1$, $\delta = 0.05$ and $R = 10^3$, 10^6 and 10^{10} . (○) $R = 10^3$; (□) $R = 10^6$; (◇) $R = 10^{10}$.

Tables 1 and 2 also show the change in the number of levels in the web with R and δ . The average level is defined by calculating the level of each species, averaging these for all species in each web, and then averaging these web averages over many webs for each parameter set. The maximum level is defined by calculating the maximum level present in each web, and averaging these maximum values over many webs for each parameter set. Both average and maximum levels increase approximately logarithmically with R as expected. For $R = 10^3$, 10^6 and 10^{10} the maximum possible number of levels from eqn (9) are 3, 6 and 10. For $R = 10^3$ the limiting value is always achieved. For $R = 10^6$ the mean value of the maximum level is only slightly below the limit, whereas for $R = 10^{10}$ it is considerably below. Two factors contribute to this. Firstly, the theoretical limit was based on a single food chain since this is the most efficient way of transferring resources to high levels. The webs generated by the model are multiply connected and contain omnivorous links and loops, hence the maximum attainable number of levels is reduced. Secondly, the calculated limit takes only ecological efficiency into account, but ignores evolutionary constraints, which may also limit the number of levels in the Webworld model. Well adapted level 1 species may begin to evolve from the start of a simulation run, since the environment is fixed. High level species depend on lower level ones for their resources, hence well adapted high level species tend to evolve at later stages of the simulation when the properties of the lower level species are changing less rapidly. The properties of the runs with $R = 10^{10}$ still appeared to be changing after 250000 timesteps, hence they were continued for 500000 timesteps. This led to a significant increase in the number of species and the

number of links, and a slight increase in the number of levels. Most of the late evolving species are on higher levels, hence the proportion of basal species was found to decrease significantly between 250000 and 500000 timesteps.

Also from the tables it can be seen that the average level decreases with increasing δ . This is understandable, because the level is defined as the shortest possible chain to the external environment node. If δ is large, then a species with a low score $S_{n,0}$, but a high score $S_{n,n'}$ against another species n' may successfully compete for the external resources, and will therefore count as level 1 (the link to n' would not affect the calculation of the level). If δ is smaller, the same species would only survive by being a predator of n' , and would therefore count as a higher level species. The maximum number of levels does not change much with δ . The apparent slight increase in the maximum level with δ in Table 2 is probably not significant.

The proportions of basal, intermediate and top species are given in Tables 1 and 2. Increasing δ at fixed R leads to an increase in B and a decrease in I and T . This is for the same reason that the average level decreases with δ . (However, in the following section we consider a case with extremely large δ where this trend is no longer true). Increasing R at fixed δ leads to a decrease in B and an increase in I . Again this is because increasing R increases the number of levels, and thus the proportion of species in level 1 goes down. The number of top species is always very small: $T \leq 1.5\%$ when $R = 10^3$, and no top species were observed at all for $R = 10^6$ and $R = 10^{10}$. Thus, increasing the number of levels does not mean that the number of top species increases. In

the model webs, for the parameters discussed so far, almost all species have predator species, even if they are at high trophic levels. This implies the presence of large numbers of loops in the food web and large numbers of omnivores. The behaviour of T is an important property which has been remarked upon in the study of real food webs, and we will return to it in the following section.

The tables also give the fractions of links between top, basal, and intermediate species, and the ratio of prey species to predator species. These quantities are given primarily for comparison with the real food web data. Trends in these quantities can be understood in terms of the trends discussed above in B , I , and T . For example, as δ increases at fixed R , or R decreases at fixed δ , the percentage of species which are intermediate decreases and as a consequence the fraction of the links which are between intermediate species also decreases.

5. Comparison with Real Food Webs

The problems in getting reliable data on real food webs are readily acknowledged by ecologists (Cohen *et al.*, 1993). These problems centre around the tremendous amount of effort required to observe all species and all predator-prey interactions in a given ecosystem. Data from a large number of food web studies has been assembled in the EcoWeb database (Cohen, 1989). Our analysis of the average properties of all the 181 webs in this database is given in Table 3. In addition we give data from several well studied webs which have been published recently (see caption to Table 3).

TABLE 3

Data from experimentally studied food webs: the ECOWEB database—average properties of all webs (Cohen, 1989); the Lovinkhoeve Experimental farm soil food web (De Ruiter et al., 1995); the Coachella Valley desert (Polis, 1991); St. Martin Island (Goldwasser & Roughgarden, 1993); the Ythan Estuary (Hall & Raffaelli, 1991; Huxham et al., 1996); and Little Rock Lake (Martinez, 1991)

	ECOWEB	Experimental data				
		Lovinkhoeve	Coachella	St. Martin	Ythan	Little Rock
No. species	16	15	29	42	83	93
No. links	33	30	262	203	398	1033
Links per species	2.0	2.0	9.0	4.8	4.8	11.1
Average level	2.1	2.5	2.0	2.1	2.5	2.2
Max level	3.2	3	3	4	4	3
B species (%)	21	13	10	14	5	13
I species (%)	49	74	90	69	59	86
T species (%)	30	13	0	17	36	1
TB links (%)	10	3	0	3	1	0
IB links (%)	29	10	13	19	10	9
II links (%)	29	57	87	53	51	91
TI links (%)	32	30	0	25	38	0
Prey/predators	0.89	1.0	1.11	0.97	0.67	1.13

Before the real food web data can be compared with the model it is necessary to note several points. For both the model and the real data, all statistics are for trophic species. Many webs contain detritus as a “species”, and we have followed the convention of treating this as a single basal species. Plants are often treated in a very aggregated way, e.g. the St. Martin Web divides plants into fruit, nectar, leaves, wood and roots, each of which is treated as a “species”. Several webs split taxa into adult and juvenile “species” where these have different diets. Again we have followed the conventions of the source article in these cases. In the model webs the external resources are treated explicitly as a node in the web, and basal species must be linked to this node. Real webs have no such external resources node (although evidently external resources do enter the real ecosystems). Therefore, when counting the number of links in the model webs, links to the external resources node were omitted, in order to allow comparison with the real webs. The real webs contain some cannibalistic links (particularly the Coachella web). For simplicity we included these in the count of links, whereas cannibalism does not occur in the model webs. The statistics in the table differ very little according to whether one counts or discounts cannibalistic links.

Most of the webs in the EcoWeb compilation are small, and they have been criticised as being incomplete, and biased due to observational methods (Martinez, 1991; Polis, 1991). We have chosen the individual webs since in these cases attempts have been made to be systematic and inclusive. Nevertheless, one suspects that the large difference in the number of trophic species between these data sets reflects the degree of aggregation chosen by the different workers, rather than the actual diversity of the ecosystems. The five individual webs are listed in order of increasing number of trophic species. There are some trends apparent when comparing these webs with each other, although in many ways each must be considered as a special case. There is a general trend for the number of links per species to be higher in larger webs. This would suggest that systematic study of a community over a long period of time leads to a greater increase in the number of links observed than in the number of species. It may be that the number of links is severely underestimated in some of the Ecoweb food webs. The Coachella web breaks this trend, since it has a very large number of links per species and is only fairly small.

There is a strong similarity between the figures for the Coachella and Little Rock webs, despite the difference in the number of species. They both have a high number of links per species, a low value of B ,

a high value of I and very low T . Martinez & Lawton (1995) have suggested that, in the limit of extremely large webs which represent large geographical areas, I will increase to about 95%, B will decrease to about 5%, and T will decrease to zero. Our data in Tables 1 and 2 confirm that as R increases, the number of species increases and the fraction of intermediates becomes larger ($I = 97\%$ in the run with $R = 10^{10}$, for which the average number of trophic species is 200). The data from the Ythan web appear to go against this trend, however, since there is a very high value of T (36%), even though the web is almost as large as the Little Rock web. We have used the version of the Ythan web without parasites (Huxham *et al.*, 1996). Many of the top species become intermediate species when parasites are included, however the parasites themselves form a new top level which are not themselves preyed on. The number of top species is still very large in the Ythan web when parasites are included, hence this cannot account for the large difference between the Ythan and Little Rock webs.

When comparing the model results with the real data we view R as a parameter which could change between ecosystems in different places, whereas δ is a fundamental property of the competition interactions between species which should presumably not vary much between locations. Therefore we would wish to choose a value of δ which best fits a range of real data. The model results for $\delta = 0.05$ have high I , low B and very low T , which seems to be characteristic of the well-characterised real webs. All the real webs have a maximum level of 3 or 4. We obtain this number of levels in the model if $R = 10^3$ or 10^4 . The very high value of 7 for the maximum level in the runs with $R = 10^{10}$ does not appear to be consistent with the data, however it should be noted that all the model data is for $\lambda = 0.1$. If we reduce λ then the number of levels in the model will reduce, and we will require larger values of R in order to obtain three or four trophic levels. Low values of δ seem to be preferred for matching the values of B and I in the real data, however in this case the model predicts less than two links per species. The number of links per species in the real webs tend to be higher (as much as 11 in Little Rock). It is possible to get high numbers of links per species in the model by increasing δ (see e.g. $R = 10^6$, $\delta = 0.2$). However in this case we get much higher values of B than are seen in real webs. We conclude that the properties of the model webs are generally of similar orders of magnitude to those of the real webs, but that we have not found a single set of parameters R , λ and δ which accurately match all the properties of the real data simultaneously. We have certainly not done an exhaustive search of parameter space yet for

the model: we did not change λ at all. So it is possible that the agreement between the model and the data could be improved. Also, there are many refinements which we could make to the model, such as changing the rules by which we distribute resources between species, or changing the way the scores are calculated. Consideration of all these possibilities would be justified if there were an excellent set of data on real food web structure against which to test the models. However, there are still problems with even the best experimental data, and in view of this, it does not seem worthwhile worrying too much about the precise values of the food web statistics from the model. The model may in fact make some useful predictions which are difficult to test in real life. For example, we noted above that if δ is increased, so as to give high numbers of links per species, the value of B in the model appeared too high. Real webs tend to apply a much higher degree of aggregation to low level species than high level ones, so maybe the values of B in the real webs should really be higher than they are.

Over the range of δ of order $1/L$ considered in the tables, I is a decreasing function of δ and B is an increasing function. However, as a limiting case, we also carried out a simulation with $R = 100$ and $\delta = 25$. With this very large δ there were almost no extinctions due to competition. After 500 speciations there were approximately 90 different species which had average population sizes just greater than 1. Extinctions occurred only due to the rule that a minimum population size of 1 is necessary for viability. In this run we found that $I = 99\%$ and $B = 1\%$. This implies that there is a reversal of the trend in B and I for very large values of δ . We do not think that this very large δ value is a reasonable one for comparison with real webs, however this simulation does illustrate a limiting case of our model: in the absence of competition very large highly connected webs arise which are almost entirely intermediate species.

We wish to comment further on the meaning of trophic levels in the Webworld model. The simple picture of ecosystems which is often envisaged supposes that organisms can be grouped uniquely into trophic levels representing plants, herbivores, carnivores, secondary carnivores etc. This picture supposes that each level only interacts with the levels immediately above and below it. Although it was argued from some early food web data that omnivores (i.e. species feeding on more than one trophic level) were rare (Cohen *et al.*, 1990), it has since been argued that omnivory in well-characterized webs is frequent, that organisms apparently assigned to the same level are far from equivalent in their

dynamics and interactions, and hence that the concept of trophic levels is of little use (Polis & Strong, 1996). We found that omnivory is frequent in the model, and that it is not possible to assign species to levels such that interactions are only with the levels immediately above and below. However, we maintain that the idea of level which we use here is a useful one, since it is a measure of food chain length: the level of a species is the length of the shortest chain from the external resources to the species (including the link to the external node). This is a different definition of chain length and trophic level from that used in many other studies. For example, Martinez (1991) calculates the average length of all food chains leading to each species in the Little Rock web using two algorithms which differ in the way they deal with loops (it is necessary to exclude loops in some way or else chain length is infinite). He then defines the trophic level as the closest integer to the average chain length + 1. Since there are huge numbers of chains in large webs, algorithms which involve averaging all possible chains are slow. Martinez was limited by computer time to looking at aggregated versions of his web using his algorithm. In analysing the model data we have thousands of webs, each with hundreds of species, rather than just one real web, therefore we must use a rapid algorithm for practical reasons. The maximum level is 3 in the Little Rock trophic species web using our definition, whereas using Martinez's algorithm the maximum level is 9. It is clear that the Little Rock web is extremely complex and that long chains occur frequently, however, this is a statement about the combinatorial properties of highly connected graphs, and may not be significant from an ecological point of view. Our algorithm shows that there is no species in the Little Rock web which does not have a chain of length 3 or shorter. We believe that shorter chains are much more important energetically than longer ones. This is certainly true in the model webs, since there is an efficiency factor of $\lambda = 0.1$ associated with every additional link. It is probably true also in real webs, and could be tested using data which measures energy flow along each link. Therefore we believe that our algorithm for chain length and trophic levels is justified ecologically as well as on grounds of practicality.

Since real webs are likely to be incomplete due to observational difficulties, Goldwasser & Roughgarden (1997) investigated the effect of incompleteness of data by deliberately omitting links from the original St. Martin island web. They have shown that most web properties vary strongly as links are removed. We carried out the following procedure in order to investigate the effect that incompleteness of data

TABLE 4
The effect on the web properties of removing a fraction of the links at random

	All links	$\delta = 0.05, R = 10^6$		
		10% removed	30% removed	50% removed
No. species	150	150	140	130
No. links	240	220	170	125
Links per species	1.6	1.5	1.2	1.0
Average level	2.5	2.3	2.3	2.1
Max level	5.2	4.5	4.2	4.0
<i>B</i> species (%)	10	16	24	30
<i>I</i> species (%)	90	79	57	43
<i>T</i> species (%)	0	5	19	25
<i>TB</i> links (%)	0	2	8	16
<i>IB</i> links (%)	22	25	29	31
<i>II</i> links (%)	78	68	47	31
<i>TI</i> links (%)	0	5	15	21
Prey/predators	1.1	1.2	1.1	1.0

would have on the food webs in our model. Beginning with a set of webs generated from the model with $R = 10^6$ and $\delta = 0.05$, we deleted a certain proportion of links randomly. Deleted links represent real predator-prey interactions which were not observed due to poor experimental resolution. After removal of the links, if there were any species which were left unconnected to the rest of the web these species were also removed from the web. The deletion of the links

was carried out on the original species web, and the trophic species web for the new set of original species interactions was then found. As with all the tables in this article, figures refer to the trophic species webs. Table 4 shows the results of this process. T increases rapidly as links are removed, I decreases rapidly, and B increases more slowly. There are consequent changes in the proportions of TB , IB , II and TI links. The number of links per species, the average level and

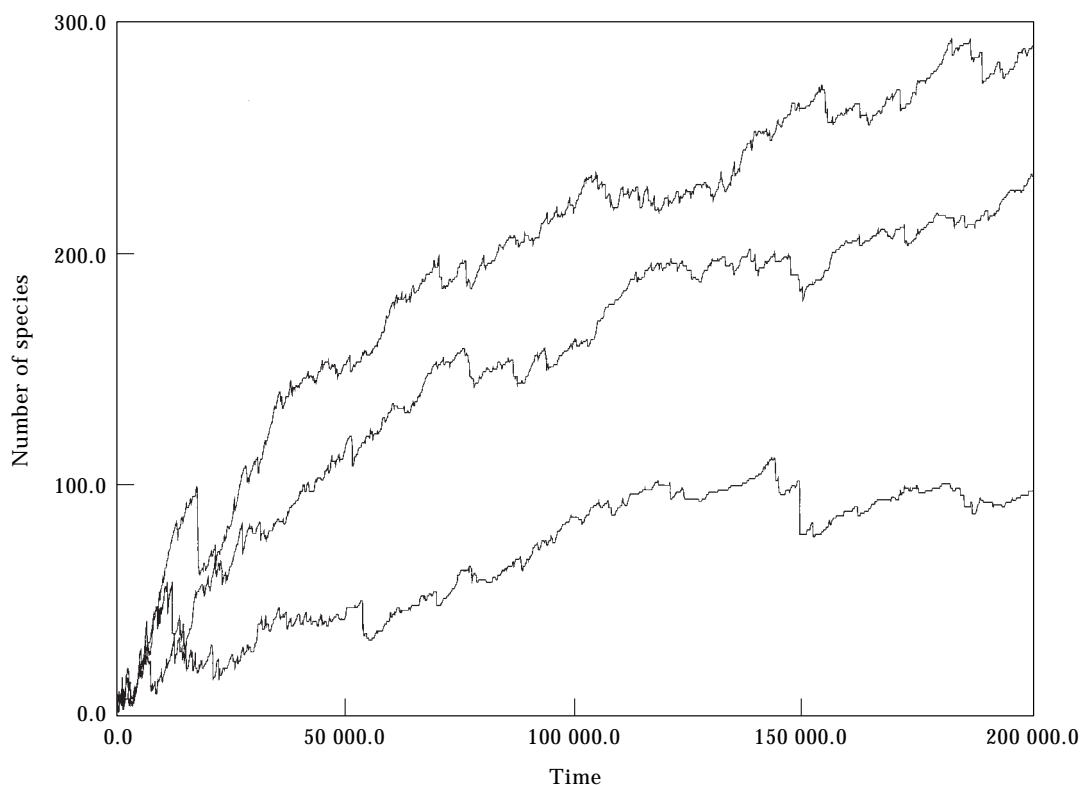


FIG. 3. The number of species in the web is shown as a function of time for three different runs of the Webworld model with the same parameters $R = 10^6$, $\delta = 0.05$ and $\lambda = 0.1$.

the maximum level all decrease as links are removed. All these trends are the same as those observed when links are removed from the St. Martin web (Goldwasser & Roughgarden, 1997). The proportions of *B*, *I* and *T* species after removal of a substantial fraction of links are similar to those in the EcoWeb data, whereas before removal of the links they are close to the values of the more highly resolved webs like Little Rock. This supports the hypothesis that many of the webs in the EcoWeb collection suffer substantially from incompleteness. Real webs are also influenced by the degree to which species are aggregated into clusters. Martinez (1991) has shown that aggregation of species within the original Little Rock web results in smaller webs with statistics which are closer to those of the EcoWeb compilation than the full web, which suggests that the smaller webs are also influenced significantly by aggregation. We have not yet considered aggregation effects in our model webs, but we expect that the changes will be similar to those observed with the Little Rock web.

6. Results—Evolutionary Dynamics

Figure 3 shows the number of species as a function of evolutionary time for three runs of the simulation with the same parameter values. The numbers of species differ significantly between different random assignments of the m_{ij} matrix. In each case the number of species tends to increase fairly rapidly at first, but after a certain time the system tends to a steady state with fairly constant species number. Extinction avalanches are visible as sudden drops in the species number. The figure shows the number of original species, but the curves for the number of trophic species follow the same pattern with slightly smaller numbers, and show extinction events occurring in the same places. In previous models of macroevolution, attention has focused on the dynamics of extinction events when the model is in a stable state. The avalanche size distribution has been measured and has been observed to have a power law shape for some of these models (Bak & Sneppen, 1993; Solé & Bascompte, 1996). In the Webworld model we may define the avalanche size at a given timestep as the number of species which become extinct due to the addition of one new species (if the new species adds stably to the web this is an avalanche of size zero). We intend to discuss the sizes of extinction events in our model in more detail in a subsequent paper. However, our initial results suggest that the size of avalanches tends to decrease with time in the Webworld model. Once the system has reached a steady state, fluctuations in species number tend to be small, whilst

in the initial stages of the simulation large avalanches can occur. Initially there are relatively few species, and these are relatively poorly adapted. If we consider only level 1 species initially, then we expect that the scores $S_{n,0}$ of species will gradually increase as better adapted primary producers evolve. In the early stages of the simulation there is a reasonable chance that a new species will be substantially better than existing ones, and an extinction avalanche may occur when the new species evolves. As time goes on it will become increasingly more difficult to evolve species which are better adapted, and when improvements do occur, scores are likely to increase by smaller amounts. Hence avalanches are likely to decrease in size and in frequency as time goes on. Since the level 1 species tend to change less rapidly as they become better adapted it follows that conditions for higher level species become more stable. Hence level 2 species can become increasingly better predators of the existing level 1 species, and so on throughout the web. Therefore evolutionary changes on all levels of the web are likely to slow down in the same way.

Self-organized models of evolution are designed in such a way that the stationary state is critical and has interesting dynamics. In these models the avalanche size distribution and the species lifetime distribution are power laws. We believe that after a very long time our model would reach an absolutely stationary state where it would be impossible for any new species to evolve. None of our simulations ever reached this point entirely, although the probability that a new species survives on the first timestep in which it evolved became very small toward the end of the runs. The time to reach this point of evolutionary “stagnation” should depend on the total number of possible species in the model. The number of combinations of 10 features out of 500 possible ones is approximately 2.5×10^{20} , which is large but still finite. We intend to investigate the effect of changing the total number of possible features K in future work.

The initial period which shows large avalanches is an interesting feature of our model, and we believe it may tell us something about the real world. Is the real world in a stationary state? Are the properties of ecosystems today statistically equivalent to those in earlier geological periods? We do not know how to answer these questions, but we believe they are important questions to ask. It is clear that the model has a finite number of possible species, but it is not clear whether this is true for the real world. The Earth is obviously much more complex than any computer model, however it is still finite in terms of the available space, energy and raw materials. If the

Earth were unchanging, it does not seem unreasonable to suppose that real ecosystems would gradually perfect themselves to the external conditions, and that the consequent rate of evolutionary change would decrease, just as in the model. The origin of life probably occurred about $3.5\text{--}3.8 \times 10^9$ years ago. It is not clear whether this is a long or a short period measured on the time-scale of what is evolutionarily possible. Measures of diversity in the fossil record (Sepkoski, 1993) show a general increasing trend in species numbers between the Cambrian and the present, despite several very large extinction events, and there is no real indication of any levelling off in diversity.

Of course, the conditions on Earth are not fixed: climatic change occurs on a wide range of time-scales. If we view the non-living world as continually changing, then the living world must also continually change, and never has the opportunity to reach evolutionary stagnation. There is also the possibility that the external conditions might change by sudden rare cataclysmic events, such as meteorite strikes, rather than by smooth gradual change. Such a large-scale external event might cause a large-scale extinction, and might change conditions sufficiently that the evolutionary clock would effectively be set back to an early stage where ecosystems were poorly adapted to the environment. This would enable a new burst of evolution, with many novel species arising. This suggests a picture of the real world where there is a considerable rate of inherent evolutionary change and considerable fluctuation in species numbers, and where external events causing major changes happen sufficiently often to prevent evolutionary stagnation from occurring. Stenseth & Maynard Smith (1984) have also distinguished two possibilities for the long term behaviour of evolving ecosystems—either “red queen” behaviour (in which evolution is continuous even if the external environment is constant) or stasis (in which continued evolution depends on external changes in the environment). The NKC model (Kauffman, 1993) also can show either stasis or a chaotic phase of continued evolution, depending on the parameters. The data in the fossil record may some-day be complete enough to give some answers to these questions. In the meantime there are still many useful issues which can be addressed by studying models such as ours.

7. Conclusions

The Webworld model describes the interactions of coevolving species. The model makes predictions concerning the structure of food webs which can be

compared with data on real webs. There are only three parameters in the model— R , λ , and δ —hence, the number of testable predictions is much larger than the number of parameters. The measured quantities such as the number of links per species, the number of trophic levels, and the proportions of top, basal and intermediate species, 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 web data as closely as possible. However, given the uncertainties in most of the present food web data, we have not tried to match these data too closely. Instead we have tried to point out the major qualitative trends in food web properties which occur when the parameters are changed. These trends make sense from an ecological point of view. We would like to contrast our model with the cascade model of food web structure (Cohen, 1990; Cohen *et al.*, 1990). Even though the cascade model successfully describes many food web properties, it is basically just a set of probabilistic rules for assigning links between nodes in a graph. The justification of these rules comes entirely from comparison of model webs with real data. In contrast, the parameters in our model have an ecological meaning: the available external resources, the fraction of resources transferred from prey to predator, and the strength of competition are all meaningful quantities in real webs.

An important question in food web theory which has had considerable attention recently is the issue of food web assembly (Luh & Pimm, 1993; Morton & Law, 1997). In assembly models species are invading the ecological community from an external species pool and are therefore unrelated to existing species, whereas in the Webworld model new species are arising by evolution and are therefore similar to the species from which they evolve. We intend to develop the model to compare properties of webs generated by invasion and by evolution. One observation in assembly models is that the probability of successful invasion of a community tends to decrease with time. This seems to have a parallel in Webworld, where the survival probability of a newly generated species tends to decrease with time.

This work was motivated in part by the wish to explore recent claims that models of evolution may have a tendency to “self-organise” into a critical non-equilibrium state which has avalanches on all scales. We approached the problem by trying to design a realistic model for coevolution in which the evolutionary dynamics can be studied, rather than by deliberately designing a very simple model with interesting dynamics, but which is more difficult to

relate to real evolutionary and ecological phenomena. This article has concentrated on the ecological properties of the food webs, and we are currently investigating the evolutionary properties of Webworld in more detail.

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