

Models of food web evolution

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While it is often possible to model the nature of the dynamics with which constituents of a fixed network interact with each other, it is frequently much more difficult to specify the range and nature of the topologies and interaction strengths of possible networks. Here we argue, in the context of food webs, that it is necessary to go beyond simply studying dynamics on a network with a fixed number of constituents and fixed interaction strengths, and to couple this dynamics to processes connected with the construction of the network. This could include a dynamics for the introduction and deletion of constituents and for the changing of interaction strengths depending on the states of the local constituents. In the case of food webs, where the constituents are species and the interactions are predator-prey relationships, this involves going beyond conventional population dynamics to include mechanisms which allow for the introduction and extinction of species and changing of feeding preferences. We review a model of food web evolution which we have been involved in developing over the last few years which encapsulates

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this philosophy. We also discuss a variety of other models which have been put forward.

1 INTRODUCTION

The complexity and seemingly unlimited variation found in ecological communities prove endlessly fascinating. It is a daunting task to try and establish any general principles which govern the structure of such systems. One aspect of multispecies communities which may have universal attributes is the network of predator-prey links: the community food web. Empirical work carried out over the last decade or two indicates that a range of measured quantities which characterize the web display measurable trends [15]. Food web data is notoriously difficult to collect, but it is improving all the time, as is our ability to identify important characteristics which are common to some food webs and those which are specific to a particular web.

If there are similarities between food webs in such diverse communities (for instance, marine, desert or lake communities) then these must be due to rather fundamental aspects of the community structure; perhaps general principles which govern predator-prey relationships, flexibility in the choice of prey, body size of predators versus prey, and so on. If this is so, then it follows that we should be able to reproduce the universal aspects of the food web data by building models which incorporate these attributes, but neglect less essential details. Of course, the difficulty lies in determining what these attributes are. However, the number of possibilities is not so large as to prohibit a systematic investigation. In this way it should be possible to identify the important ingredients which dictate basic food web structure.

To pursue this program requires us to “construct” food webs based on various general principles, and compare the results with empirical webs. One way forward is to construct typical networks which represent food webs by assigning links between species according to a rule which captures some structural attributes of real webs. A large number of model webs are generated using this algorithm, and average properties of these webs compared to empirical webs. The best known example which exemplifies this approach is the niche model [38]. We will not be discussing models of this type here: we believe that a more realistic web structure will be obtained by allowing the web to evolve. In this approach the web will again be constructed according to reasonable rules, but now these rules will govern the dynamics of web evolution. This has an advantage, since there will be properties of the webs which are important, but which are not known *a priori*, and which only emerge when the webs are allowed to evolve. An example of such a property is the existence of many weak links in evolved webs [16, 34] — a feature that also seems to be present in real webs [29, 8]. This is a property of webs which was not suspected until relatively recently. There may be many other attributes which are currently unknown, and so cannot be included in the

construction of static webs, but which are instead emergent properties and so will be present in dynamical constructed webs.

We will also not be concerned with “assembly models”, in which new species are introduced into the system from a “species pool” simulating the process of immigration [11, 12, 25, 31, 27, 26]. However, the species pool does not consist of species which have co-evolved. Instead they typically consist of species which are labeled “plants”, “herbivores”, “carnivores”. and so on, and so have already been assigned a position in the web to some extent. The interaction coefficients are assigned according to some plausible rule, perhaps involving body size or allowing for a mix of specialists and generalists. The same objections as were raised in the discussion of static models above, can be raised here: much of the structure and properties of the system are put in by hand instead of being allowed to emerge dynamically.

This article is therefore devoted to models of food webs where the network is created purely dynamically. This involves both the introduction and elimination of species and/or individuals and the determination of the existence and strengths of predator-prey links between species. The introduction of new species/individuals can be by immigration from another geographical region or by speciation of existing species in the community. Extinction would naturally occur when the number of individuals fell to zero. A model incorporating all of these aspects of web dynamics has not yet been constructed. It would presumably be an individual based model (IBM) with speciation due to changes in characteristics of an individual and immigration due to the arrival of one or more individuals from another location. The model would have to operate over a large range of time scales from the very short time intervals on which link strengths might change through timescales on which immigration might occur and to the very long evolutionary time scales. Such a model would take up a formidable amount of computing power to gain results.

To add to the computational problem of analyzing such a complicated model, there is also the problem of identifying the origin of any novel behavior that would be observed. If instead successive models of increasing complexity are built, it is easier to understand the predictions of model since one can keep track of them as they appear in successive versions. Two obvious simplifications to the full model described above that we can make is to first study the non-spatial version of the model and also to look at a population-level model, rather than an IBM. This would mean that new species would not be introduced by immigration, and that since there would now not be discrete individuals an artificial cut-off below which species are assumed extinct N^{\min} (of order one) would have to be introduced. For a similar reason speciation would consist of the reduction of the number of individuals of one species by N^{child} (also of order one), and the creation of a new species containing N^{child} individuals.

A model of this kind would still be quite complicated, because of the requirement that it spans such a wide range of time scales. One of the simplest ways to deal with this is to try to separate out the most important mechanisms

into processes occurring on different time scales. On short time scales we expect that the number of species will be fixed and so the dynamics will essentially be that of conventional population dynamics. Of course, there will be some crucial differences to the majority of population dynamics found in the literature, for instance, there will be a large number of species, not just two or three, and they will have a complex set of predator-prey relationships among each other. The reason why the population dynamics of a large number of species have been little studied in the past is because there would be literally hundreds of parameters in the model (the interaction strengths) which would make it impossible to draw any conclusions. In the approach we are advocating here, the interaction strengths between the species are determined by dynamics at different scales: the existence of links (that is, if two species are linked in a predator-prey relationship) by the dynamics of web formation which occurs at a longer time scale, and the strength of the link by this, and also by an adaptive dynamics in which individuals vary the amount of effort that they put into preying on species depending on the amount of resources they get out. In the absence of a dynamics for the existence and strengths of links there is no way to predict interaction strengths other than through some kind of plausible rules which is the approach that we have already argued against in the case of static models.

From these comments it is clear that the choice of dynamics on time scales different to the ecological time scale — the one on which population dynamics operates — will have a significant impact on the result of calculations using population dynamics. The converse is also true, so there will be a considerable amount of feedback between these various types of dynamics. While population dynamics is a relatively well studied subject (albeit with only a small number of species present) [28, 32, 36], the other types of dynamics we have mentioned have hardly been studied at all. This is largely because population dynamics can be simply formulated in terms of coupled ordinary differential equations for the population sizes of the species in the system, the other types of dynamics we have alluded to will involve a variable number of species (due to the speciation and extinction dynamics) and a link strength which will vary adaptively to take into account other changes in the system (adaptive foraging). Both these are not easy, if not impossible, to deal with analytically, and moreover there is no obvious choice for the form of the dynamics. Therefore they will have to be introduced in the context of numerical simulations and modeling choices will have to be made.

Although we have tried to provide a discussion of the issues surrounding the modeling of food webs in this introductory section, we have naturally concentrated on issues which are relevant to the approach to modeling food webs that we are familiar with. In section 2 we will describe this approach in more detail and in particular describe the model which we have been investigating for the last few years [14, 33, 30, 16, 34, 35]. In section 3, we explore the predictions of our model. Using this model as a basis, we will discuss other evolutionary models and their predictions in section 4. We will conclude in section 5 with a summary and a look to the future.

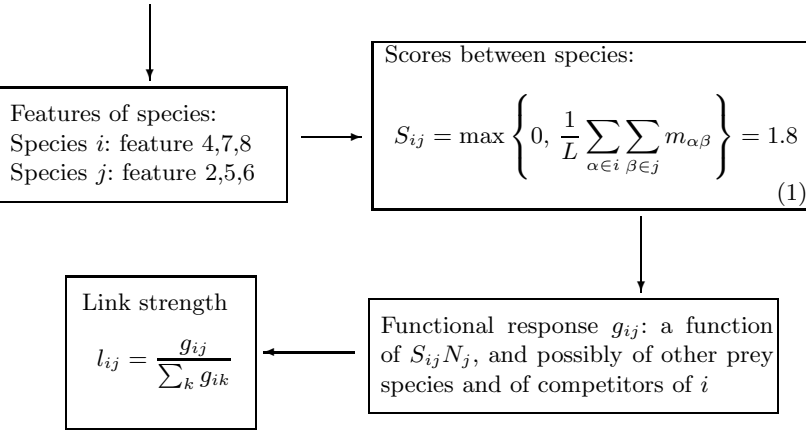
2 A MODEL OF EVOLUTIONARY DYNAMICS

We have highlighted some of the desirable properties that a model of the evolution of food webs should have in section 1. Here we will make some choices which lead to a particular model, and attempt to justify them.

One of the novel aspects of modeling this system is that the space of variables which describe the system (the number of species in the community, for example) keeps changing due to speciations and extinctions. The space of “possible species” is essentially infinite dimensional, but at any given time we are only exploring a small part of it. Which small part we are exploring keeps changing with time, however. In addition we need to characterize species in some way, that allows us to produce “child species” which are a “mutation” of a “parent species”. Therefore, the child species should be “close” to the parent species in some way. One way to deal with both these problems is to characterize species by traits or *features* which are behavioral or phenotypical characteristics of that particular species [9, 14]. This is a macroevolutionary description — there is no attempt at a genetic description, even though ultimately this is supposed to be the origin of the change. We suppose that every species is characterized by L features out of a possible set of K possible features. We make no attempt to identify these features with any real attributes of individuals belonging to any species (being warm blooded, nocturnal,...); they are just taken to be integers $1, 2, \dots, K$. Note that they could equally well taken to be sets of intervals on the real axis of a multidimensional space, or some other set of distinct objects. One requirement is that there should be (effectively) an infinite number of possible species. If we take $L = 10$ and $K = 500$, as we often do in our simulations, then since $\binom{500}{10} \sim 10^{20}$, this is the case. The representation of species in terms of features allows us to define two important quantities which describe the relationship between any two species i and j . The first one of these is the *overlap* q_{ij} , which is a measure of the similarity of the two species and is defined as the number of features that are shared by species i and species j , divided by the number of features, L . The second quantity is the score of species i against species j , S_{ij} , which indicates how well species i is adapted to prey on j . We would expect that the score should depend on the quality of the features of one of the species against the other, and therefore we first need to introduce a more primitive notion of the score between constitutive features. These scores are more fundamental and will not change with time; they will be fixed at the start of a simulation run. The simplest assumption is to define a score matrix for feature α against feature β , denoted by $m_{\alpha\beta}$, as a $K \times K$ antisymmetric matrix of random numbers. The numbers are random, since we have no other information with which to choose them. we usually take them follow a Gaussian distribution with zero mean and unit variance, but clearly other choices are possible. A preliminary investigation of the consequences of making other choices for the structure of the matrix $m_{\alpha\beta}$ suggests that the exact form is not crucial for the eventual nature of the resulting food web. In box 1, we illustrate how the scores between species are obtained as

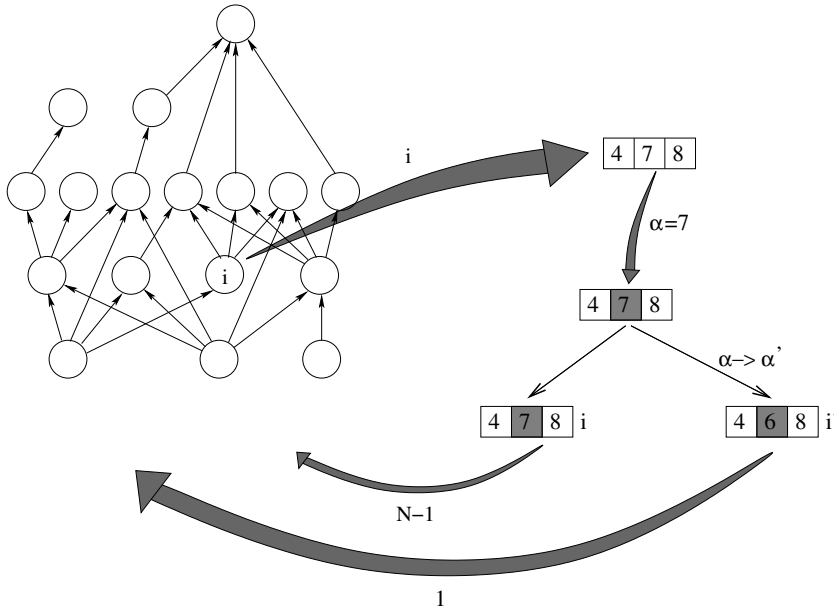
Box 1: From features to link strength

Score matrix $m_{\alpha\beta}$ for features:										
		f	e	a	t	u	r	e		α
		1	2	3	4	5	6	7	8	9
f	1	0	2.5	-0.2	0.1	1.7	-1.2	-1.2	-0.6	-0.6
e	2	-2.5	0	1.6	0.9	0.9	1.0	-0.4	0.1	-0.1
a	3	0.2	-1.6	0	0.7	0.3	-0.2	-0.7	-0.1	1.3
t	4	-0.1	-0.9	-0.7	0	-1.4	-1.0	-1.1	1.8	-0.4
u	5	-1.7	-0.9	-0.3	1.4	0	0.9	-0.2	-2.2	-1.8
r	6	1.2	-1.0	0.2	1.0	-0.9	0	-1.0	2.2	0.5
e	7	1.2	0.4	0.7	1.1	0.2	1.0	0	0.6	-0.6
	8	0.6	-0.1	0.1	-1.8	2.2	-2.2	-0.6	0	0.5
β	9	0.6	0.1	-1.3	0.4	1.8	-0.5	0.6	-0.5	0



First, the scores between all pairs of features are assigned. Then, for each species a set of features is chosen. The scores between species result from the sum of the scores between their features. The scores S_{ij} enter the functional response, which will be discussed further below, together with the population sizes. From the functional response the link strength is obtained, which is the proportion of prey j in predator i 's diet.

the sum of the scores of each feature of i against each feature of j . Note that if i is adapted to be a prey of j , the definition (1) returns a value zero; the strength of the interaction between i and j can be determined from S_{ji} , which is this case is guaranteed to be positive. Below, we will see how the scores affect the population dynamics and the link strength.

Box 2: The speciation process

Species i is picked at random to speciate. A further random choice picks out feature α belonging to species i to change into feature α' to create species i' . If there were N_i individuals of species i before speciation, $N_i - 1$ are put back into the system after speciation, along with 1 individual of species i' .

A speciation event consists of changing one of the features at random to another random feature. An example should make this clear. Suppose that $K = 9$ and $L = 3$ (not realistic choices, but conveniently small for illustrative purposes), then species i having a population of $N_i(t)$ individuals at time t might be characterized by the features $\{4, 7, 8\}$ and species j having a population $N_j(t)$ might be characterized by the features $\{2, 5, 6\}$. A speciation might then take place and result in an individual belonging to species i creating a new species, i' , which would have the features $\{4, 6, 8\}$. The child species i' differs by a single feature from the parent species i . Clearly the order of features is not important, there should not be repeated features in a particular species, and if a speciation results in a species already present in the system, it should not be designated as a new species. After this change, the population of species i will be $N_i - 1$, of species j it will still be N_j and of species i' it will be 1. The overlap between parent and child species is $q_{ii'} = (L - 1)/L$. The speciation dynamics is illustrated in box 2.

The extinction dynamics is very simple: whenever the population level falls below a certain number N^{\min} , then eliminate the species from the system. We have frequently taken $N^{\min} = 1$ in simulations. In addition, the environment (from which basal species extract resources) is denoted as species 0. It has the same structure as other features, except that it is not subject to speciation: once it is chosen at the beginning of a simulation it remains unchanged. These rules specify the web dynamics.

The other kind of dynamics which is novel occurs on much shorter time scales: the change in the link strengths between a predator and its prey which takes place because the predator is trying to optimize its intake of resources against a background of changes in, for instance, population sizes. An example would be a predator which had two prey which were very similar, but one of which had just suffered a decrease in population size. All else being equal, the predator would presumably now switch to putting more effort into preying on the prey which had increased in population. This is adaptive foraging: the continuous adaptation of foraging strategy to try to optimize the gain in resources for a given amount of effort. To formulate this mathematically, let us introduce two quantities which are central to the model. The first, is the fraction of effort (or available searching time) that species i puts into preying on species j . We denote this by $f_{ij}(t)$, and obviously these efforts must satisfy $\sum_j f_{ij}(t) = 1$ for all i . The second quantity is the functional response which plays a central role in theories of population dynamics. It is the rate at which one individual of species i consumes individuals of species j and is denoted by $g_{ij}(t)$. The choice of efforts of any species i such that the gain per unit effort g_{ij}/f_{ij} is equal for all prey j can be shown to be an evolutionarily stable strategy (ESS) [14], that is, if a population has efforts chosen in this way, there is no other choice of efforts which can do better. Using the normalization condition for the f_{ij} this condition may be written as

$$f_{ij}(t) = \frac{g_{ij}(t)}{\sum_k g_{ik}(t)}. \quad (2)$$

Since in any theory of population dynamics the functional response would be specified, this equation determines the efforts, and so the dynamics of adaptive foraging. As the efforts are identical to the proportion of prey j in predator i 's diet, they are also useful measure of link strength.

Having specified these novel types of dynamics, all that remains is to define what we have called “conventional” population dynamics. The problem, however, is that while the population dynamics of one or two species has been studied for over a century, there have been few studies of multispecies communities, and even fewer where there are large number of species each of which will typically have several predators and prey the identity of which will vary with time. We therefore had also to develop this part of the dynamics. We chose to do this by

beginning with the general balance equation

$$\begin{aligned} \frac{dN_i(t)}{dt} = & [\text{Rate of increase of new individuals of species } i \text{ due to predation}] \\ & - [\text{Rate of decrease of individuals of species } i \text{ due to predation}] \\ & - [\text{Death rate for species } i \text{ in the absence of other species}] . \end{aligned} \quad (3)$$

We will assume that the resources invested in a particular species is proportional to the number of individuals of that species, and will choose the constant of proportionality to be 1. Since $g_{ij}(t)$ is the rate at which one individual of species i consumes individuals of species j , $N_i(t)g_{ij}(t)$ is the rate at which species i as a whole consumes individuals of species j . Summing over all the prey j of species i gives the total rate of gain of resources for species i . However only a fraction, λ , will be used to create new individuals of species i . Thus the first term on the right-hand side of eq. (3) is $\lambda \sum_j N_i(t)g_{ij}(t)$. By a similar argument, the second term on the right-hand side of (3) is $\sum_j N_j(t)g_{ji}(t)$, where now the sum on j is over all *predators* of i . Finally, the third term is $d_i N_i(t)$, where d_i is a (constant) death rate. For simplicity we will take all the death rates equal to 1. Clearly it is possible to be more sophisticated about the choice of death rates, as well as about the ecological efficiency, λ , but for the present at least we will content ourselves with these simple choices.

The population dynamics is now completely specified if the functional response $g_{ij}(t)$ is given. If there is no predator-prey relationship between species i and j , g_{ij} is zero, so it also defines the network at a given time. The form that $g_{ij}(t)$ takes for a given network is quite complicated, since it needs to reflect several biological mechanisms. The functional response depends on the scores S_{ij} . A simple linear functional response would take the form, $g_{ij}(t) = S_{ij}N_j(t)$, however, many choices are possible, most of which build in a greater degree of biological realism. An analysis of some of these choices [16] reveals that the ratio-dependent functional response has many advantages ranging from purely theoretical ones, such as satisfying consistency requirements [14], to empirical ones, such as giving rise to evolved webs which do not collapse to networks with a single level [16]. In box 3 we build the functional response up gradually by constructing a form for $g_{ij}(t)$ in three simple situations. These are: a predator-prey pair and a triplet of species consisting of one predator with two prey and two predators with the same prey.

This describes the essentials of the model. In practice, a simulation run begins with a randomly generated species 0 (the environment) and species 1 which evolves according to the rules described in the section. There are, inevitably, a few technical points which are concerned with the running of the simulation, but which are not important to the overall understanding of the model. We have glossed over these here; anyone interested in them should seek out the original paper on the model [14]. The result of a typical run, with the model parameters in an appropriate range, is shown in figure 1. It seems to have many of the broad

Box 3: The functional response

In the case of a system with a single predator with a single prey the ratio-dependent functional response is taken to be (reference)

$$g_{ij}(t) = \frac{S_{ij}N_j(t)}{bN_j(t) + S_{ij}N_i(t)}. \quad (4)$$

The constant b controls the effectiveness of predation, and is one of the few parameters of the model (another is λ , the ecological efficiency).

The generalization of (4) to a system of three species — two prey consumed by one predator — might be thought straightforward: if i is the predator and j and j' are the prey, $g_{ij'}$ could be simply obtained by replacing j by j' in (4). However, this does not satisfy the consistency condition that if the prey are equivalent from the predators point of view (i.e., $S_{ij} = S_{ij'}$), then the dynamics of the predator population should be identical to the case where there is just one population of size $N_j + N_{j'}$. This condition can be satisfied if the efforts $f_{ij}(t)$ and $f_{ij'}(t)$ are used in constructing the functional response. It is straightforward to check that the choices

$$g_{ij}(t) = \frac{S_{ij}f_{ij}(t)N_j(t)}{bN_j(t) + S_{ij}f_{ij}(t)N_i(t)}, \quad g_{ij'}(t) = \frac{S_{ij'}f_{ij'}(t)N_{j'}(t)}{bN_{j'}(t) + S_{ij'}f_{ij'}(t)N_i(t)}, \quad (5)$$

do satisfy this consistency requirement. Another system which brings out an important aspect of the structure of the functional response, is the case of two predators, i and k , having a single shared prey, j . We would then expect the functional responses are reduced by the competition from the other predator, that is,

$$g_{ij}(t) = \frac{S_{ij}N_j(t)}{bN_j(t) + S_{ij}N_i(t) + \alpha S_{kj}N_k(t)}, \quad g_{kj}(t) = \frac{S_{kj}N_j(t)}{bN_j(t) + S_{kj}N_i(t) + \alpha S_{ij}N_i(t)}. \quad (6)$$

Here α is a constant which reflects the degree of competition between species i and species j . Typically, this will less the fewer features i and k have in common with each other.

Such considerations, applied to very simple web structures, suggest the following form for the functional response between any two species i and j belonging to an arbitrary web:

$$g_{ij}(t) = \frac{S_{ij}f_{ij}(t)N_j(t)}{bN_j(t) + \sum_k \alpha_{ki} S_{kj}f_{kj}(t)N_k(t)}, \quad (7)$$

where

$$\alpha_{ki} = c + (1 - c)q_{ki} \quad (0 \leq c \leq 1). \quad (8)$$

Here k labels all predators of j , including i . Notice that if the species are identical, $k = i$, $\alpha_{ii} = c + (1 - c) = 1$ and if they have no features in common $\alpha_{ki} = c$. The competition c is another one of the parameters of the model.

characteristics of real webs, and as we will discuss in section 3, the average values

of quantities of interest over an ensemble of these webs is in good agreement with food web data.

In section 4, we will review other evolutionary approaches to food web modeling and compare these with the model which we have just described.

3 COMPARISON WITH DATA

Although we have been advocating a program of modeling food web evolution, it is far from clear that a first attempt at formulating a model designed for this purpose would be successful. Even if a stable web were formed, it might be clearly incorrect: having only basal species or far too many levels, for instance. So the first test for any model webs is not strictly a comparison with data, but simply that the webs constructed using the model are “reasonable”, in the sense that they look like real food webs. Once this has been achieved, more stringent tests can be applied. These are carried out by performing a large number of runs with the same parameter values, and averaging measured characteristic web properties over all the webs which have been generated. Finally, if it appears that the model is producing realistic webs, it can begin to be used to study other aspects of food webs. These may act as other tests for the model, or they may be “numerical experiments”, the analogs of which would be difficult or even impossible to carry out in the field.

We now present some results obtained with the model discussed in section 2. As we have mentioned already, it turns out that a web can be grown only for certain choices of the functional response $g_{ij}(t)$. So, for example, if the simplest type of population dynamics, Lotka-Volterra dynamics was chosen, a typical food web which results (after enough time has been allowed to elapse so that a stationary structure can form) is shown in figure 2 [16]. All species feed on the internal resources and on the other species as well. For short, transient, periods the web may have species on a second level, but it soon collapses back down to a web with a single level. Moreover, simulations which started from a complex web with several trophic layers which was stable under the population dynamics, soon collapse under the evolutionary dynamics. Such a collapse also occurred with other types of functional responses, such as the Holling [19, 18] or Beddington [7] forms. Only with ratio-dependent functional response [4, 17, 5, 2, 1] or with the introduction of artificial mechanisms which allow only the best predators to feed on a given prey [9], were realistic food web structures found. It appears that the ability of predators to concentrate on the prey that they are best suited to exploit, rather than on all possible prey, is essential for the production of realistic food web structures.

If such a dynamics is chosen, then evolved webs such as shown in figure 1 seem to resemble real webs. It is therefore now possible to go on to the second stage of comparison with empirical webs and carry out a more detailed assessment of web properties. Table 1 shows such a comparison for a choice of basic parameters

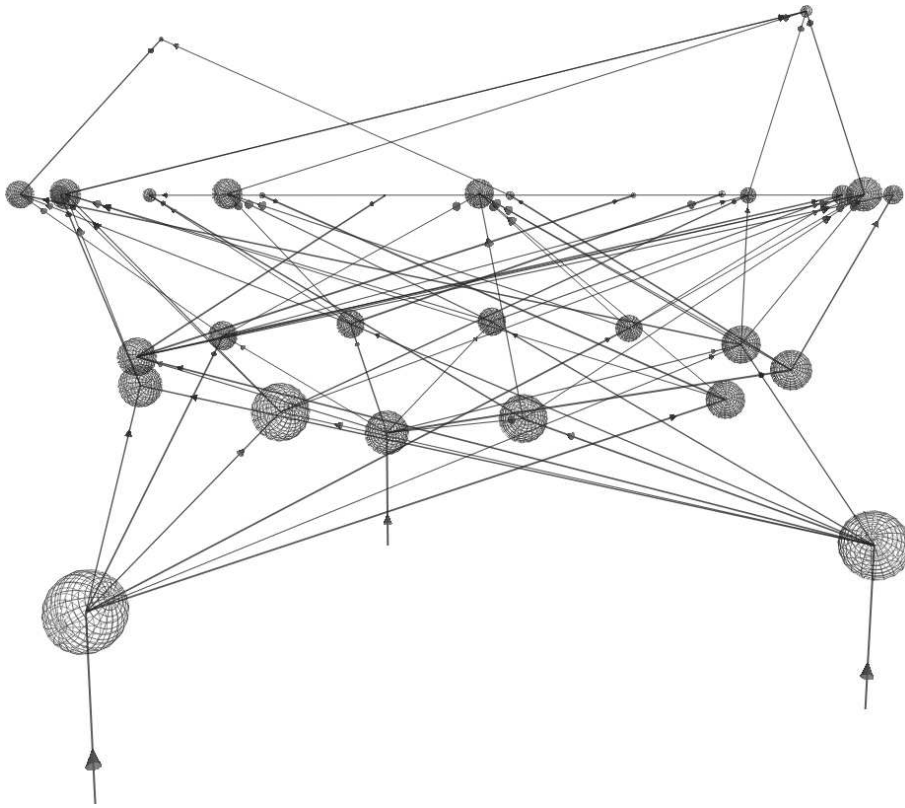


FIGURE 1 Example of a food web resulting from the evolutionary model described in section 2. The radius of the spheres which represent the species are proportional to the logarithm of the population sizes.

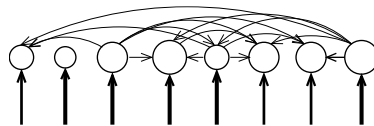


FIGURE 2 Example of a food web resulting from the evolutionary model described in section 2, but with Lotka-Volterra population dynamics.

of the model: R (the rate at which resources enter the system), λ (the ecological efficiency), c (the competition parameter, see eq. (8)) and b (the effectiveness of predators, see eq. (4) or eq. (7)). The agreement is reasonable, but not perfect. In particular, the ratio of the number of links to the number of species seems to be too low. However, this figure only includes links which have efforts which are greater than 1%. This is an arbitrary cut-off; it is difficult to assess how to make this choice in order to make the best comparison with data.

R	10^5	10^5	10^5	10^6
c	0.4	0.5	0.6	0.5
No. of species	79	57	55	270
Links per species	2.33	1.91	1.70	2.96
Av. level	2.38	2.35	2.28	3.07
Av. max. level	3.69	3.9	3.91	4.4
Basal species (%)	8	9	9	11
Intermediate species (%)	90	89	90	89
Top species (%)	2	2	1	1
Mean overlap level 1	0.22	0.34	0.37	0.27
Mean overlap level 2	0.08	0.12	0.13	0.15
Mean overlap level 3	0.07	0.09	0.09	0.12

Table 1. Results of simulations of the model with $\lambda = 0.1$, $b = 5 \times 10^{-3}$ and for various values of R and c .

The web structure in this model is in a very real sense emergent — species are not assigned to a particular level and their predator-prey interactions are not assigned beforehand in any way. Therefore, measurements of various web attributes are not influenced by preconceptions and have the potential to yield novel insights. For example, when the distribution of link strengths is measured [34], it is found that there are a large number of weak links, as shown in figure 3. This is in line with various recent suggestions [8]. The stability of food webs may also be defined in a way which is closer to that favored by empiricists, since numerical experiments may be carried out in order to investigate the stability of webs to the deletion of species [35].

4 SCOPE OF EVOLUTIONARY MODELS OF FOOD WEBS

In section 1 we have tried to argue that the notion of evolving food webs in the context of computer simulations is a very natural one and in section 2 we have given a concrete example of a model of this kind. The description of this model illustrated the need to introduce dynamics of a novel kind at timescales larger and shorter than those at which population dynamics operates on. The freedom associated with the specification of these processes reveals that there is a wide scope for the introduction of a variety of models.

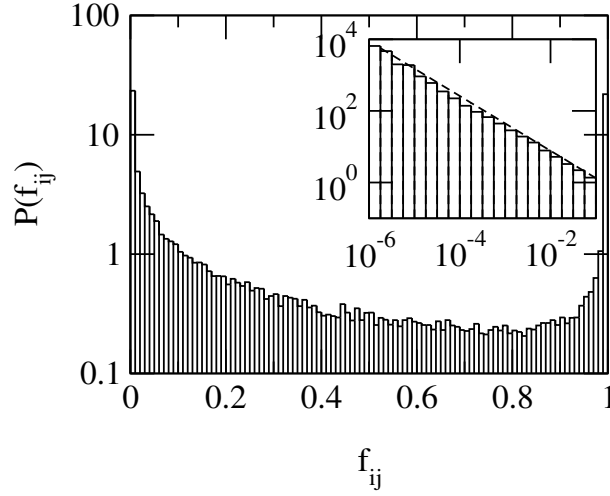


FIGURE 3 Link strength distribution resulting from the evolutionary model. The inset shows the distribution for small link strength on a log-log plot. The straight line indicates a power law with an exponent -0.75 .

Although there are a large number of models that are possible in principle, in practice studies of this kind have only begun in recent years and so the number of distinct models is relatively small. In this section we review those that are published, but we are also aware of relevant work being undertaken by several groups as we write this article.

4.1 THE MODEL OF BASTOLLA, LASSIG ET AL

The model by Bastolla, Lassig et al, [6, 24] is among all those to be discussed in this section the one that is closest to our model. It includes dynamics on two time scales. On the shorter time scale, the model has population dynamics of the type (3), using a Lotka-Volterra type functional response. In addition, the authors include a competition term $-\sum_j \beta_{ij} N_i N_j$ on the right-hand side, with the sum being taken over all competitors of species i (including species i itself). On the evolutionary time scale, speciation events occur. A new species is obtained by modifying the strength of a link or by adding or deleting a link of an existing species. The authors have performed a mean-field calculation of the expected properties of the resulting food webs analytically, finding realistic results for the mean number of species on different trophic levels. However, they have so far not published any complex food webs containing several trophic layers obtained by computer simulations of their model, and it remains to be seen whether this

model is capable of generating multi-layer webs if Lotka-Volterra dynamics is used. As we have shown, the choice of functional response has a large effect on the resulting web structure.

4.2 AN EVOLVING NETWORK OF MOLECULAR SPECIES

A model for evolving networks of interacting molecular species was introduced by Jain and Krishna [20, 21, 22, 23]. Although this model is not a food web model, it has some similarities with ecological models. In this model, species depend on other species for growth, but in contrast to food web models, there is no negative impact on a species that facilitates the growth of another species. Furthermore, this model contains no external resources, implying that stable species configurations have a core of species that mutually sustain each other. The population dynamics are $\dot{N}_i = \sum_j c_{ij} N_j - \phi N_i$, with $c_{ij} = 1$ if j catalyzes the growth of i , and zero otherwise. Evolutionary dynamics consists in replacing the species with smallest population size with a new species that has random couplings $\{c_{ij} \in \{0, 1\}\}$ to the existing species. The probability for a nonzero value of c_{ij} to occur is p , which is the parameter of the model. The total number of species is conserved in this model. After some time, a small autocatalytic set emerges, which then expands until it comprises the entire system. The core of the autocatalytic set collapses from time to time and is replaced by a different one, accompanied by crashes in the population size. The immediate application of this model is to the study of the origin of life. However, cores of mutually sustaining species are also found in two ecological models described below, and occasional crashes of the structure are observed in one of these two.

4.3 THE APPROACH OF CATTIN ET AL

Cattin et al [10] suggest a method of constructing food webs that indirectly takes evolution into account. The model is similar to the niche model insofar as species are ordered according to a “niche value”. However, motivated by the existence of phylogenetic constraints, the species are made to form a nested hierarchy of consumers in the following way. First, species are ordered according to their “niche value”, just as in the niche model, and the number of prey for each consumer is fixed in the same way as in the niche model. Then, trophic links are assigned in a two-stage process for each species i , starting with the species that has the smallest niche value. In stage one, prey species of consumer i is randomly chosen among species with rank less than i . Depending on this randomly chosen prey, j , two cases are possible: (1) Prey j has no consumer and therefore the next prey of consumer i will again be randomly attributed. (2) Prey j already has one or more consumers and therefore consumer i joins the group of species j ’s consumers, and the next prey of i is then randomly chosen among the set of prey of this group. However, if the number of prey in the group is too small for choosing all remaining prey of consumer i , the remaining prey

are again randomly chosen among prey without consumers. The second stage is needed if prey still cannot be attributed; the remaining prey is then chosen from species with rank greater than or equal to i . By creating nested groups of consumers, this model is capable of faithfully reproducing the structure of real food webs. However, it differs from the other models discussed in this article as it does not explicitly model an evolutionary process.

4.4 MODELS THAT INCLUDE MUTUALISTIC COUPLINGS

Tokita and Yasutomi [37] introduce an evolutionary model for ecosystems that also includes mutualistic couplings. Population dynamics is of the Lotka-Volterra form, with species that contain less than a fraction δ of all individuals being deleted from the pool, i.e. they become extinct. A new species may be introduced in three different ways: with random couplings (an “invasive species”), or with all couplings of the parent species modified by a small random amount, or with only one pair of couplings of the parent species being modified. All three types of rules were investigated one after the other. It is found that species number and average coupling strength increase with a power law in time for the third type of evolutionary dynamics. With the two other types of rules, the species number settles at a small value (around 10), and the average coupling strength remains small. This behavior is explained by the rapid growth of groups with mutualistic mutants, which is only possible with the third type of evolutionary dynamics.

Yoshida [39] introduces a model that is similar to the one by Tokita and Yasutomi. The main difference is that the couplings are derived from more fundamental properties. These properties are the positions in a 10-dimensional niche space, and the ranges of reactivity with respect to positive and negative interactions. The positions in niche space are similar to our features: they are 10 numbers out of 100 possible numbers, but there are two such sets of features for each species: those features that are used to determine if species harm each other, and those that are used to determine if species benefit from each other. The ranges of reactivity are random numbers between 1 and 10 and are chosen for each species for each set of features. For instance, if the difference between the n th niche values of the two species is smaller than the reactivity of a species, this increases the probability that the species harm (or benefit) each other. Mutations occur in the space of these properties, and modified couplings are calculated from these. Dynamics is again of the Lotka-Volterra type. Evolution leads to large stable networks that are dominated by species that harm others. However, from time to time a group of mutualists takes over, eventually destabilizing the system.

Of the above models which relate to food webs obtained through an evolutionary process, none make sufficiently detailed predictions about food web properties that they may be compared directly with our model described in section 2. It is for this reason that we have discussed the predictions of our model

in section 3, and used this section to illustrate the range of models which have been considered to date, and tried to put them in context.

5 DISCUSSION

The construction of model food webs using evolutionary dynamics and their comparison with real food webs is still at an early stage. Here we have reviewed one model in some detail, since it is capable of producing model webs which have a degree of realism that allows them to be compared with real webs. We also discussed a number of other models, although in less detail, since for various reasons they did not lead to stable evolved predator-prey networks which could be compared to data in the same way.

The model which we have largely focused on here is well-developed enough that we can examine it in the light of the comments on models of dynamically evolving webs which were made in section 1. By this we mean that the essential character of the model is clear and well established, so the various aspects which are important or largely irrelevant to the construction of realistic webs can be systematically investigated. The possible extensions discussed in section 1 can also be examined. Again a judgment can be made as to whether or not these extensions would lead to a significant change in the web structure, but ultimately it may be necessary to carry out these modifications to determine their actual importance. For example, as we saw in section 3, the choice of functional response in the population dynamics is important for the creation of realistic evolved webs. Within the context of the model we have identified some factors which the population dynamics should have in order to successfully lead to acceptable webs. One is that predators should not spread their efforts over a large number of different prey, but should focus on one or two of the species that they are best adapted to exploit. In some cases this choice may emerge naturally from the population dynamics, but in other cases it may have to be imposed as a constraint, since the model typically allows a predator to have a large number of prey. Another important factor is the explicit inclusion of terms f_{ij} which specify the fraction of effort that species i puts into preying on species j , and which change in an adaptive way that reflects other changes in the web. Such terms were not included in the first version of the model [9], and lead to webs which reached a state where new species could no longer be introduced.

It seems clear, however, that many choices made in the construction of the model will be unimportant to the final web structure. So while it may be objected that the way species are defined, with no reference to the underlying genetics, and the way that speciation occurs, as a single stochastic event which changes one of the phenotypic or behavioral features, are to an extent arbitrary, we believe that other reasonable choices would have resulted in similar webs. Of course, this is an assertion which has to be tested, and this is being undertaken as we write. To begin with, the number of features, the nature of the $m_{\alpha\beta}$ matrix,

the precise form of the speciation mechanism, and other specific factors can be varied and the resulting effects on web structure monitored. Later on, attempts could be made to alter some of the more fundamental aspects of the structure of the model. In addition, it is not obvious that extending the model in some of the ways outlined in section 1 would improve the type of webs produced. For instance, reformulating the model as an IBM would take a lot more computer time and might not be worth the effort. The functional responses would have to be translated into interactions between individuals which could be quite complicated, although alternatively it might turn out that this could be modeled by a relatively simple set of mechanisms. The birth-death process would now be stochastic, with no need to enforce species extinction. Speciation could take place as before, except that assuming a constant rate of speciation for each individual would make the choice of species undergoing speciation proportional to the population of the species. This was in fact the choice made in the original version of the model [9], and we do not believe that it is an important choice. Of the possible extensions discussed in section 1, one of the most interesting and probably the most important is the introduction of some spatial aspect. Clearly, making the model spatially explicit would be very costly in terms of computer time, but introducing some notion of biogeography would be valuable.

While some indications of the factors that need to be considered when model building are emerging from the study of the principal model which we have described, whether these are necessary remains to be seen. So few different kinds of models have been explored that it is premature to be too dogmatic about the necessary ingredients for evolutionary models. For this reason a large diversity in the types of evolutionary models which are produced is to be welcomed, and it is also for this reason that in our discussion of other approaches, we included models which were not strictly evolutionary models of food webs. These included a model where the nodes of the evolving network were molecular species, discussed in more detail by Jain in another article in this volume (Ref).

At the same time as the developments we have described in this review were occurring, other researchers were investigating the evolution of other kinds of networks [3, 13]. Among these networks are social networks, the internet, and citation networks. These types of networks typically grow by adding new nodes that become connected to several existing nodes. The emerging structure of the network depends on the growth rule, and there are some models that can even be evaluated analytically. Characteristic features of such networks are the *small-world* property, which means that the average distance between nodes grows only logarithmically with the number of nodes, and the property of being *scale free*. This means that the number of nodes with a given connectivity is a power law in the connectivity. These growth models are simpler than food web models based on evolutionary dynamics, since they are usually confined to the evolutionary scale and in addition do not include short-term dynamics of a process happening on the network. Certainly, there exist such processes that might determine further growth or survival of nodes, and the progress made with food web models at

combining the different time scales may inspire a similar progress in those types of models. On the other hand, the methods developed for studying structure and growth of these other types of networks could inspire new approaches to food webs. In any event, we expect that the number of evolutionary models of food webs which will appear in the next few years will increase significantly, and the greater variety of these models should bring the outlines of the subject into a sharper focus.

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