

The impact of nonlinear functional responses on the long-term evolution of food web structure

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Abstract

We investigate the long-term web structure emerging in evolutionary food web models when different types of functional responses are used. We find that large and complex webs with several trophic layers arise only if the population dynamics is such that it allows predators to focus on their best prey species. This can be achieved using modified Lotka–Volterra or Holling/Beddington functional responses with effective couplings that depend on the predator's efficiency at exploiting the prey, or a ratio-dependent functional response with adaptive foraging. In contrast, if standard Lotka–Volterra or Holling/Beddington functional responses are used, long-term evolution generates webs with almost all species being basal, and with additionally many links between these species. Interestingly, in all cases studied, a large proportion of weak links result naturally from the evolution of the food webs.

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1. Introduction

The debate over what stabilizes complex food webs has been an active one for over a quarter of a century (McCann, 2000). While it is found that the stability of a randomly linked food web model tends to decrease with the proportion of links and the number of species (May, 1972), real food webs display a high degree of stability, in spite of being very complex. Clearly, real food webs have features that are ignored in randomly linked models. For example, the distribution and strength of links in real food webs are far from random. More realistic approaches use link values taken from real food webs (Yodzis, 1981), or assemble a food web by repeated addition of species from a large species pool that contains different types of species such as “plants”, “herbivores”, “carnivores”, and “top predators” (Morton and Law, 1997; Law, 1999). Using Lotka–Volterra-

type dynamics, assembly models of this type lead to large complex webs. These Lotka–Volterra-type models lack nonlinear effects such as predator saturation, which many consider important for food web dynamics. The species pool is usually composed of a large number of species which are generated in an ad hoc manner, by pre-defining the possible types and value ranges of links. A complementary approach to food web stability focuses on more realistic dynamics (that include predator saturation, for instance) of small systems consisting only of a few species. These small systems can be viewed as a small part of a food web. It has been found that the presence of many weak links and the use of nonlinear growth rates, that prevent predators from feeding successfully on many prey at the same time, stabilize the dynamics of these small systems by reducing population fluctuations (McCann et al., 1998). Again, the possible types and values of links are pre-defined in these studies.

In real food webs, the link strengths and the linkage pattern can change with time through invasion and replacement with related species, and through adaptive

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evolutionary processes (Thompson, 1998). It is therefore desirable to investigate food web models that implement such long-term changes due to modification of existing link strengths and linkage patterns. In the following, we call this long-term change of the food web “evolution”, with the meaning of “development of the food web structure in time”, while the “true” biological evolution is of course happening on the level of individuals. Our approach is different from the species assembly models insofar that the new species are not picked irrespective of the web composition, but are similar to existing species. Our approach is also different from models for evolving ecosystems such as the one by Tokita and Yasutomi (2003), which usually include mutualistic interactions in addition to trophic interactions.

Considering the long-term change of food webs adds a new dimension to the complexity-stability debate: even though species die out and are replaced with others during the course of time, ecosystems as a whole persist in time. Except for rare catastrophic events due to external causes, food webs preserve their general structure. This means that typical structural features of food webs, such as the total number of species or the number of trophic layers, do not collapse to zero, but rather fluctuate around some mean value far away from zero. This definition of stability is perhaps more relevant for understanding the complexity of ecosystems, than some of the other definitions found in the literature. Persistence in time of a complex ecosystem of course also requires a certain kind of stability of the population dynamics: while population dynamics does not need to reach fixed points, oscillations must be small enough such that the population sizes of the majority of species remain positive after the introduction of a mutant or invading individual. If this were not so, each change in the web composition would lead to a collapse of the web, and complex ecosystems could never arise.

In this paper, we therefore study evolutionary food web models and investigate under which conditions these models show a persistent complex structure with several trophic layers. The evolutionary model that we use was studied previously with specific types of population dynamics (Caldarelli et al., 1998; Drossel et al., 2001). Here, we explore the effect of changing the functional response used in the model. We chose a representative selection of functional responses found in the literature and modified them such that they are suitable for many-species communities. Our aim here is to show that biologically realistic requirements, in particular the capability of predators to adjust their feeding rates and focus on their best prey, are essential to the construction of large complex webs, the structure of which persists under evolutionary dynamics. This finding is not in contradiction with the fact that there exist large complex model webs with other types of functional responses that are stable under population

dynamics. However, the structure of these model webs does not remain complex under long-term evolution unless the above-mentioned requirements are met.

2. The model

The governing equation for the population $N_i(t)$ of species i is taken to have the form

$$\frac{dN_i(t)}{dt} = \lambda \sum_j N_i(t)g_{ij}(t) - \sum_j N_j(t)g_{ji}(t) - d_i N_i(t) - \sum_j \alpha_{ij} N_i(t)N_j(t), \quad (1)$$

which naturally accounts for the four processes which lead to a change in the population number $N_i(t)$. The function $g_{ij}(t)$ is the functional response, i.e. the rate at which an individual of species i feeds on species j ; it depends on the population sizes, and its analytical form will be specified below. The constant λ is the ecological efficiency at which consumed prey are converted into predator offspring. The first term describes population growth due to food consumption, while the second term describes population decline due to predation. The death rate, d_i , will be assumed to be equal to 1 for all species. The last term describes direct interference competition between two predators i and j . It is needed to represent intra-specific interference competition, which ensures bounded solutions when the functional response is independent of predator density. This term also allows the incorporation of inter-specific interference competition into such models, which facilitates comparison with the predator dependent functional responses. Species, the population size of which drops below 1, are removed from the system.

On a larger time-scale, species undergo changes, either by replacement with invading similar species, or by evolutionary change. In order to implement these changes, each species was characterized by a set of 10 out of 500 possible features (Caldarelli et al., 1998). This representation gives a measure of similarity between species (the number of features they have in common) and allows for “mutations” or “invasions” by randomly replacing one feature of one individual with another. Scores between features were assigned in a random and asymmetric fashion. They are a measure of how useful a feature is for its carrier at feeding on a species carrying another feature. The interactions, or scores, a_{ij} , between species were obtained by adding the mutual scores between all pairs of features carried by the two species. Positive scores indicate that the first species can feed on the second species and negative scores mean that the first species is consumed by the second. In the latter case the score was set to zero, since this information was already contained in the (positive) score where the two

species are interchanged. Therefore all scores were such that $a_{ij} \geq 0$. The external resources were represented as an additional species of fixed (and large) population size, which does not feed on any species. The evolutionary dynamics consisted of the following steps: starting from some initial species configuration (usually the external resources plus one basal species feeding on it), one individual was picked at random, and one of its features was changed. Under the dynamics (1), this new species either died out, or added to the system, or drove one or several other species to extinction. When the dynamics had reached an equilibrium, the next “mutation” occurred, and the process was repeated.

In the following, we list the different functional responses used in our computer simulations. We have used common functional responses, generalized to multispecies systems. All of them satisfy the logical requirement given by Arditi and Michalski (1996): that the population dynamics should not be modified when identical species are pooled into one species. Lotka–Volterra dynamics are recovered by taking

$$g_{ij} = a_{ij}N_j. \tag{2}$$

A Holling type II functional response, which implies saturation of consumption rates at high prey abundance, is given by

$$g_{ij} = \frac{a_{ij}N_j}{1 + \sum_k b_{ik}N_k}, \tag{3}$$

where the sum in the denominator is taken over all prey k of species i .

More complicated functional responses for multi-species systems can only be found in the recent literature. Arditi and Michalski (1996) suggest the following generalized Beddington form:

$$g_{ij} = \frac{a_{ij}N_j}{1 + \sum_k b_{ik}N_k + \sum_l c_{il}N_l}, \tag{4}$$

where the first sum is again taken over all prey k of species i , and the second sum is taken over all those predator species l that share a prey with i . We chose the c_{il} such that individuals belonging to the same species competed more strongly with each other than individuals belonging to different species.

Arditi and Michalski (1996) also suggest the following ratio-dependent functional response, which implements the idea that predators share the prey:

$$g_{ij} = \frac{a_{ij}N_j^{r(i)}}{N_i + \sum_{k \in R(i)} b_{ik}N_k^{r(i)}} \tag{5}$$

with the self-consistent conditions

$$N_j^{r(i)} = \frac{\beta_{ji}N_i^{C(i)}N_j}{\sum_{k \in C(j)} \beta_{jk}N_k^{C(i)}}$$

$$N_k^{C(i)} = \frac{h_{jk}N_j^{r(k)}N_k}{\sum_{l \in R(k)} h_{lk}N_l^{r(k)}}.$$

Here β_{ij} is the efficiency of predator i at consuming species j , h_{ij} is the relative preference of predator i for prey j , $R(i)$ are the prey species for predator i , $C(i)$ are the species preying on prey i , $N_j^{r(i)}$ is the part of species j that is currently being accessed as resource by species i and $N_k^{C(i)}$ is the part of species k that is currently acting as consumer of species j . The advantages and disadvantages of using ratio-dependent functional responses has been so extensively discussed in the literature that we do not wish to repeat the arguments. Instead we refer the reader to a paper by two of the leading workers in this area (Abrams and Ginzburg, 2000) who discuss this issue in more detail, and to a review where we present our views on the matter (Drossel and McKane, 2003).

Finally, in a recent paper (Drossel et al., 2001), we used the ratio-dependent expression

$$g_{ij}(t) = \frac{a_{ij}f_{ij}(t)N_j(t)}{bN_j(t) + \sum_k \alpha_{ki}a_{ki}f_{kj}(t)N_k(t)}, \tag{6}$$

where f_{ij} is the fraction of its effort (or available searching time) that species i puts into preying on species j . These efforts are determined self-consistently from the condition

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

This condition is such that no individual can increase its energy intake by putting more effort into a different prey. The sum in (6) is over all species k which are predators of j . The competition strength α_{ik} is set equal to one only for $i = k$, and is smaller than 1 otherwise. For this model, or for any other model with a functional response which depends on predator density, the last term in Eq. (1) should be dropped.

3. Simulation results: food web structure

Let us first present results for the simplest type of population dynamics, which is Lotka–Volterra dynamics, Eq. (2). Starting with one species and the external resources, input at a rate R , we allowed for enough time for the system to evolve towards its characteristic stationary structure. A typical food web resulting after sufficiently long time is shown in Fig. 1. All species feed on the external resources, and additionally on other species. Only for short transient periods of time does the web have species on the second trophic level, and virtually never on the third. We also performed simulations that started from a complex web with several trophic layers, which was stable under the population dynamics. However, the evolutionary

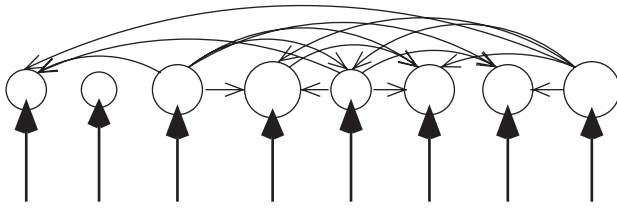


Fig. 1. Example of a food web resulting from an evolutionary model with Lotka–Volterra population dynamics. The arrow direction indicates the flow of resources, and the arrow thickness is a measure of link strength defined according to Eq. (8). Links are only drawn if a species obtains more than 1 percent of its food through that link. The radius of the circles increase logarithmically with population size.

dynamics caused this structure to collapse, and the resulting structure was again similar to that shown in Fig. 1. These results were obtained without inter-specific direct competition, i.e. with $\alpha_{ij} = c\delta_{ij}$ where δ_{ij} is the Kronecker delta defined by $\delta_{ij} = 0$ for $i \neq j$ and $\delta_{ii} = 1$. They are still true when direct inter-specific competition is included, as in a different evolutionary model described by Lässig et al. (2001) and also in our model if we set $\alpha_{ij} = c\rho_{ij}(1 + q_{ij})/2$ in Eq. (1). Here ρ_{ij} is equal to one if i and j share at least one prey and is zero otherwise, and q_{ij} is the fraction of discrete features shared by the two species.

Our interpretation of these results is as follows. When a modified species that can feed on more prey than a parent species is introduced into the model, the modified species takes over. This is due to the linear growth rates of Lotka–Volterra systems that allow a species to feed on each of several prey just as easily as it would feed on one prey, if only this prey was present. If allowed to evolve, an artificially constructed Lotka–Volterra food web will therefore tend to a simple web structure where each species feeds on many other species and in particular on the most abundant resource, the external environment. Clearly, this feature of the model is unrealistic as there are evolutionary trade-offs that do not allow species to feed very easily on an arbitrarily large number of species. In particular, species cannot normally feed on external resources and on many other types of prey.

In the light of these arguments, a Holling- or Beddington-type functional response is more realistic, since it naturally limits the total amount of prey taken by a predator. Indeed, the need for nonlinear growth rates in the context of multispecies communities has often been discussed in the literature (Pimm, 1991; Rosenzweig, 1995; Vandemeer et al., 2002). Functional responses of the form (3) were used by McCann et al. (1998) in their investigation of the effects of weak links. They have the biologically meaningful feature that predators cannot maintain a high feeding efficiency on many prey at the same time, and they have a stabilizing effect on the dynamical equations, at least for sub-

systems consisting of up to four species (McCann et al., 1998). Additional direct inter-specific competition can be introduced in a natural way by using functional responses of the Beddington form (4). However, when evolutionary dynamics by modification of existing species are added to either of these models, we find again that complex webs with several trophic layers are not stable and that after some time the webs consist merely of basal species, with a structure very similar to that shown in Fig. 1.

It appears that even for the Holling- or Beddington-type functional response too many species can feed on the same food source, and that the model does not have a mechanism that prevents possible links (i.e. $a_{ij} > 0$) from being realized. In the models we are considering here, there is always a possible predator–prey interaction between any two species i and j , either $a_{ij} > 0$ and $a_{ji} = 0$ or $a_{ji} > 0$ and $a_{ij} = 0$. Thus the ecosystems are potentially highly connected with one half of all inter-specific links realized. However, species usually focus on those prey to which they are best adapted. We therefore must introduce a mechanism which would limit the number of species a predator actually feeds on, with potential links becoming active only when the preferred prey is scarce or unavailable, or after a change in the composition of the web. One way to (artificially) realize this feature is to allow only the best predators to feed on a given prey. We did this by replacing the interactions a_{ij} with adjusted interactions $a'_{ij} = a_j^{max}(1 - (a_j^{max} - a_{ij})/\delta)$ (Caldarelli et al., 1998), with δ being a small parameter and a_j^{max} being the largest interaction against j . Negative a'_{ij} are set to zero. Fig. 2 shows a food web obtained from Lotka–Volterra dynamics with this artificial constraint. Table 1 shows the mean number of species, of links per species, and the mean occupation numbers of the trophic levels for this model, for $R = 1 \times 10^4$, $\lambda = 0.1$, $c = 1.0$ and $\delta = 0.2$. For comparison, the

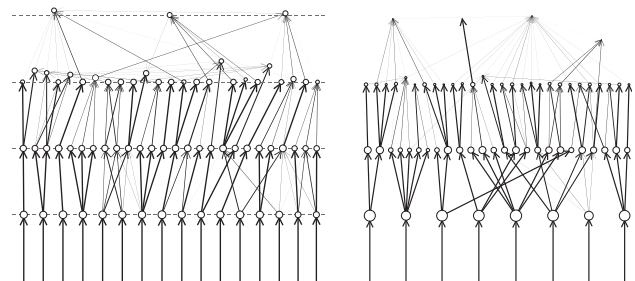


Fig. 2. On the left: Example of a food web with 70 species resulting from an evolutionary model with Lotka–Volterra population dynamics and adjusted interactions ($\delta = 0.2$). On the right: Example of a food web with 65 species resulting from an evolutionary model with a ratio-dependent functional response given by Eq. (6). The same conventions apply as for Fig. 1 except that vertical position is now proportional to the average path length from the species to the environment weighted by diet proportions. Notice that the population sizes vary much more across trophic levels when a ratio-dependent functional response is used.

Table 1
Food web statistics for the two Lotka–Volterra models: without and with adjusted interactions

Model	Number of species	Links per species	Trophic level					
			1	2	3	4	5	6
Number of species—frequency of occupation								
Lotka–Volterra without adjusted interactions	40.6(2.5)	2.3(0.1)	40.5	1.6	—	—	—	—
			1.000	0.061	—	—	—	—
Lotka–Volterra with adjusted interactions	69.8(20.4)	1.4(0.1)	20.9	22.1	19.1	7.5	1.4	1.0
			1.000	1.000	1.000	0.987	0.140	0.003

The results are averaged over 10 different simulations (lasting 200,000 iterations) and over the last 20,000 iterations of each simulation. The quantities in brackets give standard deviations over the 10 runs for the number of species and links per species. Only links between non-environment species that constituted greater than 1% of the predator’s diet were counted in the calculation of the links per species.

results for the original Lotka–Volterra model with the parameters for $R = 1 \times 10^4$, $\lambda = 0.1$, and $c = 3.0$ are also shown. Similar web structures were obtained including direct inter-specific competition or using Holling and Beddington forms with the same type of adjusted interactions.

This shows 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 complex, multitrophic food web structures.

Next, let us discuss evolutionary food web models with ratio-dependent functional responses. Ratio-dependent functional responses naturally limit the number of actual prey of a predator by dividing the available prey among its predators. One such ratio-dependent form, given by Eq. (5), was suggested by [Arditi and Michalski \(1996\)](#). However, it leads to such strong competition that only one predator species can feed on a given prey species and thus cannot give rise to complex food web structures. (One can conclude this directly from the published webs ([Arditi and Michalski, 1996](#)) or from an analytical calculation with two predator species and one prey species). In reality, however, different species exploit a food source in different ways and therefore competition between individuals of different species is less than between individuals of the same species.

This feature is implemented in the functional response (6), which was introduced by some of us ([Drossel et al., 2001](#)). Furthermore, Eqs. (6) and (7) have several other biologically meaningful features: when prey is very abundant, the consumption rates saturate due to the term containing b in the denominator. Additionally, predators divide their effort (or time) among the available prey in order to obtain the maximum possible amount of food. The condition (7) is an evolutionarily stable strategy and allows species to swiftly adjust to a modified situation, thus endowing the food web model with the flexibility found in real webs. Finally, Eqs. (6) and (7) are invariant if identical species are aggregated into a single species. This feature is shared by the other

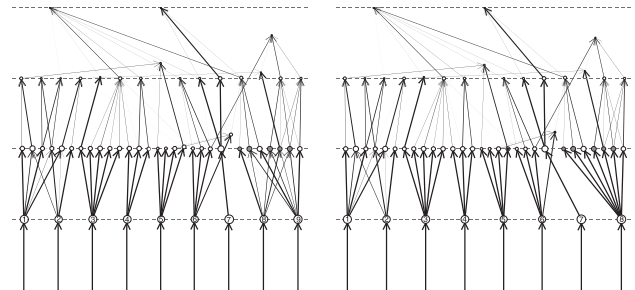


Fig. 3. A model web generated using the functional response (6) before (left) and after (right) deletion of basal species 8. The five shaded species feeding on it managed to survive by feeding at a higher rate on other species.

models used in this paper if the last term in Eq. (1) is either set to zero or present for any pair of species but not if, for instance, only inter-specific competition is included.

Using the functional response (6) in the evolutionary model, we rapidly obtain, for a wide range of parameter values, large and complex food webs with a stable structure, although there is an ongoing turnover of species in the system. The dynamics (1) converge quickly to a fixed point. The food webs generated by this model share many features with real food webs, such as the fraction of top, intermediate and basal species, and the mean number of links per species. This is discussed in detail elsewhere ([Drossel et al., 2001](#); [Quince et al., 2004a](#)). A typical food web resulting from our simulations is shown in [Fig. 2](#).

The webs generated by this model often preserve their structure under changes in the species composition. [Fig. 3](#) shows a web before and after a basal species was deleted. One can see that in this case all other species manage to survive, with the strength of several links being modified, illustrating the flexibility and resilience of the model food webs. Of course, the deletion of a randomly chosen species is not always buffered in this perfect way. A useful measure of the ecosystem stability to deletion is the fraction of species that can be removed

without causing further extinctions (Pimm, 1979). This statistic depends on the model parameters; for the values used to generate Fig. 3 it is 57%. For the deletions which do cause further extinctions the distribution of event sizes decays roughly exponentially with a characteristic size of just a few species (Quince et al., 2004b). We believe that similar results can be obtained using other (non-ratio-dependent) functional responses, if only they allow for a similar degree of predator flexibility.

We conclude this section by comparing the food web statistics for the webs generated by the Lotka–Volterra model with adjusted scores, the model with a ratio-dependent functional response, and real food webs. Some real food webs do indeed resemble closely the webs generated by our models, as for instance the Grassland food web shown in Fig. 4.

Other real webs look different. Table 2 compares different structural features of the three types of webs. In the calculation of the statistics in Table 2 only those links comprising greater than 1% of a predator's diet were used. An omnivorous species was defined as one with prey in more than one trophic level. Trophic levels are defined as the minimum number of links between a species and the environment. One can see that the webs with the ratio-dependent functional responses are closer to real food webs than the webs generated with Lotka–Volterra-dynamics and adjusted scores. None of them is completely realistic, since the average number of links per species is smaller than for real webs. The reason for this might be that we have only counted links above a minimum strength. Many potential links are not realized in our model webs, but they could become realized if the species composition or the population sizes changed. In

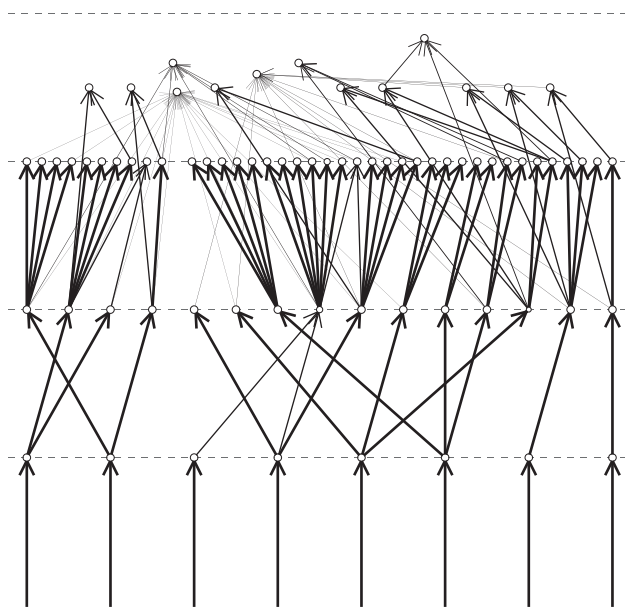


Fig. 4. Example of a real food web with 75 species. This is the Grassland food web of Martinez et al. (1999). In this diagram the circle radius is a constant independent of the species population size.

Table 2

Simple food webs statistics compiled for webs generated by the Lotka–Volterra model with adjusted scores, the model with a ratio-dependent functional response (Eq. (6)), and real food webs

Food web statistics	Lotka–Volterra with adjusted interactions	Ratio-dependent functional response	Real food webs
Sample size	10	80	14
Number of species	69.8 (20.4)	63.4 (5.2)	91.2 (50.9)
Links per species	1.37 (0.08)	1.69 (0.07)	6.38 (3.49)
Fraction of basal species	0.29 (0.06)	0.12 (0.01)	0.21 (0.20)
Fraction of intermediate species	0.68 (0.06)	0.78 (0.03)	0.56 (0.22)
Fraction of top species	0.02 (0.01)	0.10 (0.02)	0.23 (0.21)
Fraction of omnivorous species	0.08 (0.04)	0.16 (0.05)	0.36 (0.23)

For the evolutionary models the statistics are averaged over multiple simulations, the number given in sample size, and over the last 20,000 iterations of each simulation. The real food webs come from fourteen of the sixteen food webs used in Dunne et al. (2002), the two webs from unpublished data in that study, Lake Tahoe and Mirror Lake, not being used. The results are for food webs not aggregated into trophic species. The figures in brackets show standard deviations.

real webs, temporal and spatial fluctuations may be the reason for the visibility of more links, but probably not all of them are realized at the same place and at the same time (Tavares-Cromar and Williams, 1996).

4. Simulation results: link strength distributions

There has been an increasing realization that food webs have a large proportion of weak links (Paine, 1992; Tavares-Cromar and Williams, 1996; Berlow et al., 1999; Neutel et al., 2002), and that weak links tend to stabilize population dynamics (McCann et al., 1998). For this reason, we evaluated the link strength distribution in our model webs. We found that for all functional responses that generated large ecosystems either the link strength distributions were skewed towards zero or a large fraction of links were zero. This is a highly non-trivial result as in contrast to other work on the topic of weak links, the link strength distributions in our model are an emergent property of the system and not put in by hand. It is a strong indication that weak links are the natural outcome of long-term ecosystem evolution coupled to population dynamics.

In the literature there are different definitions of link strength, ranging from the biomass flowing through a link per unit time to the response of one population size to a small change in another population size (Laska and

Wootton, 1998). Here, we evaluated link strength distributions based on the following two definitions: (i) the proportion of the prey in the predator’s diet after the population dynamics had equilibrated,

$$l_{ij}^{(1)} = \frac{g_{ij}}{\sum_k g_{ik}}, \tag{8}$$

and (ii) the per-capita interaction strength $l_{ij}^{(2)}$. These are sometimes known as the elements of the “community matrix” (Laska and Wootton, 1998), although this phrase is also used to refer to the unnormalized matrix of partial derivatives (May, 1973). It quantifies the strength of all direct interactions, both predator–prey interactions and interference competition. It is defined as

$$l_{ij}^{(2)} = \frac{1}{N_i} \left(\frac{\partial \dot{N}_i}{\partial N_j} \right). \tag{9}$$

Definition (i) typically leads to a U-shaped link-strength distribution, with a peak at weak links and another one near the maximum link strength 1, indicating that many predators have one main prey. (Note that the second peak does not occur if the link strength is defined as the biomass passing through a link, since in this case the link strength is not normalized to $\sum_j l_{ij} = 1$). Definition (ii) typically leads to broad distributions with or without a peak at zero.

Fig. 5 shows the distribution of link strengths $l_{ij}^{(1)}$ for the two Lotka–Volterra models (without and with adjusted scores), and for the model with the ratio-dependent functional response. The results are averaged over multiple food webs. For small link strength, the

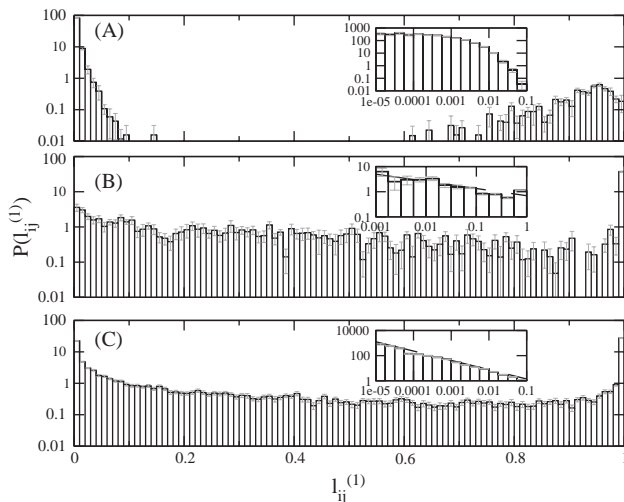


Fig. 5. The distribution of link strengths $l_{ij}^{(1)} > 0$ for the Lotka–Volterra model without adjusted scores (A) with adjusted scores (B) and the ratio-dependent functional response (C). The y-axis on all graphs are scaled logarithmically. The insets show the data with both axes scaled logarithmically, for B and C these include power-law fits which had exponents -0.74 and -0.29 , respectively. These results were averaged over multiple food webs, and the grey bars show the estimated errors in these averages.

distribution for the ratio-dependent functional response resembles a power law with an exponent around -0.74 , while the Beddington model with adjusted scores shows an exponent around -0.9 , and the Lotka–Volterra model with adjusted scores shows an exponent around -0.29 (if a power law fit should be attempted at all). The Lotka–Volterra model without adjusted scores does not have several trophic layers, and its link strength distribution appears to decay exponentially at small values. For the Beddington functional response without adjusted scores, the decay is much steeper than with adjusted scores, but not exponential. All the above-mentioned models are skewed towards small values except for the Lotka–Volterra model with adjusted scores where the approach to the origin is quite flat. For this model however, only a small proportion, 3%, of links have $l_{ij}^{(1)} > 0$. We conclude that for the models capable of generating large ecosystems only a small fraction of links were realized or $l_{ij}^{(1)}$ had a large weight at small values. We can summarize this by calculating the fraction of links with $l_{ij}^{(1)} < 0.01$ including zero, which gives 91% and 97% for the Lotka–Volterra models (without and with adjusted scores) and 97% for the ratio-dependent model.

We can investigate these ideas further by examining the link strength according to the definition (ii); this can be either positive or negative. In the case of the Lotka–Volterra models, the only direct inter-specific interactions are between predators and prey with $l_{ij}^{(2)} = \lambda a_{ij}$ and $l_{ji}^{(2)} = -a_{ij}$ if i predate j . Thus in Fig. 6 we only need to show the positive half of the $l_{ij}^{(2)}$ distribution. From this we see that, whereas the Lotka–Volterra model without adjusted scores has a distribution of $l_{ij}^{(2)}$ values that is skewed towards zero, the model with adjusted scores has a maximum at an intermediate value of $l_{ij}^{(2)}$. However, as was the case for $l_{ij}^{(1)}$, we find a much higher proportion of

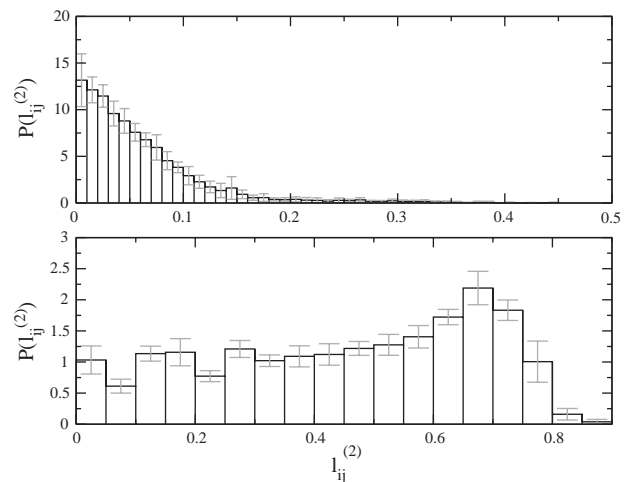


Fig. 6. The distribution of link strengths $l_{ij}^{(2)} > 0$ for the Lotka–Volterra models without adjusted scores (A) and with adjusted scores (B). The grey bars give standard errors.

non-zero links in the model without adjusted interactions (51% as compared to 3%).

If we introduce direct inter-specific competition into the Lotka–Volterra models as in Section 3 by setting $\alpha_{ij} = c\rho_{ij}(1 + q_{ij})/2$ in Eq. (1), where ρ_{ij} is equal to one if i and j share at least one prey and is zero otherwise and where q_{ij} is the fraction of discrete features shared by the two species, we find that, even if adjusted interactions are used, only small webs can be evolved. The reason for this seems to be that the resulting direct competitive interactions which are allowed by the adjusted interactions are both strong and non-zero for a large fraction of species pairs in the web. This is illustrated by Fig. 7 where the distributions of the quantity $-\alpha_{ij}$ when $c = 5.0$ are plotted for the model with and without adjusted scores. We plot $-\alpha_{ij}$ because it is the contribution of direct competition to $I_{ij}^{(2)}$. Note that because q_{ij} is discrete so is α_{ij} and that the range of non-zero α_{ij} is $-5 \leq -\alpha_{ij} \leq -2.5$.

The model with the ratio-dependent functional response, Eq. (6), also includes direct inter-specific competition, as a result of the implicit sharing of prey between predators. However this does not lead to the strong competitive interactions seen in Fig. 7, probably because this competition occurs through the predator–prey terms, which as was shown in Fig. 5, are themselves very diffuse. This can be seen in Fig. 8, where the distribution of $I_{ij}^{(2)}$ values for all competitive interactions and where the shared prey comprised greater than 1% of both competitors diet, is shown. This distribution, although bimodal, is heavily weighted towards the

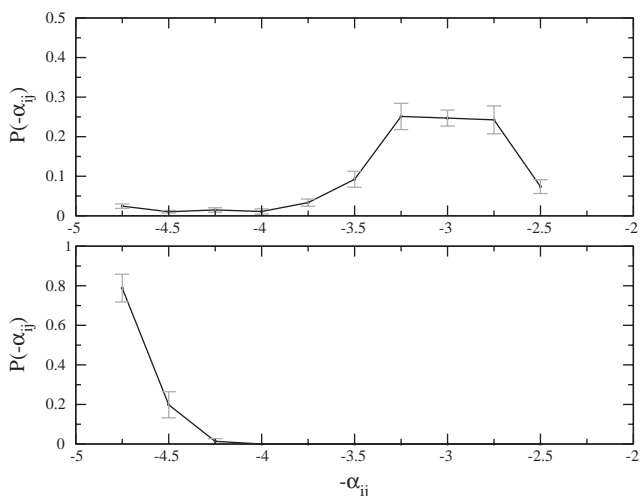


Fig. 7. The distribution of non-zero $-\alpha_{ij}$ for the Lotka–Volterra models with direct inter-specific competition. These results have been averaged over many webs and the magnitude of the estimated errors are given by the grey bars. The results for the model without adjusted scores is shown in A and with adjusted scores in B. The fraction of inter-specific interaction with non-zero α_{ij} was 100% for the former model and 23% for the latter. Note that the non-zero α_{ij} are clustered near to the smallest allowed magnitude of 2.5 in A and near to the largest allowed magnitude of 5 in B.

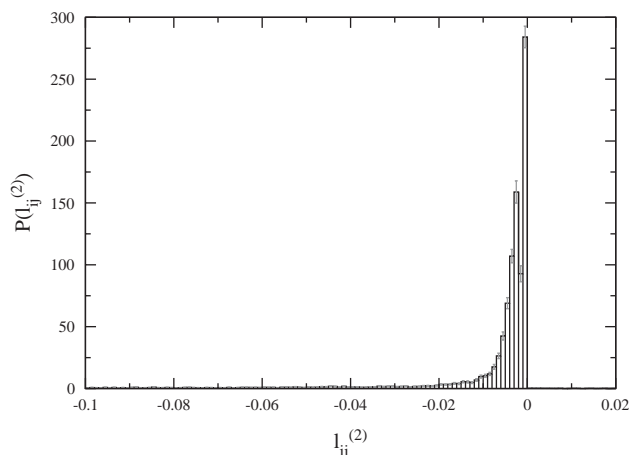


Fig. 8. The distribution of $I_{ij}^{(2)}$ for competitive interactions where the shared prey comprised greater than 1% of both competitors diet estimated for the ratio-dependent model. This condition was satisfied by 5% of all species pairs. The grey bars give standard errors.

origin. This then explains why the ratio-dependent model with inter-specific competition is, in contrast to the Lotka–Volterra models discussed immediately above, capable of evolving large complex ecosystems.

This finding of ours is complemented by a recent paper by Kondoh (2003), who investigates randomly linked food web models and the cascade model based on Lotka–Volterra dynamics with adjustable foraging efforts. He finds that incorporating adaptive foragers turns a negative relationship between stability and complexity, defined in terms of species number and potential connectance, into a positive one. This result had already been found, albeit over a more limited range of parameters, by Pelletier (2000). These results are strictly different to ours in that the stability criterion, community persistence defined as fraction of species surviving for some long time in a stochastic environment, is different. However the mechanism that allows the generation of large webs with high potential connectance, the reduction in the number of non-zero realized links and the reduction in strength of those links that are realized due to the foraging dynamics, is very similar to that proposed above. In fact, this mechanism is arguably just May's original hypothesis, that strong links or a large fraction of links will destabilize ecosystems, placed in an adaptive context (May, 1972).

5. Discussion

The form that a realistic functional response might take has been the subject of a large number of papers in the literature but few, if any, of these suggestions were implemented in a model of multispecies communities in order to test their effectiveness. In this paper we have used an existing model to investigate the effect that

different choices for the functional response have on food web structure. We studied models with a wide range of functional responses: Lotka–Volterra with and without direct inter-specific competition, Holling and Beddington forms, all of these but with a mechanism to limit the number of species a predator actually feeds on, and ratio-dependent functional responses. We found that in the first two cases complex webs could not be built up, but in the last two cases they often could. More specifically, unless an (artificial) mechanism was introduced which restricted predator choice to prey which they were best suited to exploit or alternatively a ratio-dependent functional response was used, then stable webs consisting of more than one trophic level could not be built up.

Our second major conclusion was that, given we chose a functional response which gave rise to complex, stable webs as described above, the link strength distributions were skewed towards zero. For the Beddington functional response with adjusted scores or ratio dependence, the link strength distribution followed a power law, but this was much less clear in the case of the Lotka–Volterra model, where only a small fraction of the links were realized i.e. a large fraction of the links were zero. Some insight into the mechanisms involved in these effects was also gained by looking at the strength of a direct inter-specific competition introduced into the Lotka–Volterra equations. Without adjusted scores, interactions were present, but not particularly strong. However with adjusted scores, about three-quarters of the interactions (for the parameter values we used) were zero, but the remaining quarter were strong. In this case we found that, even with adjusted scores, large complex webs could not be grown. We concluded that the existence of strong competitive interactions might also destabilize food webs.

In summary, we found that the type of functional response used in the population dynamics of multispecies communities has to be chosen carefully if a large complex community is to be sustained. If this is achieved, then a large proportion of weak links arises naturally from the evolution of the food webs. These conclusions were arrived at within the context of a class of evolutionary food web models. It would be interesting to investigate if these results could be obtained from other starting points or with different model assumptions.

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