Evolving complex food webs

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with

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1. Introduction

Food webs are networks of “who eats whom” in a particular geographical location — for example an island, a lake, an estuary,...

Ecologists have for some time catalogued food webs by drawing graphs where species are nodes and predator-prey interactions are the connecting links (edges)

Most of the food webs documented early on were small, and the data collected as a by-product of some other project

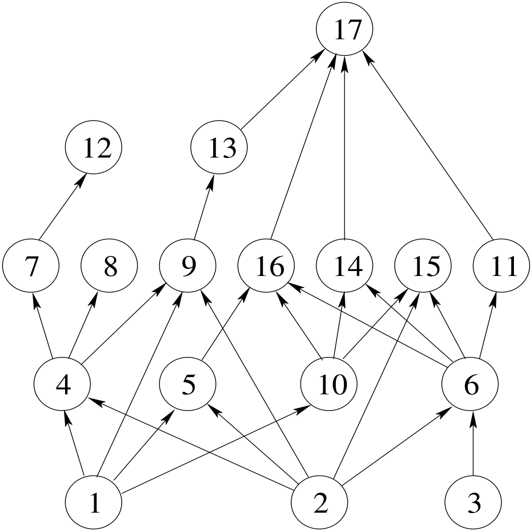
Food webs models were not formulated till much later...the first models were either static (random graph model, cascade model) — postulating certain types of web on the basis of one or two plausible rules, or had very simple dynamics on a random graph

Instead, to model food webs, we construct them from scratch using biologically reasonable dynamics, rather than postulating a given graph structure with no population dynamics, or defining a population dynamics on a fixed graph

Two types of dynamics are required: (i) a “network dynamics”, which gives rise to new species in the web (by speciation or immigration) and eliminates them from the web (extinction), and (ii) a more conventional population dynamics, which describes the interaction between individuals when the number of species present in the community is fixed

We will first create species on a mainland, or metacommunity, purely through speciation (with extinctions and population dynamics). Later we can use these as a species pool to study immigration into islands, or local communities

The networks that are constructed will be emergent — species are not positioned in the network “by hand” and will change their links to increase the resources available to them



Narragansett Bay food web

2. The Webworld model

To devise a model which enables us to “grow” a food web we introduce three distinct time scales into the model:

On the longest time scale, new species are introduced. They are variants of a randomly chosen species already in the system

On the intermediate time scale, the number of species is fixed, and the dynamics is that of conventional population dynamics

On the shortest time scale, the populations of each species are fixed, but the choice of diets of predators may change: species may alter their feeding habits to take advantage of recent changes in population sizes

Before setting up the dynamics, need to introduce features which characterise species, so that we can describe speciations

Species are defined by choosing a set of L features out of a pool of K possible features (in the simulations I will present here, $L = 10$ and $K = 500$)

Features represent phenotypic and behavioural characteristics; the number of features species have in common gives a measure of the similarity between species

Example

Species 1 is defined through the features

$$\{34, 75, 135, 176, 285, 324, 356, 432, 437, 476\}$$

and Species 2 is defined through the features

$$\{12, 75, 152, 178, 276, 298, 325, 337, 391, 439\}$$

In this case only feature 75 is common.

The measure of how useful a feature is for its carrier (at feeding on a species carrying another feature) is assigned at the beginning of a run in terms of an antisymmetric matrix $m_{\alpha\beta}$ $(\alpha, \beta = 1, \ldots, K)$

In the standard version of the model the entries $m_{\alpha\beta}$ $(\alpha < \beta)$ are taken to be Gaussian random variables with zero mean and unit variance, but many other choices have been investigated, and have not significantly changed the nature of the results

The effectiveness of the set of features belonging to species i, against the set of those belonging to species j, gives a measure of how well i is adapted for predation on j and is given by the *score*

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

The score matrix will appear in the equations describing the population dynamics

Dynamics

Evolutionary dynamics (network dynamics)

At each evolutionary time step a speciation occurs: a species is randomly chosen, and one of its features is randomly replaced by another

The population of the parent species is reduced by 1 and the new species is introduced into the community with a population of 1

The population dynamics (discussed below) is applied to the new community, and new population densities calculated

If the population density of any species falls below 1 during this period it is eliminated (extinction)

Choices made above relating to the way species are chosen, number of new species introduced into the community, thresholds for extinction,...do not significantly change the nature of the results obtained

Population dynamics

The governing equation for the population dynamics is taken to be

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

• The term $\sum_j N_j(t) g_{ji}(t)$ represents the loss from predation by species j on species i. The quantity $g_{ij}(t)$ is the functional response — which is the rate at which an individual of species i feeds on species j

• The term $\lambda \sum_j N_i(t) g_{ij}(t)$ represents the gain from predation by species i on species j. Here λ is the ecological efficiency at which consumed prey is converted into predator offspring

• Finally, d_i is the death rate, which we assume to be equal to 1 for all species

It only remains to model the functional response. This is done in as realistic a way as possible.

Let's recall some of the forms proposed for a single predator P and single victim V:

$$\begin{aligned}
g(P,V) &= aV \quad \text{(linear functional response)} \\
g(P,V) &= \frac{a_1 V}{1 + a_2 V} \quad \text{(Holling)} \\
g(P,V) &= \frac{a_1 V}{1 + a_2 V + a_3 P} \quad \text{(Beddington)} \\
g(P,V) &= \frac{a_1 V}{a_2 V + a_3 P} \quad (\text{ratio} - \text{dependence})
\end{aligned}$$

So, going back to our previous notation, for a single predator i feeding on a single prey j:

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

If there are several species preying on j:

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

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

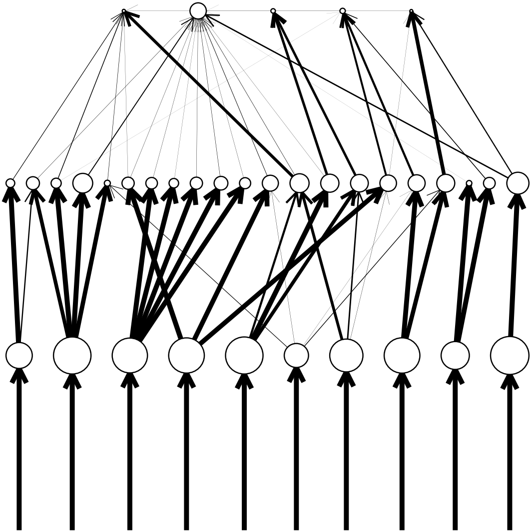
If predators have more than one prey as well:

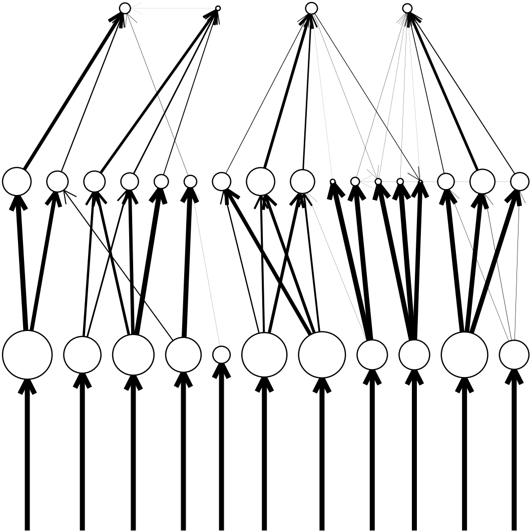
$$g_{ij}(t) = \frac{S_{ij}f_{ij}(t)N_j(t)}{bN_j(t) + \sum_k \alpha_{ki}S_{kj}f_{kj}(t)N_k(t)}$$

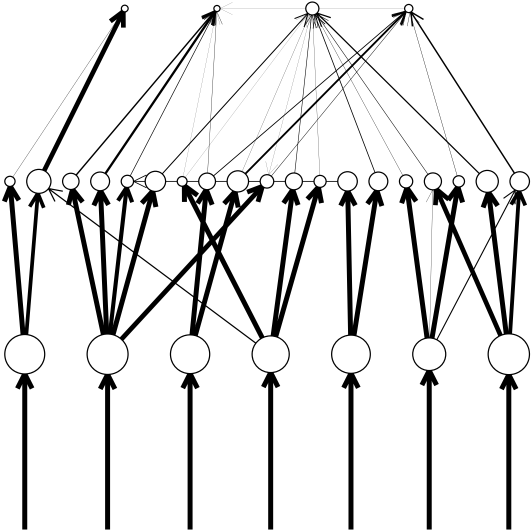
where the "efforts" satisfy

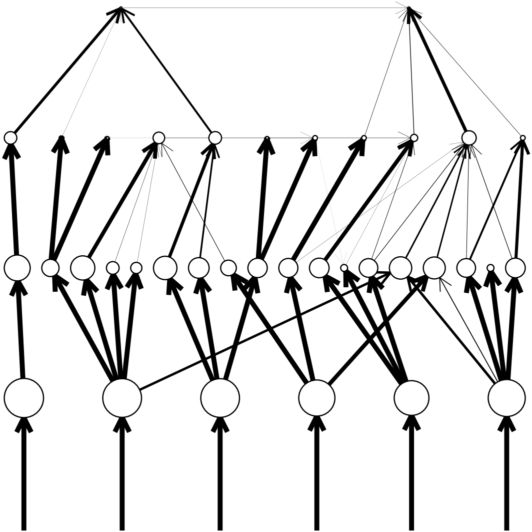
$$f_{ij}(t) = \frac{g_{ij}(t)}{\sum_k g_{ik}(t)}$$

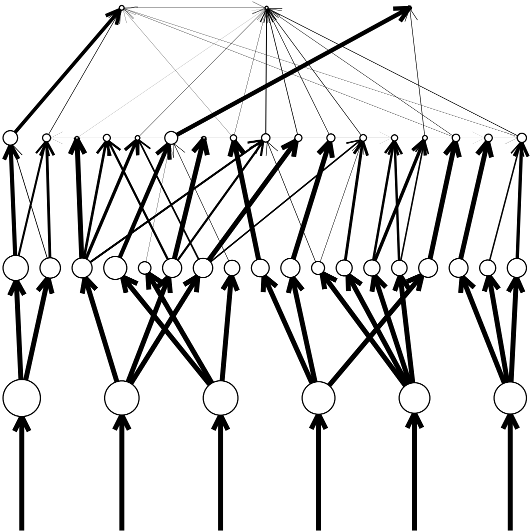
3. Examples of Constructed Webs

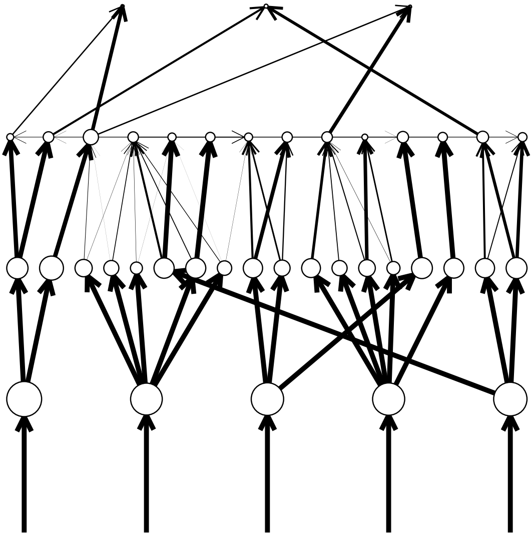












4. Results

Many simulations were performed, each with

- different random matrices for the scores of features against each other
- different random feature sets for the environment

Each run was for 100,000 evolutionary time steps, except when very large webs were created, when the model was run for 200,000 evolutionary time steps

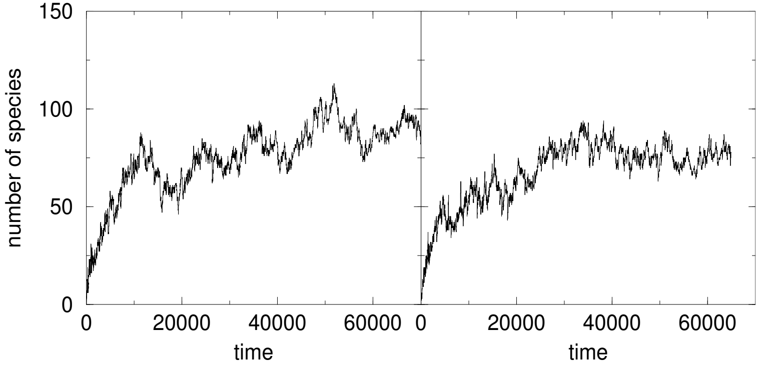
Main parameters of the model:
R: Total resources
c: Competition parameter ($0 \leq c \leq 1$)
λ: Ecological efficiency ($= 0.1$)
b: Saturation level of g_{ij}

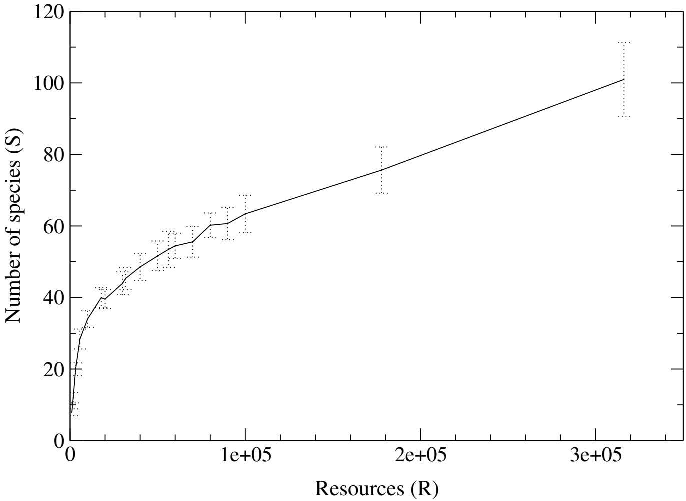
Two different runs

$$R = 3.5 \times 10^5$$

$$c = 0.5$$

$$b = 0.005$$





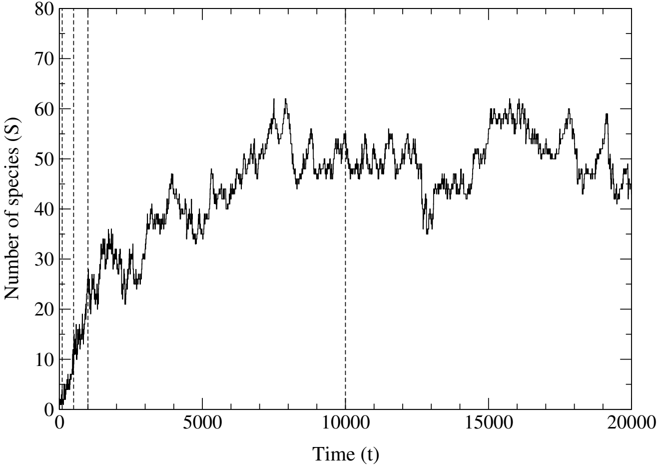
Mean number of species versus input of resources over many runs with the same set of parameters

$c = 0.5, \quad b = 0.005, \quad \lambda = 0.1$

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

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

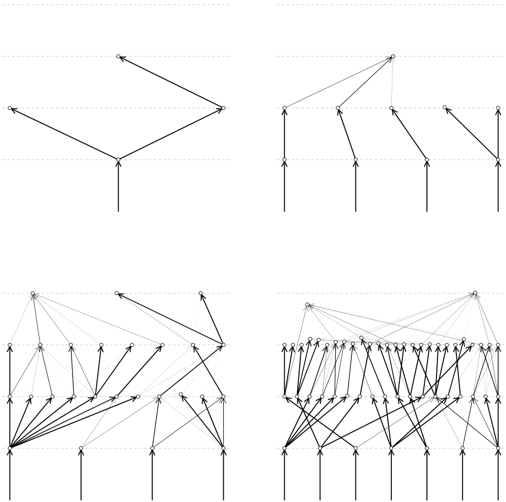
Time evolution of a single ecosystem



Dashed lines are at times 100, 500, 1000 and 10000

Simulation had parameters $R = 1 \times 10^5$, $b = 0.005$, $c = 0.5$ and $\lambda = 0.1$

Food webs produced in the previous simulation sampled at times 100, 500, 1000 and 10000



Other aspects of the model which have been investigated:

- Web structure obtained using other forms of functional response (Lotka-Volterra, Holling, Beddington, Arditi-Michalski). A large proportion of weak links result naturally from the evolution of food webs [J. Theor. Biol. **229**, 539–548 (2004)]

- Distribution of interaction strengths in the evolved web — is this skewed towards weak links? [Ecol. Modelling **187**, 389–412 (2005)]

- Stability of model ecosystem to removal and addition of species. No evidence that complexity, in terms of increased species number or links per species, is destabilising [Oikos **110**, 283–296 (2005)]

- Robustness of the model to changes in its structure, by changing the nature of species interactions and thresholds such as the number of individuals of a species required to be present before that species is said to be extinct. We found that the model was remarkably robust to such changes [Ecol. Complexity **5**, 106–120 (2008)]

• Does making the model more complex led to a richer set of predictions, or if it is made simpler, can contact be made with even simpler models, which could be studied analytically. There is essentially a whole class of food web models, which are related to the original, which give broadly similar results, and which run from the relatively simple to the quite complex [Jour. Theor. Biol. **252**, 649–661 (2008)]

• Measured the species abundance distribution. Seems to be the first time that this has been measured in a non-trivial model with several trophic levels. We found that the power-law normal distribution was a better fit to the form of the distribution than was the conventional log-normal [Jour. Theor. Biol. **255**, 387–395 (2008)]

• Unified the evolutionary approach to foodweb modelling discussed above, with an alternative modelling procedure: assembly models. So now immigration, as well speciation, is the mechanism for the introduction of new species and hence for the construction of ecological communities. Allows for test of species-area relation [Ecol. Complexity **6**, 316–327 (2009)]

5. Conclusions

The dynamical model of food web evolution described here covers time scales from the very short (e.g. changing foraging strategies) to the very long (e.g. when evolutionary dynamics reaches a state where the number of originations and the number of extinctions balance on average)

The networks that are formed are truly emergent, with species finding their own niche within the web and continually changing their foraging strategies to maximise their gain in resources

Results are intuitively appealing and in broad agreement with food web data from real ecosystems. They are also robust to changes in various parameters in the model

The approach can be extended to include immigration by evolving a mainland which can be used as a species pool for constructing island communities

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