Evolution of stabilising weak links in food webs

Graeme J. Ackland & Ian D. Gallagher

School of Physics and Astronomy, The University of Edinburgh, Edinburgh Scotland EH93JZ

Conventional ecological models[1-4] show that complexity destabilises food webs, suggesting that food webs should have neither the large number of species nor the large number of interactions. However, in nature the opposite appears to be the case. More recent work[5] shows that the introduction of nonlinearity and weak interactions can enhance stability, and the observation of weak interactions in real systems is taken as justification for this. Here we show that if the interactions between species is allowed to evolve, such stabilising feedbacks and weak interactions emerge naturally. Moreover, we show that trophic levels[4] also emerge spontaneously from the evolutionary approach, and the efficiency of the unperturbed ecosystem increases with time.

Ecosystems are a classic example of complexity[6], being formed from a myriad of interactions between various species. The mathematical study of ecosystems has a long history[1-11], dating back to the work of Lotka and Volterra[7,8]. Such models tread a delicate balance between including so much detail that they lose the capability to make qualitative predictions, and being so simple as to be wholly wrong. Striking features of ecosystems are their tendency to be arranged into a heirachical structure with different trophic levels, its development of many complex interactions, and its chaotic population dynamics. In setting up a mathematical model, it is necessary to decide which of these observed qualities will be built into the model, and which (one hopes) will emerge from solving the model. For example, in May's work based on random matrices the trophic structure was not assumed, but the number of interactions and their distribution of strengths was. May showed that such simple ecosystem models captured chaotic population dynamics and stability[1,2]. Further work by Pimm and coworkers [4,6,12,13] showed that webs with an imposed heirarchical trophic structure (i.e. the absence of "trophic cycles": formally defined by loops in the directed graph) were more stable than random webs. However, large model food webs still tended towards instability. Subsequently, McKane and coworkers[14] investigated webs created by continuous introduction and extinction of species of preset trophic level and interactions, success depending on population dynamics. These webs evolve to contain large numbers of species, and are persistent even though species are continually being introduced and going extinct. However, in all of these models increasing the number of interactions per species leads to instability.

McCann *et al* addressed this latter issue by investigating simple webs with weak interactions[5], showing that weak interactions act to dampen oscillations and stabilise highly connected systems. Their argument for weak interactions is based on studies of interaction strengths in real food webs.

Here we show that stable, highly connected food webs with chaotic dynamics and many weak interactions arise from a generalised Lotka-Volterra model[4] with evolution of the interactions strengths (box 1).

Our calculations differ from previous work primarily in allowing evolution of the interaction strength. Such evolution may arise from various biological phenomena, including genetic and behavioural evolution, and changes in the spatial overlap of populations.. The interaction strength represents the balance of power between the species, each species tends to evolve more effective means of dealing with the other, but the interaction strengths, representing *differences* in effectiveness may increase or decrease. It cannot, of course, change sign as the role of predator and prey cannot be reversed. We assume that the overall effect is that large populations of predators become less well adapted to capturing rare prey, since other food sources are available, while small populations of prey become better able to avoid their major predators. Thus we simulate coupled population and evolutionary dynamics, starting with a pool of species and eliminating any population drops below a minimum threshhold.

Preliminary calculations with constant interaction strengths showed that this strategy produces large, feasible, viable food webs, but that the complexity of the interaction network remains low, on average just one link per species, independent of web size. This is consistent with previous numerical work on evolved webs [14] and the exact result for random webs[4]. Hence, as with all previous models, selection by extinction of failing species does not reproduce the observed complexity.

By allowing the interactions to evolve, we introduce one new parameter (the interaction evolution rate). We also eliminate two assumptions – neither the number of interactions per species nor the distribution of interaction strengths need be determined *a priori* – the system is able to evolve its interactions or make them so weak as to effectively remove them altogether. The model also does not preassign trophic levels or (almost equivalently) preclude trophic cycles.

We find that in our evolving-interaction model, when very weak interactions (less than 0.0001 of the maximum) are neglected, a cycle-free trophic structure with chaotic dynamics almost invariably emerges (Fig.1). Moreover, the distribution of interaction strengths (Fig 2) exhibits a power-law tail with an exponent of –0.83, independent of web size (for large webs). This means that the predators obtaining most of their resources from a few strong interactions; the effect of the many weak interactions is to stabilise the web, particularly by becoming stronger in times of declining population.

Behaviour of our food webs can be monitored by the flow of resources through the system[4]. We monitored this during our simulations and found a remarkable result – the total flow of resource (and hence total biomass) increases with time reaching a plateau after many thousands of steps – the steady-state link-strength distribution appears to maximise the use of resource. This type of optimisation is consistent with other ecological models [15,16]

In sum, we have shown that simply by allowing the strength of interactions to evolve in a GLV model, several features of observed food webs emerge spontaneously. These include chaotic dynamics, maximal use of resources, stability engendered by many weak links and absence of trophic cycles. While previous models have shown some of these phenomena, others have had to be assumed in the formulation of the models. This work emphasises the powerful effect of evolution in structuring the food web patterns of nature.

Mathematical details.

Lotka-Volterra-type models [4] consider populations as their basic objects, modelling the interactions between the various populations. The Lotka Volterra model[7] considers two species with populations x_1 (prey/autotroph) and x_2 (predator/heterotroph). x_2 has constant death rate, c and per capita reproduction proportional to the amount of prey abx_1. x_1 has a per capita death rate due to predation by x_2 and a regeneration rate constrained by environmental resources as described by the logistic map. This gives the following equations for two species:

$dx_1/dt = gx_1 - gx_1^2/K - a\, x_2\, x_1$; $dx_2/dt = a\, b\, x_1 x_2 - c\, x_2$.

This model can be readily generalised to N species.

For autotrophs, with x_0 setting the limit on the population

$dx_i/dt = x_i - x_i^2/x_0 + \Sigma_j M_{ij}\, x_i\, x_j$.   (1)

For heterotrophs,

$dx_i/dt = \Sigma_j M_{ij}\, x_i\, x_j - c\, x_i$.   (2)

We take c=0.01 and draw the initial M_{ij} randomly from a flat distribution between 0 and 1. This food web forms a directed graph where the species form nodes connected by interactions of strength $M_{ij.}$ We define resource flow (Fig 3) into the network as the sum of positive terms in (1) and (2) and flow out as sum of negative terms. Predation is not efficient, and following Lotka Volterra we assume that for positive M_{ij}, M_{ji}=-b M_{ij} with a birth efficiency b.

We also allow for evolution of the link strengths M_{ij} themselves. M_{ij} represent interactions between individuals of two species and its change therefore relates to the efficiency of predation. We assume that the driving force for change in M_{ij} is proportional to the number and strength of interactions $N_i N_j M_{ij}$. Furthermore, it depends on the population size, larger populations become less well adapted to exploit rare prey. specifically it is proportional to $(1/N_i - 1/N_j)$. The net change in M_{ij} is then

$dM_{ij}/dt = \varepsilon\, (N_i - N_j) M_{ij}$ (3)

where ε sets the rate of change. We set an upper limit of 1 on the efficiency M_{ij} - without this it is possible for species to evolve so as to exist on vanishingly small amounts of prey.

In our calculations we iterate equations (1-3) in time, eliminating any species for which $N_i<0$. The dynamics can be explored using an applet located at http://www.ph.ed.ac.uk/nania/ecosse/ecosse.html

The chaotic population dynamics, which can be introduced either by finite timestep or a sharp upper limit on M_{ij}, are crucial for power law dynamics: if we take an alternate plausible evolution of the interactions for which M_{ij} is self limiting:

$$dM_{ij}/dt = \varepsilon[(1/N_i)(dN_i/dt) - (1/N_j)(dN_j/dt)]\ M_{ij} \qquad (4)$$

and use an infinitesimal timestep, then the dynamics tend to a fixed point rather than chaotic state. Trophic level structure and high numbers of weak interactions still occur in this model, but curiously, the evolved link strengths are now exponential rather than power law distributed.

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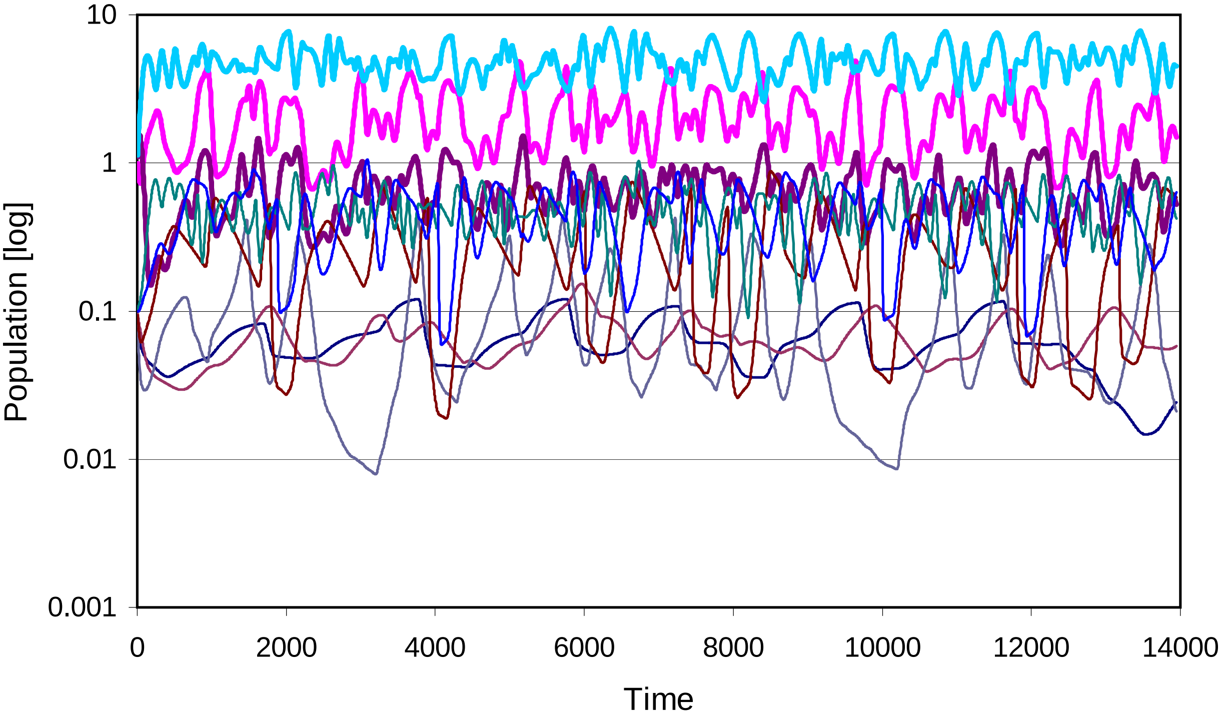
GJA designed the model, wrote the paper and wrote preliminary code, IDG improved the code, ran the simulations and prepared the figures.

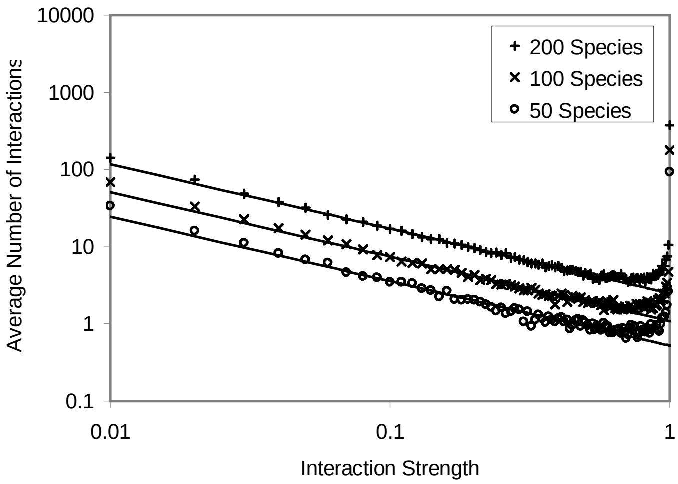
Correspondence and requests for materials should be addressed to G.J.A. (e-mail: gjackland@ed.ac.uk).

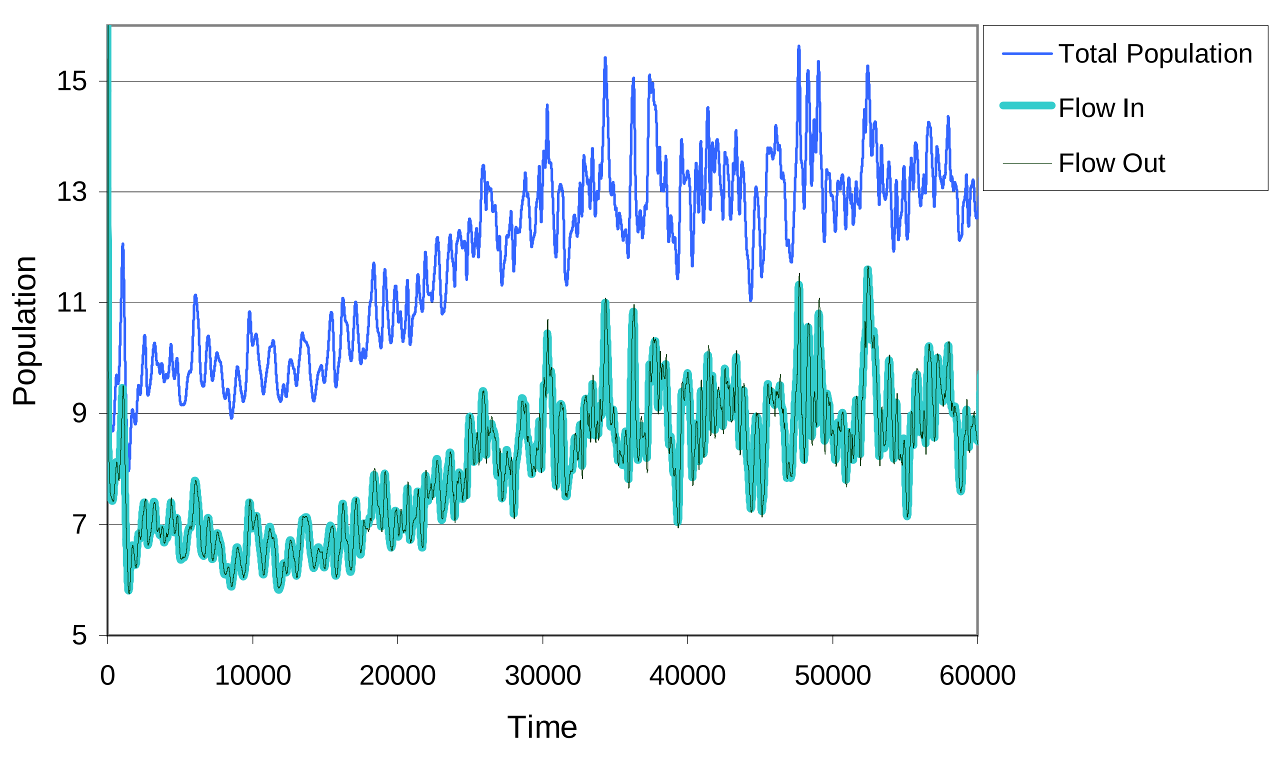
Figure 1 Time series of the populations of typical species in a typical evolving food web. Autotrophs are shown by thick lines, heterotrophs by thin. Units of population (N) are arbitrary, time is related to the death rate of 0.01 for heterotrophs (i.e. 100 is a mean lifespan). Both population dynamics and the dynamics of interaction stengths (not shown) are chaotic. Graphs of typical food webs can be seen and generated at `http://www.ph.ed.ac.uk/nania/ecosse/ecosse.html`

Figure 2. Plot of the (log) number of links against their (log) strength. The histogram is averaged over many snapshots from 100 webs of size a) 200 b) 100 c) 50. In each stable web the link strength varies with time - the interaction strengths are instantaneous not time-averaged values.

Figure 3 Total population as a function of time for a typical evolving web, and flow of resources into out of the web (see box for definition).


10
1
0.1
0.01
0.001
Population [log]
0
2000
4000
6000
8000
10000
12000
14000
Time


10000
1000
100
10
1
0.1
Average Number of Interactions
0.01
0.1
1
Interaction Strength
200 Species
100 Species
50 Species



Population
Time
Total Population
Flow In
Flow Out
15
13
11
9
7
5
0
10000
20000
30000
40000
50000
60000