

Chapter 1

On the evolution of structure in ecological networks

Matthew Labrum

Department of Mathematics, University of Idaho

Terence Soule

Department of Computer Science, University of Idaho

Aaron Blue

MMBB Department, University of Idaho

Stephen M. Krone

Department of Mathematics, University of Idaho

krone@uidaho.edu

Previous research on simulated ecological networks has often focused on issues such as the distribution of the number of links between species, without generally categorizing the types of inter-species relationships that develop, unless those relationships are of some predesigned form (e.g., food webs). In this work we use a model system to examine general, dynamically-evolved ecological networks that are subject to occasional invasion by novel species. Keeping track of the specific types and numbers of interactions between species over time leads to insight on how these affect network stability, fragility and evolution. We discuss the role that assembly rules play on the evolutionary trajectories of randomly initialized communities. We also investigate the occurrence of certain types of interactions (e.g., cyclic) and quantify their destabilizing effect on the network. In particular, extinctions and secondary extinctions (“avalanches”) are related to these issues.

1.1 Introduction

The structure of an ecological species network is influenced to a large degree by the historical nature of its construction [4]. This contingency effect, wherein the outcome of some event depends on the sequence of events that preceded it, can make the details of network architecture difficult to predict. In addition, there is a high degree of nonlinearity in the system due to the elaborate feedback between different parts of the network. Nevertheless, there is a great deal of regularity in the structure of many networks, both biological and non-biological. What causes this regularity and what are its effects? To what extent is network structure influenced by assembly rules, and how much of it is the result of general organizing principles that are relatively insensitive to the details of the model? There is a tension between the forces of self-organization and species–species interactions that combine to give the network its structure. Species interactions lead to perturbations in the network and the network forms the framework which gives these interactions their meaning. These interactions are never absolute. A species that fares well in one community may be doomed in another.

Real ecological networks have been shown to exhibit clustering and small world organization, and this influences community stability and diversity [6, 9, 5].

Our goal is to simulate ecological networks that are allowed to evolve as freely as possible rather than imposing some *a priori* structure. For example, we do not assume that our networks have food web topologies. It must be acknowledged, of course, that assumptions must be made in any model and these can bias the system. For example, species with negative intrinsic growth rates are obligate predators. Such species tend to have more interactions with other species than do those with positive intrinsic growth rates. It is for this reason, as well as our vast ignorance regarding the detailed interactions in most biological communities, that it is essential to let *in silico* ecological networks evolve on their own rather than simply assigning the interactions at random. Evolution and shared history are hallmarks of real communities.

Although the observations generated by our simulations should be applicable to a large range of ecosystems, we are particularly interested in microbial communities. In such a setting, our knowledge of inter-species interactions in natural and clinical settings is very tenuous. In addition, the number of “species” can be very large; e.g., estimates of 1000 bacterial species in a gram of soil are typical.

Most studies of real ecosystems are based on a snapshot in time and many of the statistics used to study these, as well as model ecosystems, are based on observations at a fixed time. In some cases, historical observations may be available that shed light on the past history of a particular ecosystem. In microbial communities, the time scales are such that “real-time” observations can be made and temporal data on community structure can be collected, although not without considerable effort. Because of the temporal nature of community construction and the state-dependent nature of community dynamics, we suggest that the collection and interpretation of temporal data can lead to a better understanding of complex ecological networks.

Our model ecosystems can be thought of as directed graphs with vertices representing species and edges representing interactions. We explicitly model the directions and strengths of the interactions, so these graphs are both directed and weighted. The sign of the interactions determine the types of pairwise interactions (predator-prey, competitive, mutualistic).

1.1.1 The model

Our simulations are based on simple Lotka–Volterra dynamics with no spatial structure. With $u_i(t)$ denoting the density of species i , the basic equation is

$$\frac{du_i}{dt} = u_i(r_i + \sum_j a_{ij}u_j). \quad (1.1)$$

Here, r_i denotes the intrinsic growth rate of species i and the a_{ij} 's represent interaction strengths. We simulate a discretized version of this model. Interaction strengths in stable communities are typically quite small [6, 8]. It has been observed [7] in similar food web simulations that the addition of nonlinear functional responses does not have a strong effect, at least for certain statistics. For this reason, we chose to treat only the above model. It should be noted, however, that certain types of nonlinear functional response, as well as spatial structure, can strongly influence the outcomes of multi-species associations, leading, for example, to a stabilization of competitive loops [1, 2, 3]. These complications provide fertile ground for future studies of ecological network evolution and suggest that we should not be overly biased by predictions arising from simple Lotka–Volterra models.

Our simulations were set up as follows. The initial ecosystem for each run consisted of 200 species. Each species had a maximum carrying capacity generated randomly (i.e., uniformly) over the range [1000, 10000] and a growth rate generated randomly over $[-0.1, 0.1]$. These values were used to generate a species self-interaction term (a_{ii}). Each species had an initial population size of 1000.

The probability of a given (one-way) link between two species was set at X/N , where N is the number of species in the population. Our experiments used values $X = 2, 3, 4$. The sign of the link (interaction strength) between two species that are connected (in a given direction) is positive or negative with probability $1/2$ each. The strength of such a link was randomly calculated using the formula

$$|a_{ij}| = \alpha R_{ij} \min_i |a_{ii}|,$$

where the R_{ij} 's are independent random numbers uniformly chosen from the range $[0.1, 1]$, and α is a fixed constant. We used values $\alpha = 1.0, 0.75, 0.5, 0.25$ in the simulations. Small values of α correspond to weak interactions.

The maximum total population was fixed at 1,000,000. This global density dependence is necessary to keep the number of species from growing without bound; without it, non-interacting species with positive growth rates keep accumulating. To implement this in the simulation, we trim an overfull ecosystem

as follows. After a given iteration, if the sum of the populations of all species exceeds 1,000,000 by an amount P percent, then we reduce each population by P percent. This brings the total population size back down to 1,000,000 before the next iteration. If the population of a species drops below 1, that species is removed from the ecosystem; it goes extinct.

New species (immigrants) were added (i.e., invade) when the ecosystem had stabilized after the previous migrant addition. Based on preliminary experiments, we say that the ecosystem has *stabilized* if there are 100 consecutive iterations without an extinction. New species are introduced with a population size of 100 and the corresponding parameters are chosen randomly according to the same rules as for the initial species.

In several of the experiments we measured avalanches of extinctions. The *avalanche size* is the number of extinctions between the addition of a new immigrant and re-stabilization of the ecosystem. For example, assume that a new species is added (with a population of 100) during some iteration, and over the course of the next 75 iterations five species go extinct, followed by 100 iterations without any further extinctions. The system is assumed to have stabilized, an avalanche of size five is recorded, and a new immigrant species is added to the ecosystem.

We consider two kinds of statistics: dynamic (time dependent) and static (collected only at the end of a run). Both viewpoints can provide information on community structure and stability.

1.2 Simulations

In the simulations, one typically sees an initial crash as a large number of species go extinct in a short time. This is followed by a gradual build-up in the number of species until some equilibrium level is reached. Throughout this process, extinctions occur, sometimes followed by secondary extinctions, or “avalanches”. We emphasize that our extinction events are dynamically generated, not just artificial removals.

Our first figure illustrates this process and shows the dependence on the parameters X and α . Note that the ecosystem is more stable for low values (roughly, less than 1.5) of the product $X\alpha$ and becomes more unstable as this product increases. In the accompanying tables, we say that an ecosystem is “successful” if it does not lose all its species during the time of the run.

If we let b be the average absolute interaction strength, L the total number of links, and N the number of species, then both empirical and model ecosystems typically have values of $b\sqrt{L/N}$ that are roughly constant as a function of time. This quantity can also be written as $b\sqrt{CN}$, where $C = L/N^2$ is the connectance of the network. In Figure 1.2, we see that as the product $X \cdot \alpha$ increases, the corresponding trajectory (an average of 20 ecosystem runs) has larger values and is more erratic. A large part of the increased variability comes from the fact that increasing $X \cdot \alpha$ tends to decrease the number of species.

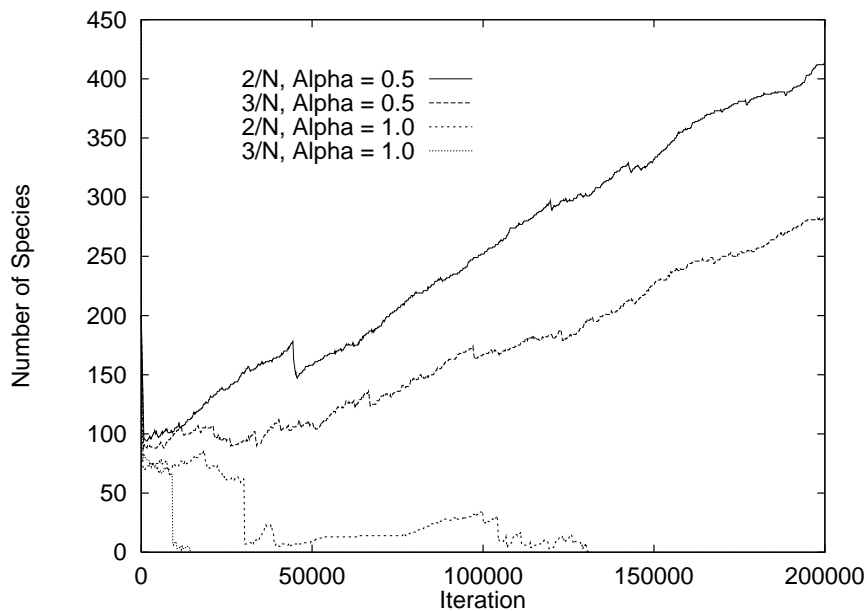


Figure 1.1: Number of species for different parameter settings. Each curve represents an average of 20 runs. Notice that diversity and stability are strongly influenced by the product $X\alpha$.

	2/N	3/N	4/N
alpha = 1.0	1	0 (49,750)	-
alpha = 0.75	16	0 (193,950)	1
alpha = 0.5	20	18	17
alpha = 0.25	-	20	20

Table 1.1: Number of ‘successful’ ecosystems out of 20. Number in parentheses is the iteration in which the last ecosystem failed.

	2/N	3/N	4/N
alpha = 1.0	13.0767 (0)	0	-
alpha = 0.75	75.125 (92.9324)	0	4 (0)
alpha = 0.5	393.5 (98.7666)	117.611 (131.196)	28.882 (48.516)
alpha = 0.25	-	476.65 (17.4822)	409.300 (124.612)

Table 1.2: Average number of species per ecosystem after 200,000 iterations. The number in parenthesis is the standard deviation.

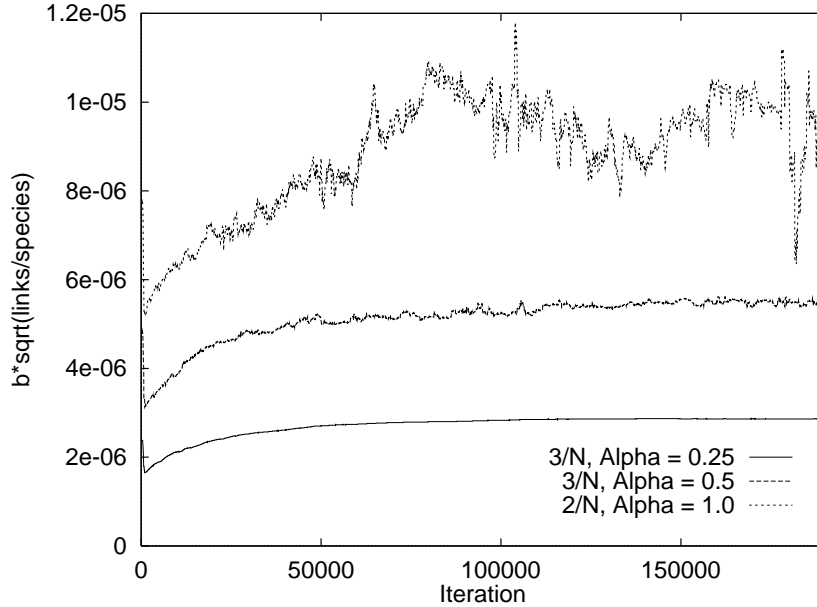


Figure 1.2: A plot of $b\sqrt{L/N}$ as a function of time. See text for parameter definitions.

1.2.1 The effect of loops

Occasionally, a group of species will become connected in a loop. If, going in a particular direction (and independent of what happens in the other direction), we have positive interactions (say $a_{i,i+1} > 0$), then we call this a *positive loop*. The ecosystems often became very unstable after the formation of such a loop. For the final set of experiments we examined the effects of positive loops directly by running a version of the model that does not allow any positive loops to form. For these trials when a new species is added to the ecosystem, it is immediately checked for positive loops that may have been created by the new species. If a positive loop is found then the new species is removed from the ecosystem and another species with different, random connections is added instead. This process is repeated until a new species is added that does not create any positive loops. This technique is also applied in generating the initial ecosystem of 200 species; so the ecosystem will never contain any positive loops.

For ecosystems with parameters that produce unstable conditions the results with no positive loops are significantly different from the results with positive loops. Figure 1.3 shows the effect on diversity and stability by recording the number of species as a function of time.

In the last figure, we show that the avalanche size distribution obeys a power law, $y = \text{const.}x^{-\gamma}$, if we let x represent avalanche size and y the number of avalanches of that size.

We also counted the total number of avalanches for all twenty runs for the

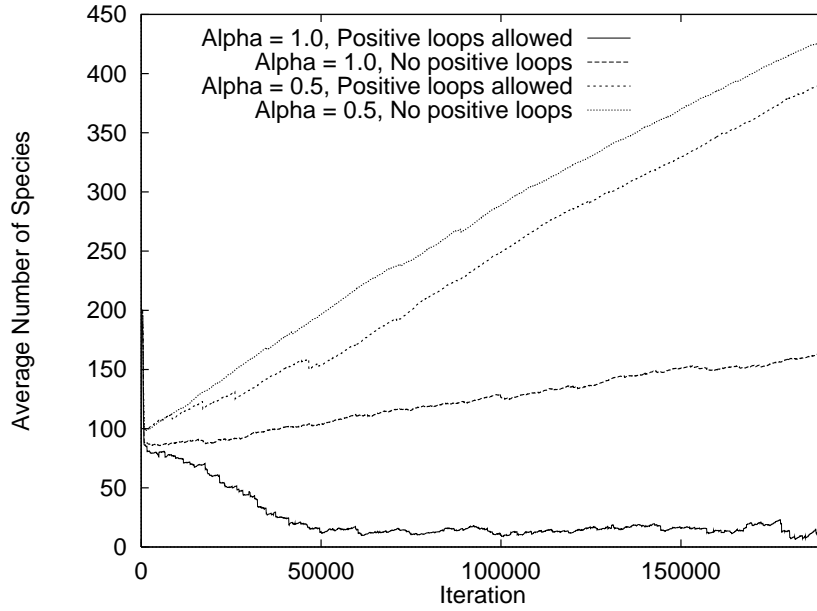


Figure 1.3: The average number of species (averaged over 20 runs, with $X = 2$) as a function of time, both with and without positive loops.

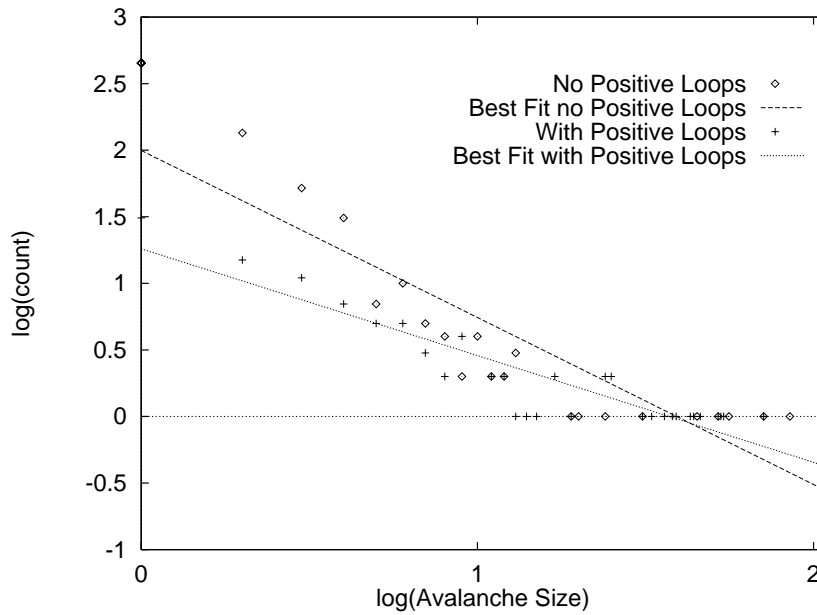


Figure 1.4: Power law behavior for avalanche size distribution, both with and without positive loops. The power law exponents are $\gamma = 0.802$ (loops) and $\gamma = 1.255$ (no loops).

unstable parameters $2/N, \alpha = 1.0$ with positive loops allowed and without positive loops. We did not count the initial species ‘crash’ that occurs in the first few hundred iterations. In both cases the smaller avalanches, those in which 1 to 36 species went extinct, obeyed a similar power law relationship. The smaller avalanches are much more frequent.

However, for avalanches larger than 36, the behaviors were very different. Without positive loops there were no avalanches larger than size 36. With positive loops there were 15 avalanches of size 37 to 100, including two of size 91. There was slightly less than one large avalanche per trial. Note that, in general, the ecosystems can only support one such large avalanche as, after it occurs, the number of species is typically less than 36. Thus, the lower number of species observed in Figure 1.4 with positive loops (parameters $2/N, \alpha = 1.0$) can be attributed to the occurrence of a single large avalanche that does not occur when positive loops are not allowed.

1.3 Acknowledgments

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