BIOU9PC: Population & Community Ecology
Lab Practical 10-11: Food Web Stability

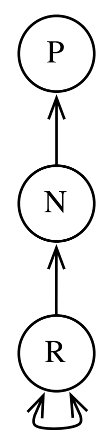
17 & 24 November 2016

Introduction
Your objective these two weeks is to determine the relative stability of ecological communities. We have already examined the degree to which the intensity of inter- and intra-specific interactions, including competition and predation, affect the abundance and persistence of organisms. This week's objective differs, in that we are interested in the effect on stability caused by the presence or absence of interactions, rather than assuming that an interaction exists, and investigating its intensity.

Why do this? Humans have manipulated the topology of food webs around the world. There are countless examples of species introductions, some of which are intentional, whereas others involve species that have unintentionally been introduced and have become invasive. Each time that we introduce a predator or a parasitoid to control an invasive pest, reintroduce previously extirpated species, or even stock game fish into a lake, we affect a food web. Today's models, though abstract, provide a useful tool for predicting the effects of ecological management and conservation actions.

Food webs may be visualized as a network of nodes connected by lines. The nodes indicate taxa, often resolved to the species level. Connecting lines indicate that an interaction exists between those nodes. Additional information, for example, the intensity of that interaction, may be indicated by the width or coloration of those lines. In this way, food web diagrams can communicate a great deal of information about the processes in an ecological community. Diagrams, however, are insufficient for analysis.

For analysis, a food web can also be represented as a square matrix, in which each species represents both a row and a column. **Columns represent the effect of a species on itself and the other species**, whereas **rows represent the effect that other species have on it**. The following matrix represents a simple three-species food chain consisting of a primary producer (R), consumer (N) and predator (P):



$$\begin{bmatrix} - & - & 0 \\ + & 0 & - \\ 0 & + & 0 \end{bmatrix}$$

The diagonal (from top-left to bottom-right) represents a species' effect on itself.
Here, we assert that primary producers compete among themselves, but other species do not. The second element in the first column in positive, because the producer has a positive effect on the consumer. The third element of the first column is 0, because the predator does not directly affect the primary producer. The two elements immediately above the diagonal are negative, reflecting that the consumer negatively affects the primary producer, and the predator negatively affects the consumer. The matrix depicted above is *qualitative*, in that the signs of the interactions are

indicated, but not their magnitudes. In the *quantitative* models that we will use today, the non-zero elements of this type of matrix are replaced with numbers (of appropriate sign), indicating the magnitude of the interaction between all pairs of modeled species.

We can assess the stability of a food web in several ways. First is to ask, do all species persist indefinitely in the system, or do some go extinct? If some go extinct, which species go extinct first? If all species are able to persist indefinitely in the community, we can quantitatively assess the stability of the system. We do so using the **return time**. A community's return time indicates the time necessary for it to return to equilibrium population sizes following a perturbation that knocks it away from that equilibrium. Remember Practical 6, in which the predator-prey models with density dependence (Model 2) showed damped oscillations. In those models, initially large deviations from equilibrium faded over time, and the system converged to a stable equilibrium. Roughly stated, the 'return time' is a measure of the amount of time necessary for oscillations to dampen, and the community to return to a stable equilibrium. In contrast, the basic Lotka-Volterra predation model explored in Model 1 of Practical 6 exhibited 'neutral stability', meaning that it exhibited stable limit cycles, but never converged to a stable equilibrium. The 'return time' of such a system is infinite. The mathematical details are not crucial for your understanding of today's practical. The important thing is that increased stability in a food web is indicated by a *decrease in return time*, and vice versa. Many other measures of stability exist, including resistance and resilience, but we will use return times for this practical.

For those who wish to dig deeper: The food web matrix (**M**) derives from the differential equations of population dynamics. It is the Jacobian matrix of these differential equations, and constructed as the partial derivatives of per-capita population growth rate for each species with respect to each species in the system, evaluated at equilibrium. The return time of a food web is calculated as `-1/max(Real(eigenvalues(M)))`. Pages 147-150 and the appendix of the Morin textbook provide more detail on this topic.

Approach

In this practical, you will begin by investigating the relative stability of food webs that I have constructed for you. Then you will generate additional food webs from real-world data, and evaluate their stability following anthropogenic perturbation(s). To obtain generalizable results, we build 1000 versions of a community, each with interaction strengths drawn randomly, as explained below. This means that the stability patterns obtained are not attributable to any specific parameter value (i.e., any particular interaction strength), but rather indicate the stability imparted by the structure (topology) of the food web itself. This is important, because interaction strengths are difficult to estimate with certainty in the real world.

Our assumptions for food web construction are as follows:

- **Primary producers have intra-specific competition**. Thus, their entries, which appear along the diagonal (top left to bottom right) are -1, with no variation (as in Practical 9).
- **At other trophic levels, intra-specific competition is assumed to be nil**. Thus, all other entries along the diagonal are 0.
- **Inter-specific competition is weaker than intra-specific competition**, and roughly symmetrical. Thus, the negative effects of interspecific competition of species i on species j, and species j on species i are drawn independently from a uniform distribution on the interval (-1, 0).

- **Trophic interactions are asymmetric**. The act of consumption has a strong negative effect on the prey, but only a weak positive effect on the predator. Thus, negative effects (predator on prey) are randomly drawn from a uniform distribution on the interval (-10, 0), whereas positive effects (prey on predator) are randomly drawn from a uniform distribution on the interval (0, 0.1). Note that herbivory and parasitism are both forms of predation.
- **It is possible to include mutualism.** Please consult with me before doing so.
- **Consult with me about other interactions you want to model.**

A key R function for this practical is `runif(n, min, max)`. `runif()` draws n random numbers from between `min` and `max`. All numbers are equally likely, as it draws from a uniform distribution

The techniques of this practical are rooted in the analyses presented by Pimm & Lawton (1977) *Nature* 268: 329-331, which is summarized in the Morin textbook on pages 147-150. Refer to those documents for further detail and background.

In-lab exercises

For each of the following questions, evaluate the effects on ecological communities that are caused by the indicated perturbation. Interpret the effects of the perturbation in terms of stability and response time. Provide graphical output to support your interpretation, where necessary.

1. *Adding higher trophic levels to an un-branched food web*. Compare Models A, B and a five-species community (which you have to make).
2. *Adding an additional primary producer*. Compare Models A, C and a three-producer community (which you have to make).
3. *Adding competition between producers*. Compare Models C, D and the model you made for Question 2, adding competition among the three producers
4. *Adding omnivory*. Compare Model B with a modified Model B in which the top predator eats both the consumer and the predator.
5. *Complexity and stability*. How does the stability of Model G vary with species richness and connectance? Does richness of connectance more strongly affect stability?
6. *Add a new consumer to a model of your choice*.

Assignment

Your task is to evaluate the stability of a real-world food web in the face of perturbations imposed by humans. First, choose a food web from the library of food webs on Succeed. Choose one that is a) interesting to you, b) contains 5-20 species[1], and c) faces anthropogenic impacts Learn about the natural history of your ecological community by obtaining the study that generated the food web using Google Scholar. Hypothesize the effects of humans on the food web. Do humans introduce a new organism? Do they remove one of the existing organisms? Will they modify the intensity of interaction(s) among the existing organisms? Establish a community matrix that describes the interactions among the organisms in their pre-perturbation state.

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[1] If you choose a community with too many species, it will be difficult to analyze. I can help you simplify large communities, if necessary.

Establish community matrices that describe the interactions among your organisms with and without the anthropogenic perturbation(s). Evaluate the degree to which the perturbation(s) affect the stability of the ecological community. Describe how the perturbation(s) could be ameliorated.

Write a brief but insightful scientific paper on your analysis of the stability of your chosen ecological community. In the **introduction** (20 marks), clearly introduce the ecological community, and the anthropogenic perturbation you will study. Be sure to provide enough motivation and background so that the reader clearly understands the context of your study. Consider your audience to be other 3^{rd} or 4^{th} year biology students. State your **hypotheses** (10 marks) clearly, justifying the predictions you make. In the **methods** (10 marks), briefly explain how you established and manipulated the model. Provide enough detail that the reader will understand the manipulations you have made. In the **results** (20 marks), lay out your findings clearly using complete paragraphs. Use **tables or figures** (20 marks) to convey your principal results. Among your figures and tables, you should present the community matrix and the community diagram. Be sure that your figures are legible, well-labelled, include complete captions, and illustrate your findings. In the **discussion** (20 marks), interpret your findings in terms of your research questions. Did your results support your hypotheses? What implications can be drawn from them? Extensive literature research is not necessary, however, you may find it useful to refer to some papers to interpret your results. Use no more than 1500 words (excluding figure captions and references).

During the practical sessions, I encourage you to work with your classmates. Your report, however, must be written in your own words. Write your reports *independently*. Turn in this assignment using Turnitin ONLY by **Friday December 2^{nd} at noon**. There is no need to submit a hard copy. Indicate your identity with your student number, and only your student number.