A. Defining and predicting keystone species in the tangled bank

B. Dimensions of keystoneness in ecological communities

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**Introduction:**

How ought one define a keystone species? The first use of the term came from Robert Paine in 1969(?) to describe the importance of sea stars (*Pisaster*) to the diversity of benthic intertidal mussel communities. He found that following the exclusion of sea stars, a generalist predator of mussels (among other prey), there was a dramatic reduction in the diversity of mussel species in the excluded area. The sea stars were preventing competitive exclusion by consuming mussels and opening up new habitat for settlement.

Ecologists soon picked up this new term, and it has come to generally mean a species that is important to the ecological system. Over the past 60 years a number of methods have been developed to identify keystone species in ecological communities. One of the more popular methods is by examining the topology of the interaction network, with the theory being that species with high degree (more interactions) or betweenness (number of pathways running through the node) should be more important to the system. Node degree and betweenness as measures of keystoneness have been derived from network studies that show that removal of hub nodes in networks, both generally (e.g., the internet) and ecologically (e.g., food webs), destabilizes the system more than random removals.

Simulated removal of species from food webs has revealed that… Something about the food web studies.

Undoubtedly there has been a bias in ecological analysis of keystone species towards trophic interactions. Recently, however, there has been a trend towards incorporating multiple interaction types into our understanding of ecological communities (proulx paper, Chilean network paper, sander et al.).

**Methods:**

*Generating a community*

We analyzed equilibrium communities using two different approaches. The first was to use initially randomly interacting species, and the second was to use the architecture of a real network of species interactions.

The random model we used was the Erdos-Renyi (ER) model implemented in *igraph* (**Csardi CITATION**). This model takes in two parameters, the number of species and the connectance, and returns a network with any two species having an equal probability of interacting with one another. The ER networks we used were initialized with 100 species and connectance of 0.2 (meaning 20% of all possible interactions are realized).

In nature, however, most ecological networks do not have random structure. To assess how non-random structure may influence our results we used the architecture of the Tatoosh Island interaction web. This network was generated from observed interactions in the intertidal zone. This network consists of 110 species and 1898 links of multiple different interaction types. The original data has 869 predator-prey pairs, 5 mutualistic links, 208 commensal, 492 amensal, and 324 competition. We generated new communities by randomly assigning each link in the Tatoosh network a new interaction type.

We used a generalized Lotka-Volterra model to simulate the dynamics of each community. The change in each species’ abundance was modeled as:

where *Xi* is the abundance of species *i*, *ri*is its growth rate, *Ki* its carrying capacity and αij is the effect of species *j* on *i*. In our simulations carrying capacity was set to a community-level carrying capacity and each species’ carrying capacity was defined as *Kcommunity/#species*. This model was implemented in R *version 3.2.3* using the deSolve package.

Growth rates for each species drawn randomly from a uniform distribution between 0.1 and 1. Interactions were drawn randomly from the absolute value of a standard normal distribution. Mean interaction strength was therefore equal across different interaction types. The community carrying capacity was set to 20.

We simulated the initial community dynamics for 4000 time steps. Species whose abundance dropped below 10^-5 were considered locally extinct and their abundance was reset to 0. The resulting equilibrium communities, composed of those species whose abundances are greater than zero at t = 4000, were then used to measure keystone status.