Alternative community structures in a kelp-urchin community: A qualitative modeling approach

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ABSTRACT

Shifts in interaction patterns within a community may result from periodic disturbances and climate. The question arises as to the extent and significance of these shifting patterns. Using a novel approach to link qualitative mathematical models and field data, namely using the inverse matrix to identify the community matrix, we reconstructed community networks from kelp forests off the Oregon Coast. We simulated all ecologically plausible interactions among community members, selected the models whose outcomes match field observations, and identified highly frequent links to characterize the community network from a particular site. We tested all possible biologically reasonable community networks through qualitative simulations, selected those that matched patterns observed in the field, and further reduced the set of possibilities by retaining those that were stable. We found that a community can be represented by a set of alternative structures, or scenarios. From 11,943,936 simulated models, 0.23% matched the field observations; moreover, only 0.006%, or 748 models, were highly reliable in their predictions and met conditions for stability. Predator–prey interactions as well as non-predatory relationships were consistently found in most of the 748 models. These highly frequent connections were useful to characterize the community network in the study site. We suggest that alternative networks provide the community with a buffer to disturbance, allowing it to continuously reorganize to adapt to a variable environment. This is possible due to the fluctuating capacities of foraging species to consume alternate resources. This suggestion is sustained by our results, which indicate that none of the models that matched field observations were fully connected. This plasticity may contribute to the persistence of these communities. We propose that qualitative simulations represent a powerful technique to raise new hypotheses concerning community dynamics and to reconstruct guidelines that may govern community patterns.

1. Introduction

The structure of a particular community is determined by the physical environment, biological interactions, episodic dis-turbances and successional sequences (Power et al., 1996; Winemiller, 1996). Communities from the same location can go through different successional stages that are driven by local and global dynamics. Successional patterns can be the

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result of different disturbance regimes, changes in species abundances, and different life history strategies, and interactions among community members (Winemiller, 1996).

Community membership can change or interactions among community members can switch, presumably as a result of functional responses. Capturing these responses present ecosystem and community ecology with a formidable task, including modeling. An observed response may be the reaction of a stable or unstable community, a community in transition from one configuration to the next, or a switch in response from one stable configuration to another. Determining community structure and stability from empirical observations is problematic because of generation time constraints among community members and of spatial and temporal scales of observations. Generation times must be measured on the ecologically dominant species, which may be exceedingly long lived (Connell and Sousa, 1983), and different life history strategies can have a particular influence in food web structure, determining the fate of community succession (Winemiller, 1996). Moreover, scaling-up predictions from small-scale experiments to large-scale ecological systems are fraught with difficulty because of lack of context (Cooper et al., 1998). It is difficult also to parameterize the strength of all important interactions within a community (Wooton and Emmerson, 2005). Therefore, only an incomplete understanding of community dynamics is possible.

When modeling ecosystems and communities, the goal is typically to find a single model that will fit the system under study. Defining models that best characterize a specific area is a difficult research question due to the lack of mathematical tools that systematically consider all the possible alternative models that might represent a particular community. Determining alternative communities requires rigorous description of all possible interactions among its members. The task is formidable if interactions among species are not known or need to be quantitatively specified. To our knowledge, the complete quantification and validation of a complex community have only been done once (Schmitz, 1997). Perturbation experiments to reveal the interaction strength of more than three species obviously are difficult to achieve, especially in harsh environments such as the subtidal zone off the Oregon Coast, where kelp forest communities are common.

In this study, we reconstruct community networks where interactions between species are neither known nor assumed constant. We do so by collecting data on change in density and interpreting these data as elements of the inverse (or adjoint) of the community matrix. From the inverse, we then can assess the community matrix itself (which mathematically speaking is the 'inverse of the inverse'). We apply this approach to members of a kelp forest community in a marine reserve off the Oregon Coast. We identified the kelp forest community members to create a reference model from which qualitative simulations were performed. We then developed an algorithm to perform qualitative simulations that generated all the plausible models from a community matrix of size N. Predictions for all simulated models were compared to changes in species abundance from year to year to identify a model or set of models that match model predictions. Models that matched the field observations and had highly reliable predictions (based on criteria in Dambacher et al.,

2002; Dambacher et al., 2003b) were selected to represent the kelp forest community structure from a particular study site off the Oregon Coast. We conclude that a dynamic community can be represented as a relatively small and closely related set of models with a highly consistent structural core.

2. Methods

2.1. Qualitative analysis

We used qualitative analysis theory that uses signed digraphs to represent a system and that analyzes a community through its 'community matrix' (Levins, 1974, 1975; Lane and Levins, 1977; Puccia and Levins, 1985). Unlike traditional food web analysis, which requires detailed information about the strength of direct and indirect interactions, qualitative (loop) analysis relies on a matrix of positive, negative and zero interactions. General applications of the technique to aquatic systems can be found in Puccia and Levins (1985), Lane and Levins (1977), Puccia and Pederson (1983), Li et al. (2000), Castillo et al. (2000), Hulot et al. (2000), Dambacher et al. (2002), Bodini (1998, 2000), Bodini (2000) and Ortiz and Wolff (2002). Qualitative analysis incorporates direct interactions between community species that are tabulated in the community matrix (A) and illustrated in signed digraphs. A recent study used qualitative analysis to demonstrate that functional diversity and indirect interactions play an important role in the response of ecosystems to perturbations, suggesting that complex food webs may be more predictive of behavior of complex systems than linear webs (Hulot et al., 2000). The method has recently been independently validated in field studies (Ramsey and Veltman, 2005).

A signed digraph consists of a network diagram of a community in which the vertices are variables that are joined by a directed line (link) indicating an interaction. A positive interaction from variable i to variable j is represented by an arrow ($\rightarrow$) and a negative one by a close circle (—●). The direct pathway between predators and prey indicated by arrows and circles (●→) signifies the benefit received by the consumer and the simultaneous loss suffered by the resource. Different direct relationships can be represented in signed digraphs: mutualism ($\leftarrow\rightarrow$), commensalism ($\rightarrow$), amensalism (—●), and interference competition (●—●) (Fig. 1).

In a particular system, site changes in the environment (natural disturbances or inputs to the system) can cause parameter changes (growth, mortality, survival) in one or more species. Each member of the community will react to this input either by increasing, decreasing or not changing in abundance. Direct and indirect paths determine how each species will respond to input from a press. The direction of change in abundance of each species after the disturbance is obtained from the inverse of the community matrix (A^{-1}) or prediction matrix (Levins, 1974, 1975; Bender et al., 1984; Dambacher et al., 2002) that predicts the effect of one input on all community members.

Predictions from the inverse matrix can be subject to a high degree of indeterminacy, as reported by Schmitz (1997) and Yodzis (1988). Theoretical qualitative predictions have been limited by the lack of a practical method to discrimi-