NICHE HIERARCHY: Structure, Organization, and Assembly in Natural Systems

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If deep general principles are to be found (in ecology) they are likely to be associated with general widely observed empirical regularities. This work is motivated by the idea that conceptions and theory should arise from observations and measurements of nature, and that the theory should be as directly and simply connected to measurements as possible.

1.1 INTRODUCTION

Three important properties of a large multispecies community are the topological structure of species interrelationships (e.g., who competes with whom), the dynamic nature of these interactions, and the resulting pattern of species relative abundance. Ideally, a logical order in which these properties might be studied would be first to obtain a sketch of the bare outlines of community organization by determining the topological constraints acting within real communities, then to color in the sketch by adding dynamic behavior to the static linkages among species, and finally to extend these insights toward understanding macroscopic patterns of species commonness and rarity. Each step, by this plan, leads naturally to the next in terms of detail and complexity.

In contrast to this ideal situation, the historical arrow has actually flown in the opposite direction. Species abundance patterns which figured prominently since the early part of this century were superseded in the 70’s by concern over the dynamic behavior of ecological
systems, and it is only recently that attention has focused on a formal study of the topological properties of communities. This realized trajectory is understandable and corresponds both to the conceptual primacy of these properties as well as to the chronological order in which the mathematical tools required for each subject were refined. Dominance and diversity are certainly more directly observable than are fluctuations in population sizes, and these in turn are less subtle to perceive than the linkage patterns of niche interrelationships. The tools for probing structure, graph theory and algebraic topology, have really only come into their own in the last few decades, compared with the better established disciplines of differential equations and statistics used to study dynamics and relative abundance patterns.

There is little doubt that the reversed ordering of events was necessary, however an apparent consequence of the historical trajectory is that connections between these three major areas are either weak or completely missing. As Robert May (1979) recently remarked, the relationships between community organization and dynamics is largely speculative and have yet to take advantage of real topological constraints such as those discovered by Cohen (1978) in the empirical data. The implications of structure and dynamics for species abundance patterns is presently also a wide open area for inquiry. This seems a bit curious especially in view of the effort devoted by earlier generations of ecologists to the species abundance problem. Whether these discontinuities are an expression of specialization, disenchantment with unyielding problems, or popular trends, it seems likely, had the flow gone from topology to abundance patterns, or from dynamics to topology that a much more unified picture would have emerged by now.

1.2 MENU

This collection of essays attempts to tie together the properties of topological structure, dynamics, and relative abundance in multispecies communities. It is anchored at either end by two provocative empirical regularities: Cohen’s (1978) discovery that real ecological ensembles can be rendered in one-dimension, and thereby represent a small subset of mathematically possible topologies, and Preston’s (1962) finding that most real taxonomic communities can be
The Beginning

uniquely described by a specific one-parameter relative abundance distribution, the so called canonical lognormal distribution of species abundance. In addition, a new empirical regularity is introduced showing that niche space has the topology of a simple solid rather than of a perforated multidimensional swiss cheese. The idea used to unify these properties is the broad concept of hierarchical organization which is developed in two senses: structural hierarchy and functional hierarchy. Structural hierarchy refers to the formal topology of trophic linkages and functional hierarchy to the dendrogram of relationships organizing the system.

Chapter 2 begins by presenting a new mathematical characterization of the niche which aligns roughly with Hutchinson’s (1958) hypervolume concept but where a species is viewed as an n-dimensional resource set (resource clique or simplex) rather than an n-dimensional hypervolume per se. This makes Hutchinson’s idea operational with available foodweb data and allows for a sensible discussion of the communal niche space—sensu Whittaker’s (1972) community hypervolume—in cases when the species involved have resource sets of different dimensionality.

Chapter 3 shows how this architectural description of the niche can be used to make sensible the question “are there holes in niche space?” This is presented as the converse of the well-known species packing problem and asks whether there are any realized minimal constraints on the structure of the niche. Tested on coarse data from a diversity of food webs, and more refined data from bird communities we find that most if not all real ensembles tend to be packed in a conservative manner that allows no holes.

Chapter 4 centers on Cohen’s finding that nature contains an excess of interval food webs. This excess is shown to be a by-product of a more fundamental property in the structure of niches, the rigid circuit property; which, in turn, leads to a simple and biologically sensible rule operating in the assembly of communities. The assembly rule is derived by mathematical deduction and is necessary and sufficient to explain the observed high frequency of rigid circuit graphs as well as the absence of holes in the niche discovered in the previous chapter.

Chapter 5 asks whether niche space is organized as a structural hierarchy i.e. whether species niches are strung together noncircutously in a tree-like fashion. By relating this formally to the question
of holes, most of the real niche spaces examined are found to be consistent with organization of this kind. Also introduced here is the notion of functional hierarchy where the binary linkages of the structural portrait are given weight and degree, and the ensemble is assembled into nested guilds, chinese box fashion, according to increasing degree of functional similarity. Results demonstrating a correspondence between functional hierarchy and properties of the underlying structural portrait are discussed by introducing the concept of compatible ordering.

Chapter 6 begins to forge the link between topology and dynamics and investigates the cause and effect relationships between observed topological patterns and their dynamic background. Preliminary results here show that observed structural patterns in niche overlaps may indeed be at least partially shaped by dynamic behavior, and that such organization in ecological communities may in turn help to make them more robust to outside perturbations.

Finally, Chapter 7 examines the consequences of hierarchical community structure for species abundance patterns. The motive here is to seek a correspondence between two separate classical ideas about structure: functional organization and species abundance distributions. Here it is shown that hierarchical organization in the niche may account for most observed abundance structures including Preston’s (1962) canonical lognormal distribution, Motomura’s (1932) geometric series and MacArthur’s (1957) broken stick distribution. Data from bird communities are used to make independent and more restrictive tests of the correspondence between functional organization and relative species abundance.

This work is not intended to be a comprehensive treatment of topology, dynamics and the species abundance problem. In particular, one specific aspect of niche topology not discussed is the directed-graph or food-web portrait of predator prey relationships investigated recently by Pimm and Lawton (1980), Auerbach (1982), and Post and Pimm (1982). Rather than focusing on the predator prey picture we will concentrate on the competitive structure of niche overlaps, mainly because this is a level where interesting regularities appear and find coherent expression.
Although the treatment of dynamics uses simple analysis based on stability and equilibrium, the results reported here are believed to be robust to these assumptions. The link between dynamics and species abundances remains indirect in these essays and is mediated by the extent to which dynamics helps to explain observed topologies. A further study that connects explicit ecosystem dynamics to abundance patterns and to fluctuations in abundance remains a focus of future work.