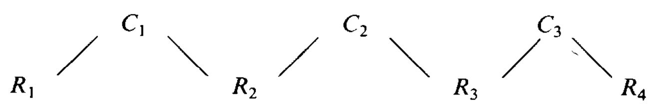
BOOK REVIEW

J. Cohen, *Food Webs and Niche Space*, Princeton U. P. Monographs in Population Biology, Princeton, N.J., 1978, 189 pp.; cloth $14.00, paper $6.95.

I first heard Joel Cohen speak on this subject at the University of Chicago in 1969. At that time he suggested that there might be a consistent pattern exhibited by food webs in nature. It was by no means clear that the pattern was real, although the available data were suggestive. But even if that pattern did exist, it was not apparent what to make of it. It wasn't predicted by an obvious dynamic theory, nor did it suggest the existence of some deeper structure which we might study. The book *Food Webs and Niche Space* is an impressively detailed and carefully thought-out elaboration of that talk. It is the result of an ambitious program and is must reading for anyone interested in population interactions, niche theory, or community trophic structure.

The original presentation included a tentative observation and a question. The observation: an interesting pattern *may* exist in nature. The question: if the pattern does exist, what does it mean? I believe this entire book can be summarized first as an attempt to make the observation less tentative, and second as speculation about the answer to the question. The work is less than totally convincing on the second count. Nevertheless it brings into focus a perplexing problem that may eventually result in totally different ways of looking at ecological communities.

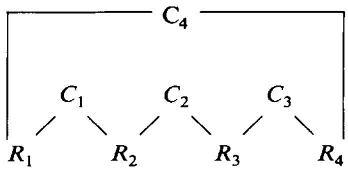
With apologies to Professor Cohen, let me crystallize the question with a heuristically motivated and thus highly oversimplified example. Suppose we begin with a very simple food web composed of three consumers and four resources as follows:



We now ask how we might add a fourth consumer to the system. The fourth consumer might be a specialist, eating only R_1, or R_2, or R_3, or R_4. Or it might be a generalist eating one of nine possible combinations of resources (R_1 and R_2; or R_2 and R_3; or R_3 and R_4; or R_1 and R_3; or R_2 and R_4; or R_1, R_2, and R_3; or R_1, R_2, and R_4; or R_1, R_3, and R_4; or R_2, R_3, and R_4). These thirteen possibilities (four for the specialist, nine for the generalist) are all within the confines of making the food web representable by an "interval graph." Adding a consumer that eats only R_1 and R_4 is the single possibility that leads to a noninterval graph. The general observation is that food webs in nature tend to be representable by interval graphs. That is, for this particular example, the only

0025-5564/79/040305+3$02.25

way of adding the fourth consumer that is *not* permissible is

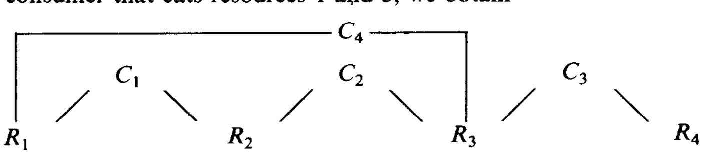


All other thirteen possible ways lead to interval graphs.

Cohen presents a convincing body of empirical data suggesting that food webs in nature tend to be representable by interval graphs, implying the existence of a natural pattern, heretofore unrecognized, that calls for a theoretical explanation. But undoubtedly the reader will have already noticed that the overwhelming presence of interval graphs may be nothing more than a statistical artifact (e.g. in the above example 13 of 14 possible graphs are interval graphs). Here Cohen makes quite a convincing argument that the high frequency of interval graphs in nature is very unlikely the result of a simple statistical artifact. The pattern seems to be a real pattern. Fifty-one pages (chapters 3 and 4) of this 131-page book are devoted to this task. I am convinced that the pattern is not a statistical artifact (prior to reading this book I was not so convinced).

The explanation of the pattern is somewhat less convincing, for a variety of reasons. The suggested explanation is that niche space is one dimensional, at least with respect to trophic niches. More accurately, niche overlaps can be represented in one-dimensional space. In my view this explanation is less than satisfactory. The ambiguity with which it begins allows a diverse array of outcomes, leaving one with a feeling that there has been more of an attempt to reconcile new patterns with old theory than to discover new theory. Indeed, I suggest that perhaps whole new ways of dealing with population interactions might be required to explain these new observations satisfactorily. It may be that dealing with traditional concepts such as niche overlap and dimensionality may shed more haze than light.

An example will illustrate my reservations. According to Cohen (p. 6), "If two kinds of organisms...both eat some kind of organism...the niches (of the two) logically must overlap... ." He then asks the question (p. 11) "Can all the overlaps...be represented exactly by connected regions in a one-dimensional space...," and answers with a resounding yes, for any trophic webs that can be represented by an interval graph. But if we forget about interval graphs for a moment and simply try to apply all this niche overlap stuff to the above example, the answer is not so resoundingly "yes." For example, if we add a fourth consumer that eats resources 1 and 3, we obtain



It is obvious that all overlaps cannot be represented by connected regions, since there is no way of ordering the four resources in such a way that the niches themselves are connected regions—if we consider the resources as orderable points in one-dimensional niche space [e.g. the niche of C_4 is the set (R_1, R_3) which is separated by R_2, and any other ordering of R's would result in some other consumer's niche being not connected]. Yet the example is an interval graph.

But this is not the concept of "overlap" and "connected" that Cohen is talking about. In Cohen's framework the overlaps must be representable in an abstract one-dimensional space. Nevertheless, the above example serves to illustrate the confusion that may result from a procedure that defines niche overlap more or less as common food habits and then claims that overlaps can be represented in one dimension even when they clearly cannot be so represented along a well-defined food dimension, necessitating the postulation of an abstract or "unknown" dimension (with an entire chapter devoted to the question "what is the dimension?"). When such results are further used to imply that mathematical models based on one-dimensional overlaps may not be so bad after all (p. 100), we dangerously approach the boundaries of unreasonable extrapolation.

Perhaps the insights of this book (and there are many) could be put into a more constructive framework if the classical notions of niche, overlap, dimensionality, etc. were abandoned. For example, might we suggest that noninterval graphs occur only when indirect competitive effects are felt through two or more competitors (in the second of the above three graphs C_2 receives no direct competitive effect from C_4 but rather receives the competitive effect of C_4 through C_1 *and* C_3)? And if so, what would the dynamic consequences be? In short, I suggest that the unswerving reliance on traditional concepts in analyzing interval graphs may be the weak part of this book.

Nevertheless, on its own terms the book is an obvious success. Even though questions of mechanisms will be raised seriously by many readers, the problems posed both directly and indirectly make this book an extremely important contribution to ecological theory. It will be read and debated for some time to come.

JOHN H. VANDERMEER
Division of Biological Sciences
University of Michigan
Ann Arbor, Mich. 48109