

D No: 17696-PR

Assigned to: \_\_\_\_\_

Prospective RM: YES  NO

Project No: 1463

F-44620-67-C-0045  
Contract No: \_\_\_\_\_

Task Order No: \_\_\_\_\_

# RAND DOCUMENT

INTERVAL GRAPHS AND FOOD WEBS:  
A Finding and a Problem

Joel E. Cohen

30 August 1968

## For RAND Use Only

DO NOT QUOTE OR CITE IN EXTERNAL RAND PUBLICATIONS OR CORRESPONDENCE

INTERVAL GRAPHS AND FOOD WEBS:  
A Finding and a Problem

Joel E. Cohen

1. THE FINDING

The theory of interval graphs can illuminate two major problems in ecology, which is the study of organisms in their relations with the environment.

The two problems concern the structure of "ecological phase space" and "the food web."

Biologists think of "ecological phase space" as a space of several dimensions such as temperature, moisture, pH, size of prey, or any other characteristics of the environment which determine whether a species can survive and maintain a stable population. The region in this space, the range of temperatures, moisture, pH, capturable prey, size, etc., in which a species lives is called that species' "ecological niche." The generalization biologists have discovered about this space is the principle of competitive exclusion: no two species have identical niches.

The major problem concerning ecological phase space is: what number of dimensions is sufficient to represent competitive relations among species living together in a biological community? and what are the labels on those dimensions?

Biologists describe the feeding (trophic) relations among species living together in a community by a "food web,"

a directed graph with vertices corresponding to species and a directed edge from  $a$  to  $b$  if  $b$  preys on  $a$  (energy flows from  $a$  to  $b$ ).

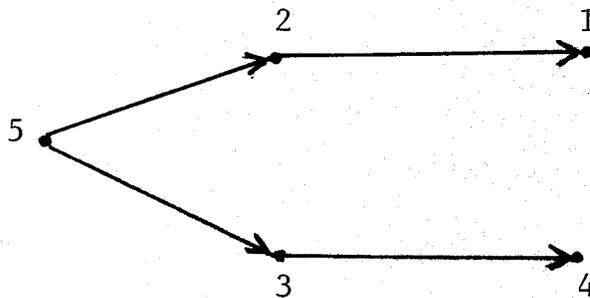
The major problem concerning the food web is to say something useful about its structure.

The results of Fulkerson and Gross on incidence matrices and interval graphs can relate and shed light on both problems.

A directed graph  $W$  (the web) on  $n$  vertices induces an  $n \times n$  incidence matrix  $A(W)$  as follows. Let the columns correspond to the vertices in some order and the rows correspond to the vertices in the same order. Let the entry in row  $i$ , column  $j$  be 1 if the graph has an edge from vertex  $i$  to vertex  $j$ , and 0 otherwise. (Think of the columns as predators, the rows as prey: then the 1's in column  $j$  tell which species (rows) are eaten by species  $j$ .) Two columns are disjoint if their dot product is 0. Two species may be said to compete if their corresponding columns are not disjoint, that is, if they take at least one prey species in common. Form an undirected graph, called the competition graph  $C(A)$  on  $n$  points (again corresponding to the species), by inserting undirected edges between two species whose columns in  $A(W)$  are not disjoint. In this competition graph  $A(W)$ , just competing species, those which take at least one prey species  $C(A)$  in common, are joined by an edge. (This is not quite the overlap

graph of Fulkerson and Gross because  $C(A)$  ignores the distinction between overlap and containment between columns.) Cannibalism, a loop in the directed graph  $W$ , leads to a 1 on the main diagonal of the incidence matrix  $A(W)$ ; but the competition graph is assumed to have no loops.

If  $W$  has the form



then only columns 2 and 3 are not disjoint in  $A(W)$ ; but columns 1 and 4 are not disjoint in  $A^2$ , reflecting the competition at one remove 1 and 4; and in  $A + A^2$ , only columns 1 and 2 are disjoint and columns 3 and 4 are disjoint. Thus  $C(A)$  may look very different from  $C(A + A^2 + \dots)$ .

If  $C(A(W))$  is an interval graph, then the direct competitive relations among the predators in the community may be represented in a one-dimensional space. More generally, the "boxicity" of the graph in the sense of Roberts tells the minimum dimension of the space (the "ecological phase space") in which the competitive relations among the predators can be represented.

Of four examples of food webs taken from the biological literature (Paine), all induced interval competition graphs. In two of the food webs, there were only two predators,

hence the induced competition graph was trivially an interval graph. A third web involved seven predators and six other prey species or species groups. The competition graph induced by such a web could have required up to three dimensions. The largest web involved eight predators and 25 other prey species or species groups, and could have required up to four dimensions.

Several biological questions arise.

1. Do food webs in nature generally induce competition graphs which are interval graphs? (Collect more examples.) If so, why? If not, what determines the boxicity of the competition graph?

2. Are the higher order interval graphs  $C(A + A^2 + \dots)$  also interval graphs?

3. What is the label on the single dimension along which competitive relations are represented, when one dimension is sufficient?

4. What is the effect on the boxicity of the competition graph of considering competition among species for resources other than prey, such as water or living space?

## 2. THE MATHEMATICAL PROBLEM

The mathematical problem is to find nice characterizations of  $W$  or of  $A(W)$  such that  $C(A)$  is an interval graph, or such that  $C(A + A^2 + \dots)$  is an interval graph.

More formally, if  $W$  is a directed graph on  $n$  (finite) vertices, where self-loops but not multiple edges in the same direction are permissible, and where  $(i,j)$  represent a directed edge from vertex  $i$  to vertex  $j$ , form the  $n \times n$  matrix  $A(W)$  by  $a_{ij} = 1$  if  $(i,j)$  is in  $W$ ,  $a_{ij} = 0$  otherwise. From  $A$  form the undirected graph  $C(A)$  on  $n$  vertices by joining vertices  $j$  and  $j'$  with an undirected edge if and only if the dot product of column  $j$  and column  $j'$  is positive. Characterize those  $W$  such that  $C(A(W))$  is an interval graph. Characterize those  $W$  such that  $C(A + A^2 + \dots)$  is an interval graph.

REFERENCES

- Fulkerson, D. R. and O. A. Gross, Incidence matrices and interval graphs. Pacific J. Math 15(3):835-855, 1965. A useful characterization of interval graphs.
- Paine, R. T., Trophic relationships of eight sympatric predatory gastropods. Ecology 44(1):63-73, 1963. A food web with eight predators and 25 other prey species of species groups.
- Paine, R. T., Food web complexity and species diversity. American Naturalist 100:65-75, 1966. Three smaller food webs.
- Roberts, F. S., On the boxicity and cubicity of a graph. In: Proc. 3rd Waterloo Conf. on Combinatorics, W. T. Tutte (ed.). New York: Academic Press, 1969. Sharp upper bounds on the dimensions needed to represent the competition graph.
- Slobodkin, L. B. Growth and Regulation of Animal Populations. New York: Holt, Rinehart, and Winston, 1961. The Concept of "ecological phase space" reviewed.