PART III

GRAPH THEORY

13

Food Webs

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Prerequisites: The prerequisites for this chapter are basic concepts of graph theory. See Sections 9.1 and 9.2 of *Discrete Mathematics and Its Applications*.

Introduction

A food web is a directed graph modeling the predator-prey relationship in an ecological community. We will use this directed graph to study the question of the minimum number of parameters needed to describe ecological competition. For this purpose we will consider how graphs can be represented as intersection graphs of families of sets.

We will also investigate the axiomatic description of measures of status in food webs.

Competition

In an ecological system, the various species of plants and animals occupy niches defined by the availability of resources. The resources might be defined in terms of factors such as temperature, moisture, degree of acidity, amounts of nutrients,

and so on.

These factors are subject to constraints such as temperature lying in a certain range, pH lying within certain limits, etc. The combination of all these constraints for a species then defines a region in n-dimensional Euclidean space, where n is the number of factors. We can call this region the *ecological niche* of the species in question.

For example, suppose we restrict ourselves to three factors, such as temperature, nutrients, and pH. Assume that the temperature must be between t_1 and t_2 degrees, the amount of nutrients between n_1 and n_2 and the pH between a_1 and a_2. Then the ecological niche these define occupies the region of 3-dimensional Euclidean space shown in Figure 1.
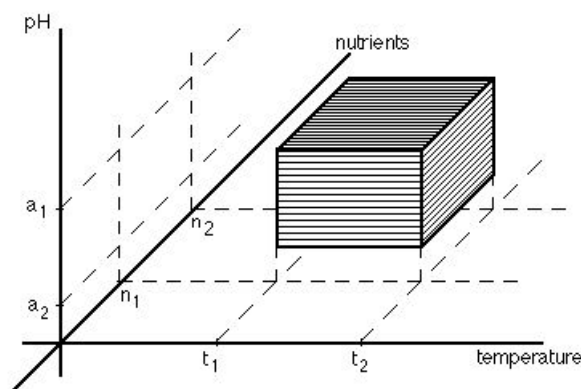

Figure 1.   An ecological niche.

Euclidean space which has as dimensions the various factors of temperature, pH, etc., is called an **ecological phase space**. Generally, no two distinct species will have the same ecological niche in phase space; however, two species **compete** if their ecological niches have non-empty intersection. A basic principle of ecology, known as the **principle of competitive exclusion**, dictates that species whose niches are too similar, or overlap too much, cannot coexist. If the factors defining the niche are independent, then the niche in phase space would be a box such as that in Figure 1. If the factors are not independent, i.e. the level of one depends on levels of others, then the niche would be some other type of set, e.g. convex, but not a box.

For example, consider the two factors temperature (t) and per cent humidity (h). We might have constraints such as: t must be between 0 and 100, and h must be between 0 and $100t - t^2$. In this case temperature and humidity are not independent; the possible values of h depend on the values of t. The region in two-dimensional space defined by these constraints is not a rectangle.

Our discussion of ecological communities and related concepts such as

species, food webs, and competition will be somewhat oversimplified in order to make a brief presentation possible. Interested readers should consult reference [1] for an in-depth treatment of these topics. Our mathematical treatment follows that of reference [6].

Food Webs

It may be difficult to know all the factors which determine an ecological niche, and some factors may be relatively unimportant. Hence it is useful to start with the concept of competition and try to find the minimum number of dimensions necessary for a phase space in which competition can be represented by niche overlap.

One approach to this question is to consider the notion of the *food web* of an ecological community.

Definition 1   A *food web* of an ecological community is a directed graph with a vertex for each species in the community and a directed edge from the vertex representing species A to the vertex representing species B if and only if A preys on B.   ☐

Figure 2 shows a simple food web for a community of seven species: robin, fox, grasshopper, raccoon, salamander, milksnake, and toad.
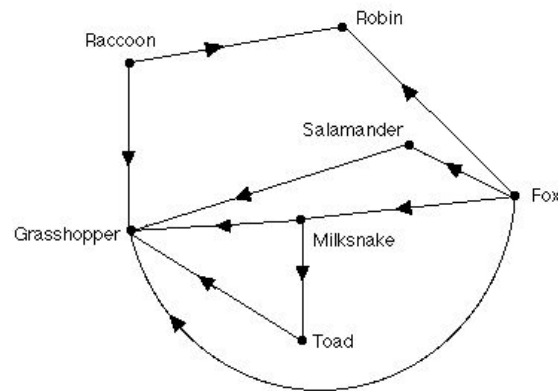

Figure 2.   A simple food web.

We can define *competition* using the food web. Two species *compete* if and only if they have a common prey. Thus, in the example of Figure 2, raccoon and fox compete (since robin is a common prey), milksnake and raccoon compete,

while salamander and robin do not compete. We use this competition relation to define a graph called the competition graph.

Definition 2   The *competition graph* of a food web is a simple graph with a vertex for each species. Two vertices are joined by an (undirected) edge if and only if the species they represent have a common prey.   ☐

Example 1   Find the competition graph for the food web of Figure 2.

Solution: The competition graph for this food web is shown in Figure 3.   ☐
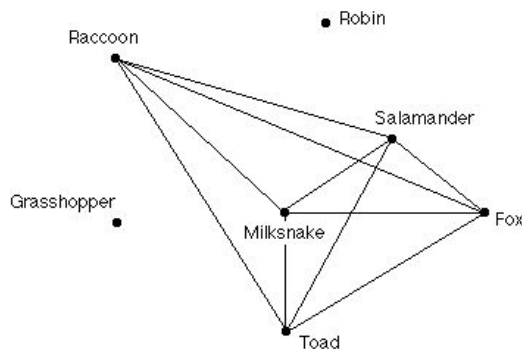
Figure 3.   A competition graph.

To represent the competition relation in phase space we want to assign to each vertex of the competition graph a subset of Euclidean space of some dimension in such a way that two vertices are joined by an edge in the competition graph if and only if the sets assigned to these vertices have non-empty intersection. Figure 4 shows a representation of the competition graph of Figure 3, using an interval for each vertex. We have thus represented the competition graph using only one dimension.

Figure 4.   Interval representation of a competition graph.

We can now state a general mathematical problem, but first we need to develop some terminology.

Definition 3   A graph is an *intersection graph* for a family of sets if each vertex is assigned a set in such a way that two vertices are joined by an edge if and only if the corresponding sets have non-empty intersection.   ☐

Definition 4   A graph is called an *interval graph* if it is the intersection graph for a family of closed intervals.   ☐

Our goal is the representation of competition graphs of families of sets in Euclidean n-space. Clearly the simplest case would be that of competition graphs that are interval graphs. This would mean that only one ecological factor is necessary to describe niche overlap.

Example 2   Find the interval graph for the family of closed intervals $A = [1, 3]$, $B = [2, 6]$, $C = [5, 8]$, $D = [4, 5]$.

Solution: We use the definition of intersection graph to obtain the graph of Figure 5.   ☐
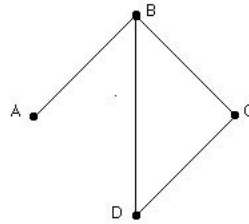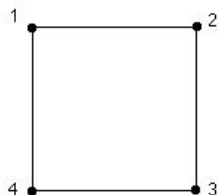

Figure 5.   An intersection graph.

Example 3   Prove that the 4-cycle graph C_4 of Figure 6 is not an interval graph.

Solution: The proof depends on the order properties of the real numbers. Let the interval corresponding to vertex n be $[n_l, n_r]$. Since the intervals for vertices 1 and 2 overlap, we must have either $1_l \leq 2_l \leq 1_r \leq 2_r$ or $2_l \leq 1_l \leq 2_r \leq 1_r$, Assume for specificity that $1_l \leq 2_l \leq 1_r \leq 2_r$. The argument for the other case is analogous.

Since the interval for vertex 3 must meet that for vertex 2 and must not meet that for vertex 1, we must have $1_l \leq 2_l \leq 1_r < 3_l \leq 2_r$. Now the interval for vertex 4 must meet those for both vertices 1 and 3, so we have to have $1_l \leq 4_l \leq 1_r$ and $3_l \leq 4_r \leq 3_r$ since interval 1 lies entirely to the left of interval 3. However, since $2_l \leq 1_r < 3_l \leq 2_r$, the intervals for vertices 2 and 4 overlap, which is forbidden.   ☐

Figure 6. A graph that is not an interval graph.

The 4-cycle can, however, be represented as the intersection graph of a family of boxes in Euclidean 2-space, as shown in Figure 7.

There are several methods known for determining whether a simple graph is an interval graph. A detailed discussion of this topic may be found in Roberts' book [6]. We simply state the characterization due to Gilmore and Hoffman [3] without proof. Before the characterization can be stated, we need some definitions.
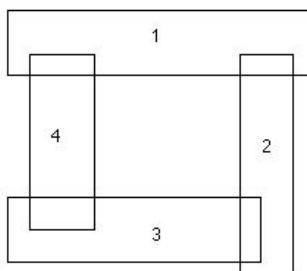
Figure 7. A box representation.

Definition 5   A graph H is a *generated subgraph* of a graph G if the vertices of H are a subset of the vertices of G and vertices in H are adjacent in H if and only if they are adjacent in G.   ☐

Definition 6   The *complement* of a graph G is the graph $\overline{G}$ where the vertices of $\overline{G}$ are the vertices of G, and two vertices in $\overline{G}$ are adjacent if and only if they are not adjacent in G.   ☐

Definition 7   An *orientation* of a graph G is an assignment of a direction to each edge in G (which makes G into a directed graph).

An orientation is *transitive* if whenever (u, v) and (v, w) are directed edges, then (u, w) is a directed edge.   ☐

The characterization due to Gilmore and Hoffman is given by the following theorem.

Theorem 1   A graph G is an interval graph if and only if it satisfies the following two conditions:

(i) The four-cycle C_4 is not a generated subgraph of G,
(ii) The complement of G is transitively orientable. ■

Our goal in our study of ecological competition is the representation of niches in Euclidean space and competition by niche overlap. It seems desirable in an ideal representation that the factors determining the dimension of the ecological phase space would be independent and the niches would be represented as "boxes", or Cartesian products of intervals. This leads us to the next part of this discussion, namely, when can we represent a graph as the intersection graph of a family of boxes in n-space.

Boxicity

Definition 8   The *boxicity* of a graph G is the smallest n such that G is the intersection graph of a family of boxes in Euclidean n-space. □

Note that an interval graph is simply a graph with boxicity equal to 1. It is not entirely clear that every simple graph has a boxicity. The following theorem resolves this difficulty.

Theorem 2   Every graph G with n vertices is the intersection graph of a family of boxes in Euclidean n-space.

Proof: Let $v_1, v_2, \ldots, v_n$ be the vertices of G. A box in Euclidean n-dimensional space is the set of all n-tuples of real numbers $(x_1, x_2, \ldots, x_n)$ such that each x_i is in some closed interval I_i. Now, for each $k = 1 \ldots, n$ and each vertex v_i, define closed intervals $I_k(v_i)$ as follows.

$$I_k(v_i) = \begin{cases} [0,1] & \text{if } i = k \\ [1,2] & \text{if } i \neq k \text{ and } \{v_i, v_k\} \text{ is an edge in } G \\ [2,3] & \text{if } i \neq k \text{ and } \{v_i, v_k\} \text{ is not an edge in } G. \end{cases}$$

For each vertex v_i define a box $B(v_i)$ in Euclidean n-space by

$$B(v_i) = \{(x_1, x_2, \ldots, x_n) \,|\, x_j \in I_j(v_i) \text{ for } j = 1, \ldots, n\}.$$

Thus, the box $B(v_i)$ corresponding to v_i is the Cartesian product of the intervals $I_j(v_i)$ for $j = 1, \ldots, n$.

Now we show that v_i and v_j are adjacent in G if and only if $B(v_i) \cap B(v_j) \neq \emptyset$. Thus the graph G is the intersection graph of the family of boxes $B(v_i)$. First, suppose that there is an edge joining v_l and v_m. If k is different from both l and m, then according to the definition, $I_k(v_l) \cap I_k(v_m)$ is $[1, 2] \cap [1, 2], [1, 2] \cap [2, 3]$, or $[2, 3] \cap [2, 3]$. In any case we have $I_k(v_l) \cap I_k(v_m) \neq \emptyset$. If k=l or k=m then $I_k(v_l) \cap I_k(v_m) = [1, 2] \cap [0, 1] \neq \emptyset$. So, if there is an edge joining v_e and v_m, then for all k, $I_k(v_l) \cap I_k(v_m) \neq \emptyset$. Hence $B(v_l) \cap B(v_m) \neq \emptyset$.

Now suppose that $B(v_l) \cap B(v_m) \neq \emptyset$. Then for each k from l to n, $I_k(v_l) \cap I_k(v_m) \neq \emptyset$. Set $k = l$ then $I_l(v_l) = [0, 1]$ and $I_l(v_m)$ must be $[1, 2]$ for the intersection to be nonempty. By definition of $I_l(v_m)$, v_l and v_m are adjacent. Thus G is the intersection graph of the family of boxes $B(v_i)$. ∎

This theorem shows that boxicity is well-defined. Unfortunately, there is no efficient algorithm known for determining the boxicity of a general graph. There is no characterization known for graphs of any specific boxicity other than 1.

In fact, there are not many general classes of graphs for which the boxicity is known. It is not hard to see that the boxicity of the n-cycle C_n is 2 for $n = 4$ or larger, and this is left as Exercise 6. Another general class of graphs for which the boxicity is known is the *complete p-partite* graphs. These are the graphs $K_{n_1, n_2, \ldots, n_p}$ defined as follows: there are $n_1 + \cdots + n_p$ vertices partitioned into p classes, where the ith class has n_i vertices. Within a class no vertices are adjacent, and every vertex in any class is adjacent to all vertices in the other classes. Roberts [6] showed that the boxicity of $K_{n_1, \ldots, n_p}$ is equal to the number of n_i that are larger than 1.

One result which helps somewhat in calculating the boxicity of a graph is due to Gabai [2]. This theorem depends on the concept of *independence* of a set of edges.

Definition 9   A set of edges in a graph is *independent* if they have no vertices in common. □

Gabai's theorem [2] is the following, stated without proof.

Theorem 3   Let G be a simple graph. If the maximum size of an independent set of edges of $\overline{G}$ is k, then G has boxicity less than or equal to k. Also, if $\overline{G}$ has a generated subgraph consisting of k independent edges then the boxicity of G is greater than or equal to k. ∎

Gabai's theorem is useful in determining the boxicity of relatively small graphs and for certain families. In any case it limits the amount of trial and error needed.

In our study of competition we search for the representation of the competition graph of a food web as the intersection graph of a family of sets in Euclidean n-space for some n. As a consequence of the theorem proved above, this representation is always possible. Furthermore, we can use the boxicity of the competition graph as an indicator of the minimum number of factors essential for describing competition in the community. Cohen [1] has studied more than 30 single-habitat food webs published in the ecological literature and has found that the competition graphs of all of them are interval graphs. That is, in all cases one dimension suffices to represent competition by niche overlap. It is not known whether this is a general law of ecology, but it does raise many interesting questions. In some single-habitat communities a single dimension for the niche space can be identified. It may be some obviously linear factor such as temperature, body length or depth in water. However, it may well be that more than one single dimension will work. And, of course, we can't expect the single-niche dimension to be the same from community to community.

Hypothetical food webs have been constructed such that their competition graphs are not interval graphs, but these combinations of species have never been observed in nature at the same time and place.

The representation of graphs as intersection graphs of boxes has important applications in ecology, as we have seen. Applications to such diverse fields as archaeology and automobile traffic control have also been investigated (see reference [6]). We conclude with an additional application of food webs.

Trophic Status

In the study of social systems it is often useful to measure the status of an individual in an organization. Harary [4] first introduced the idea of measuring the status of a species in a food web. In ecology this status is usually called the **trophic level** and is helpful in assessing the complexity and diversity of a web. The idea is that a web with many species at each trophic level has a high degree of complexity. In ecology it is generally thought that more complex ecosystems are more stable. In this section we study the question of how trophic status can be defined in a food web.

If the food web is simply a directed path (a food chain) then it is easy to define trophic status; just follow the order of the species in the chain. Some other structures also allow for an easy definition of trophic status. For example, we might think of species with no outgoing edges as being at the *bottom* of the web. Suppose that for every vertex, all directed paths to vertices at the bottom have the same length. Examples of such webs are given in Figure 8.
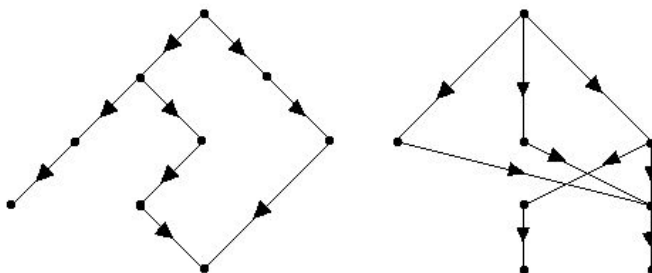
Figure 8.   Graphs of two food webs.

In this kind of web, the trophic status of a vertex can be defined as the length of a directed path from the vertex to the bottom.

In general it is difficult to define trophic status in complicated food webs. Because more than one approach may be possible, we will use the term *trophic status* in this context rather than the term trophic level which is well-known in the context of food chains. Our goal is to investigate how trophic status could be measured rather than to develop a unique possibility.

To start, we need some basic assumptions about food webs. In particular, we assume that our food web is *acyclic*, i.e. that the directed graph has no cycles. Thus, there are no species $s_1, \ldots, s_n$ such that for $i = 1, \ldots, n-1$, s_i preys on s_{i+1} and s_n preys on s_1. In particular there are no two species such that each preys on the other. Thus, the prey relationship is *asymmetric*.

We will take an axiomatic approach to defining measures of trophic status. That is, we will state conditions which any reasonable measure should satisfy in the form of axioms. A measure will then be acceptable if and only if it satisfies the axioms. The axioms will define an ideal model for the concept of measure of trophic status. Our approach will follow that of Harary [4] and Kemeny and Snell [5], who work with status in an organization, and the treatment in Roberts [6], which is more detailed.

Definition 10   In a food web a species v is a *direct prey* of a species u if there is a directed edge from u to v. A species v is an *indirect prey* of u if there is a directed path from u to v.   □

It could well happen that there are two species u and v neither of which is an indirect prey of the other.

Definition 11   If v is a direct or indirect prey of u, then the *level of v relative to u* is the length of the shortest directed path from u to v.   □

We can now state some reasonable axioms for measures of trophic status. Let $t_W(u)$ be the measure of status in the food web W. The axioms are:

Axiom 1: If a species u has no prey then $t_W(u) = 0$.

Axiom 2: If, without otherwise changing the food web, we add a new vertex which is a direct prey of u to get a new web W', then $t_{W'}(u) > t_W(u)$.

Axiom 3: Suppose the web W is changed by adding edges and/or vertices in such a way that the level of some direct or indirect prey of u is increased, and no direct or indirect prey of u has its level relative to u decreased. If W' is the new web, then $t_{W'}(u) > t_W(u)$.

These axioms make sense intuitively when we consider that we are saying that a species with no prey is at the bottom level (Axiom 1), that if the number of prey of a species increases its status increases (Axiom 2), and that the status of a species increases if its level relative to some indirect prey is increased (Axiom 3).

There is a measure of status which satisfies the axioms. Harary [4] suggested the following definition.

Definition 12   If a species u has n_k species at level k relative to u for each k, then

$$h_W(u) = \sum_k kn_k. \qquad \qquad \square$$

Theorem 4   The measure $h_W(u)$ satisfies Axioms 1-3.

Proof: If u has no prey, then $h_W(u) = 0$ because all the $n_k = 0$.

If we add a direct prey for u, then n_1 increases by 1, so the sum defining $h_W(u)$ also increases.

Likewise, if some direct or indirect prey of u at level k relative to u is moved to level $k + n$ below u and no other direct or indirect prey of u has its level decreased, the sum for h increases by at least kn, verifying Axiom 3.   ∎

Kemeny and Snell [5] also show that if t_W is any other measure of trophic status satisfying Axioms 1–3 and having all its values nonnegative, then for all species u, $t_W(u) \geq h_W(u)$. Thus, h is in a sense a minimal measure of trophic status.

While h satisfies our axioms it fails to have other desirable properties. For example, it seems reasonable that if t_W is a measure of trophic status and v is a direct or indirect prey of u, then

$$t_W(u) \geq t_W(v).$$

The measure h does not have this property. Figure 9 shows an example of an acyclic food web W with two vertices u and v for which v is a direct prey of u but $h_W(v) > h_W(u)$.
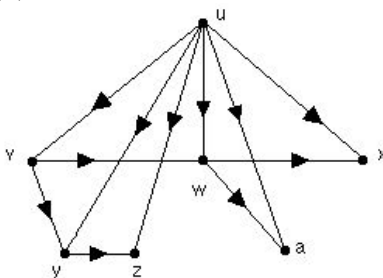
Figure 9.   An acyclic food web.

In this example, $h_W(u) = 6$ and $h_W(v) = 8$.

The problem we have found can be avoided if we modify our definition of level of one species relative to another: If v is a direct or indirect prey of u, then the *level of v relative to u* is the length of the *longest* directed path from u to v.

It is not hard to show that if h is defined by the same formula as before, but using the new definition of level, then h satisfies Axioms 1–3 as well as having the property that any species has higher status than any of its direct or indirect prey (see reference [5]). The problem we encountered here demonstrates one of the difficulties with the axiomatic approach. Our problem lay in the definition of level and this would not show up in any consideration of the reasonableness of the axioms. Ideally, all of the terms used in specifying the axioms should either be left undefined or else be checked for "reasonableness", just as the axioms themselves are. In this light we would also have to examine the new definition of level.

Without referring to the notion of relative level in a food web, perhaps the only requirement we can state for a measure of trophic status is that if there is a directed path from u to v, then $t_W(u) \geq t_W(v)$.

There are other ways to investigate complexity of food webs and relative importance of species in food webs. General methods of measuring complexity in graphs can be applied to competition graphs and food webs. For example, such ideas as the number of edges divided by the number of vertices, and the average out-degree and average in-degree might be useful. The importance, or criticality, of a species in a food web could be studied by investigating what happens to the web when the species is deleted from the web. For example, if the web is disconnected when a species is removed that would indicated a high level of importance. More information on these questions can be found in [6].

Suggested Readings

1. J. Cohen, *Food Webs and Niche Space*, Princeton University Press, Princeton, N.J., 1978.

2. H. Gabai, "*N*-dimensional Interval Graphs", mimeographed, York College, C.U.N.Y., New York, 1974.

3. P. Gilmore and A. Hoffman, "A Characterization of Comparability Graphs and Interval Graphs", *Canadian J. Math.*, Vol. 16, 1964, pp. 539–548.

4. F. Harary, "Status and Contrastatus", *Sociometry*, Vol. 22, 1959, pp. 23–43.

5. J. Kemeny and J. Snell, *Mathematical Models in the Social Sciences*, MIT Press, Cambridge, MA, 1972.

6. F. Roberts, *Discrete Mathematical Models with Applications to Social, Biological, and Environmental Problems*, Prentice Hall, Upper Saddle River, N.J., 1976.

Exercises

1. Find the ecological niche in Euclidean space of the appropriate dimensions in each case.

a) Temperature between 10^oF and 90^oF; nitrate concentration in soil between 1% and 5%.

b) Carbon monoxide in atmosphere between 0% and 1%; relative humidity between 20% and 100%; nitrogen gas content in atmosphere between 15% and 20%.

2. Find the competition graph for the given food webs in each case:
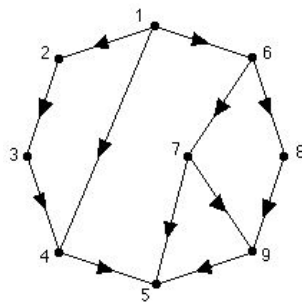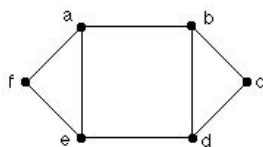
a)   b)
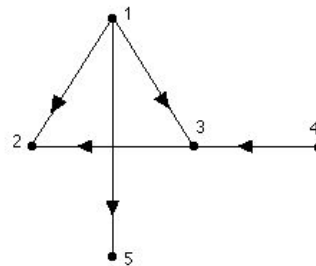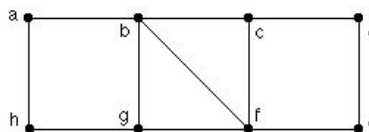
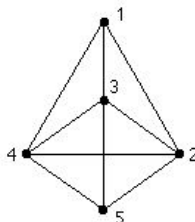**3.** Find a representation for each graph as the intersection graph of a family of rectangles in the plane.
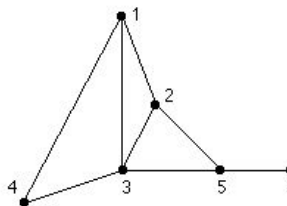
a)

b)

4. Find a representation for each graph as the intersection graph of a family of intervals on the line.

a)

b)

5. Show that if a graph G is an interval graph then it satisfies the conditions of the theorem of Gilmore and Hoffman characterizing interval graphs. *Hint:* For an interval representation let $I(v)$ be the interval assigned to the vertex v. If u and v are adjacent in $\overline{G}$, make the orientation (u, v) if and only if $I(u)$ lies entirely to the left of $I(v)$.

6. Show that if C_n is the cycle of length n, then the boxicity of C_n is 1 for $n = 3$ and 2 for $n \geq 4$.

7. According to Roberts' result quoted in the text, the boxicity of the complete bipartite graph $K(3,3)$ is 2. Find a representation of $K(3,3)$ as the intersection graph of a family of boxes in the plane.

8. Let Q_3 be the graph formed by the edges and corners of a cube in Euclidean three space. Is Q_3 an interval graph? Why? Determine the boxicity of Q_3.

9. A food web for some species in the Strait of Georgia, B.C. ([1], page 165) is given by the following table. The numbers atop columns indicate predator (consuming) species and those at the left of rows indicate prey (consumed) species. An entry 1 indicates that the predator in that column consumes the prey for that row, an entry 0 that it does not. The key identifies the various species.

	1	2	3	4	5
2	1	0	0	0	0
3	1	0	0	0	0
4	0	0	1	0	0
5	1	0	0	1	0
6	0	1	1	0	1
7	0	0	1	0	1

Key

1. Juvenile pink salmon
2. P. minutus
3. Calanus and Euphausiid furcilia
4. Euphausiid eggs
5. Euphausiids
6. Chaetoceros socialis and debilis
7. mu-flagellates

    a) Construct a directed graph for this food web.

    b) Construct the competition graph for this food web.

    c) Find a set of intervals on the real line such that the graph of part b) is the intersection graph of this family of intervals.

10. Repeat Exercise 9 for the following food web for a community of pine feeders [1], p.148.

	2	3	4	5	6	7	8	9	10
1	1	1	0	0	0	0	0	0	0
2	0	0	1	1	0	0	0	0	0
3	0	0	1	0	1	1	1	1	1
4	0	0	0	0	0	0	0	0	1
5	0	0	0	0	0	0	0	0	1
8	0	0	0	0	0	0	0	0	1
9	0	0	0	0	0	0	0	0	1
10	0	0	1	0	0	0	0	0	0

Key

1. Pine
2. Caterpillars, moths
3. Aphids, secretion
4. Digger wasps
5. Ichneumons
6. Bugs
7. Ants
8. Syrphids
9. Ladybugs
10. Spiders

11. Give an example of a food web which has two species, neither of which is a direct or indirect prey of the other.

12. In the section on trophic status two different definitions of relative level were given and two corresponding versions of the measure of trophic status h_W were also given. Calculate the trophic status of each vertex in each of the following food webs using both versions of h.
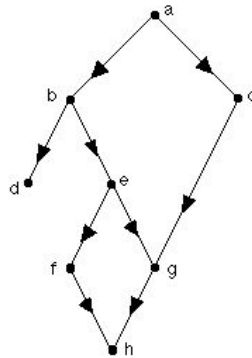
a)   b)
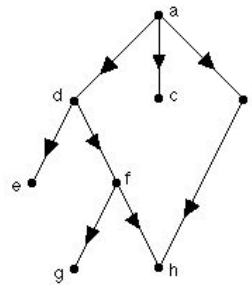
13. If the only requirement we make for a measure of trophic status t_W is that if there is a directed path from u to v then $t_W(u) > t_W(v)$, show that every acyclic food web has such a measure of trophic status.

14. (Roberts [6]) If relative level is measured using the length of the shortest directed path (our first definition), a plausible measure of trophic status is

$$t_W(u) = \sum_v h_W(v),$$

where the sum is taken over all vertices v for which there is a directed path from u to v. Show that this possible measure has the property that if there is a directed path from u to v, then $t_W(u) \geq t_W(v)$. Which of the Axioms 1–3 does this measure satisfy?

15. In our discussion of trophic status we assumed that the food web was acyclic. How restrictive is this assumption? Can you think of two species each of which could have the other as prey?

Computer Projects

1. Write a program to calculate trophic status in acyclic food webs.

2. Write a program to calculate the adjacency matrix for the intersection graph of a family of intervals given as pairs (a, b) of their endpoints.