Competition Graphs and Food Webs: Some of My Favorite Conjectures

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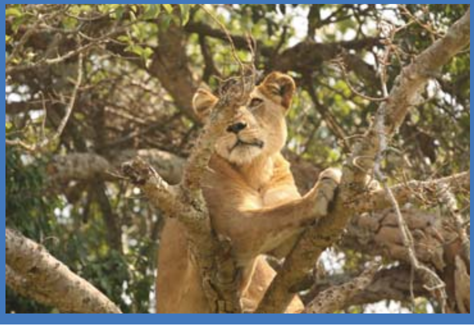
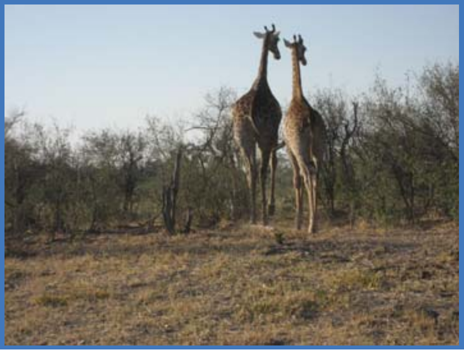
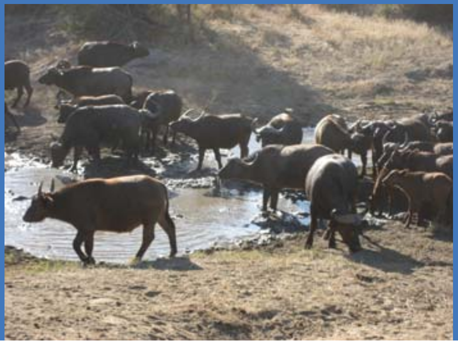
Competition Graphs & Food Webs

- Ecology is sometimes the source of interesting graph-theoretical problems.
- Competition between species is a case in point.
- Starting from predator-prey concepts in ecological food webs, Joel Cohen introduced the notion of competition graph in 1968.
- 100s of papers on this topic since then.
- And many applications outside of ecology.
- Recently, one long-standing conjecture about competition graphs was settled. But many remain.







Competition Graphs

•The notion of competition graph arose from a problem of ecology (Joel Cohen 1968)

•Key (oversimplified) idea: ***Two species compete if they have a common prey.***

•***The approach based on this idea has led to some ecological puzzles that have been unexplained for 45 years and to challenging graph-theoretical conjectures one of which was finally settled in 2011.***

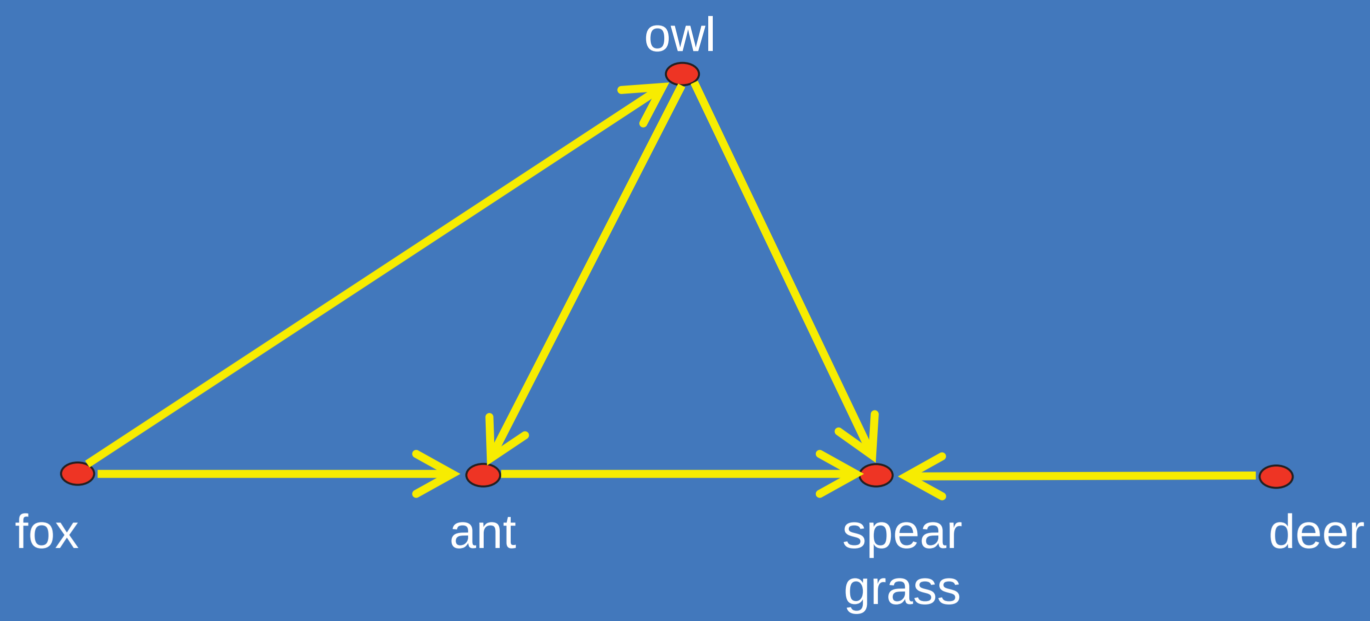
Competition Graphs of Food Webs

Food Webs

Let the vertices of a directed graph (digraph) be species in an ecosystem.

Include an arc from x to y if x preys on y.

Usual assumption for us: no cycles.

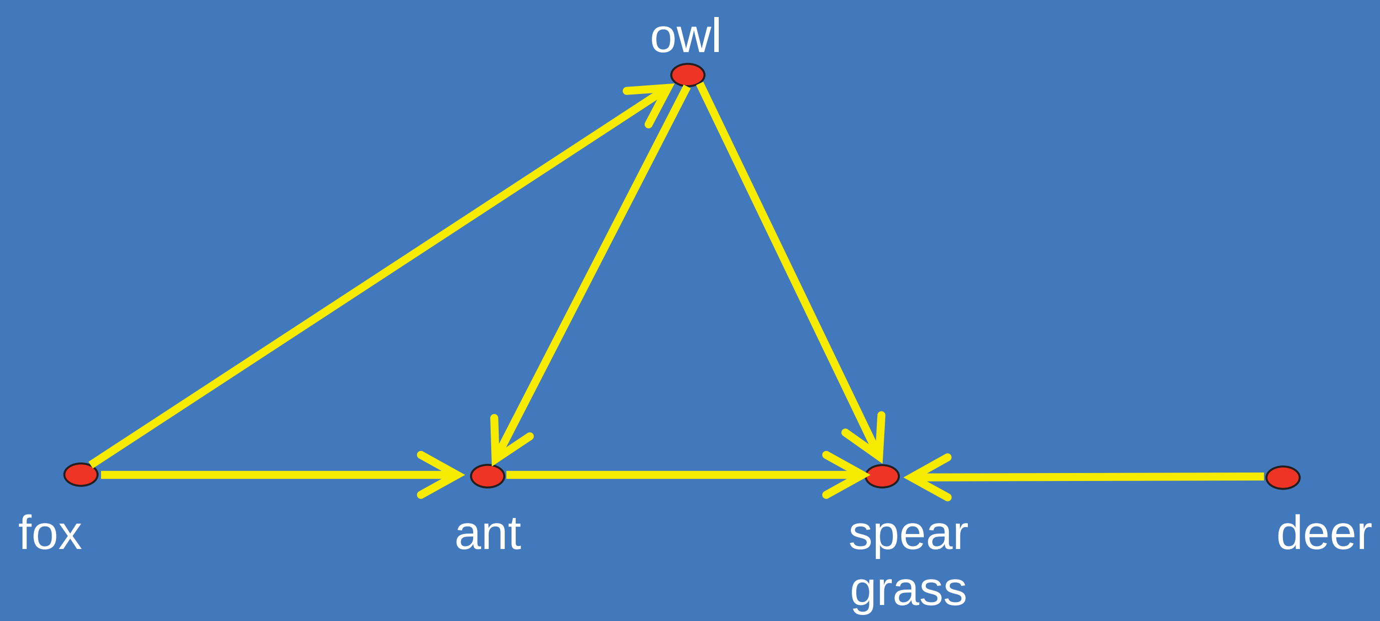


Competition Graphs of Food Webs

Consider a corresponding undirected graph.

Vertices = the species in the ecosystem

Edge between a and b if they have a common prey, i.e., if there is some x so that there are arcs from a to x and b to x.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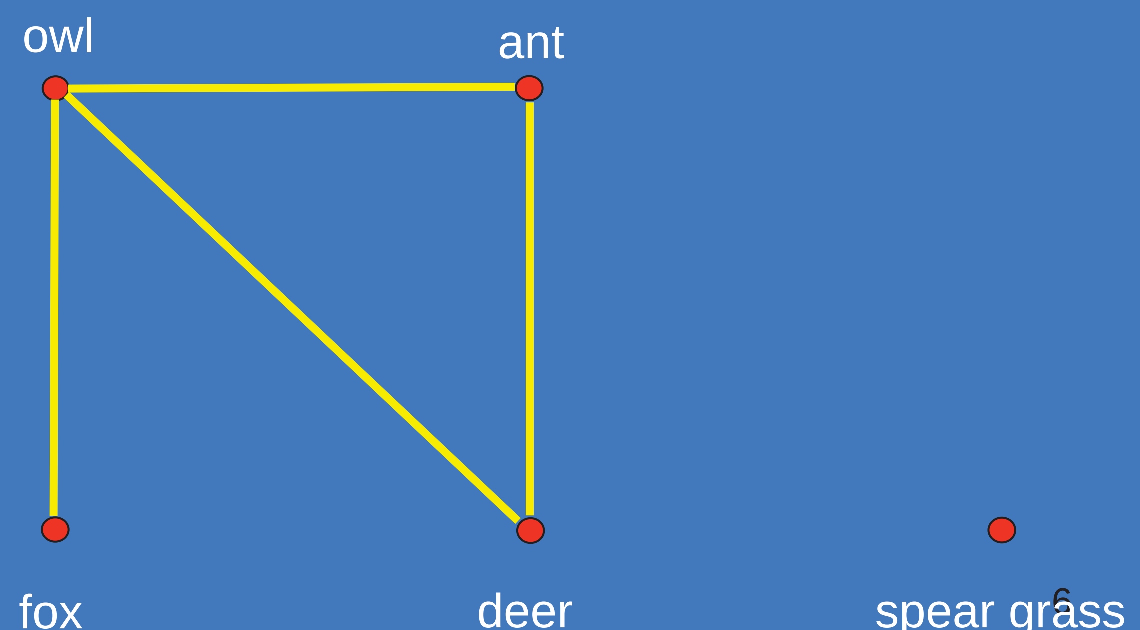
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Competition Graphs

More generally:

Given a digraph $D = (V,A)$
(Usually assumed to be ***acyclic***.)

The ***competition graph*** $C(D)$ has vertex set V and an edge between a and b if there is an x with arcs $(a,x) \in A$ and $(b,x) \in A$.

Competition Graphs: Other Applications

Other Applications:

- Coding
- Channel assignment in communications
- Modeling of complex systems arising from study of energy and economic systems
- Spread of opinions/influence in decisionmaking situations
- Information transmission in computer and communication networks

Competition Graphs: Communication Application

Digraph D:

•Vertices are transmitters and receivers.

•Arc x to y if message sent at x can be received at y.

Competition graph C(D):

•a and b "compete" if there is a receiver x so that messages from a and b can both be received at x.

•In this case, the transmitters a and b interfere.

Competition Graphs: Influence Application

Digraph D:

- Vertices are people
- Arc x to y if opinion of x influences opinion of y.

Competition graph C(D):

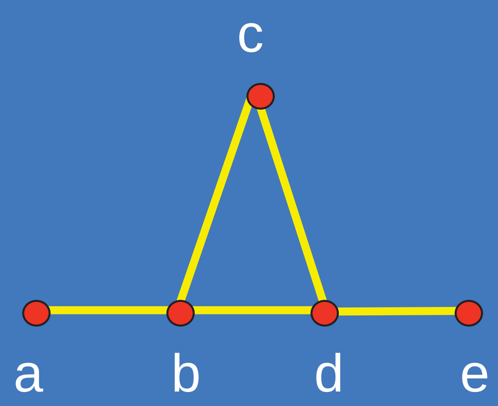
- a and b “compete” if there is a person x so that opinions from a and b can both influence x.

Aside: Interval Graphs

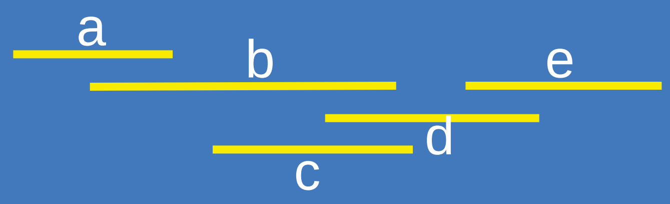
- A key idea in the study of competition graphs is the notion of interval graph.
- ***A graph is an interval graph if we can find intervals on the line so that two vertices are joined by an edge if and only if their corresponding intervals overlap.***

Interval Graphs

•Given a graph, is it an interval graph?



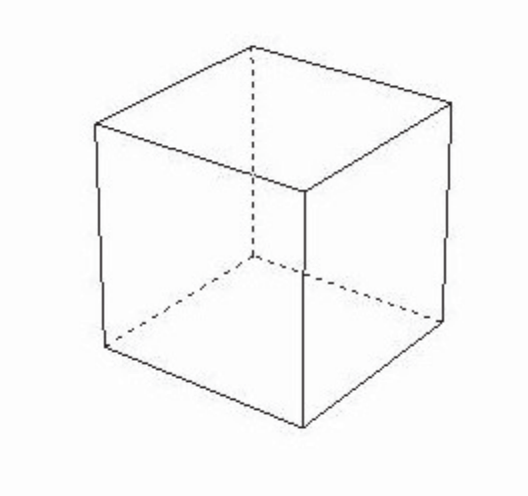
•We need to find intervals on the line that have the same overlap properties



Intersection of Boxes

More generally, we can study ways to represent graphs where the edges correspond to intersections of boxes in Euclidean space.

The ***boxicity*** of G is the smallest p so that we can assign to each vertex of G a box in Euclidean p-space so that two vertices are neighbors If and only if their boxes overlap.



Well-defined (Roberts 1968) but hard to compute.

Intersection of Boxes

- Interval graphs are the graphs of boxicity 1.

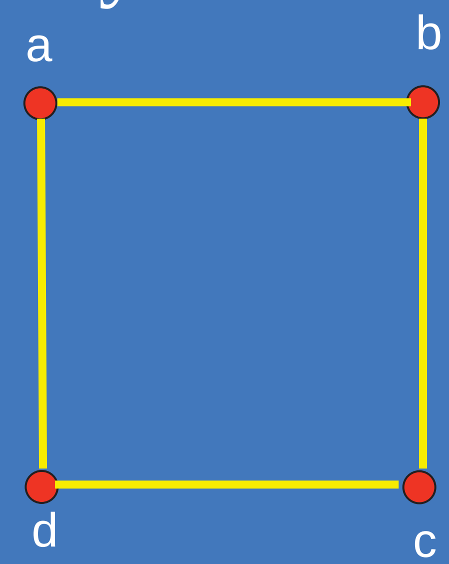
- Consider the graph C_4.

- It is not an interval graph.

- However, it can be represented as the intersection graph of boxes in 2-space.

- So, boxicity of C_4 is 2.

$G = C_4$



Intersection of Boxes

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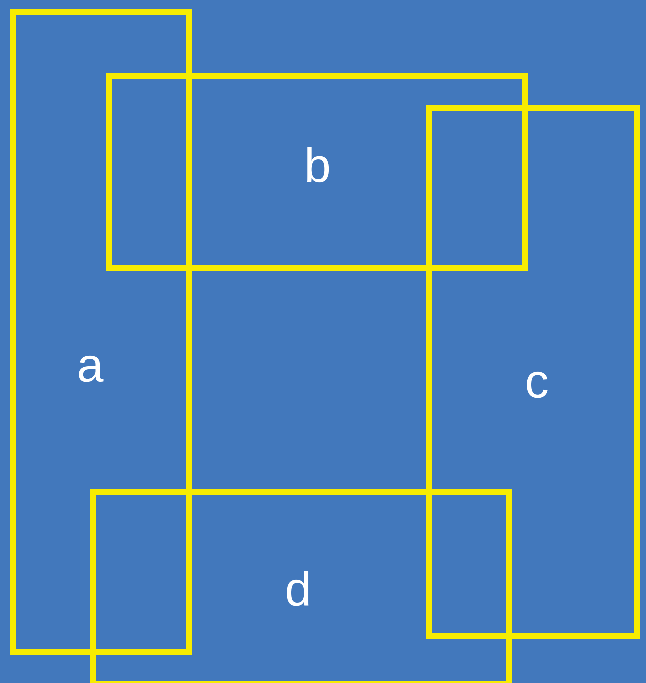
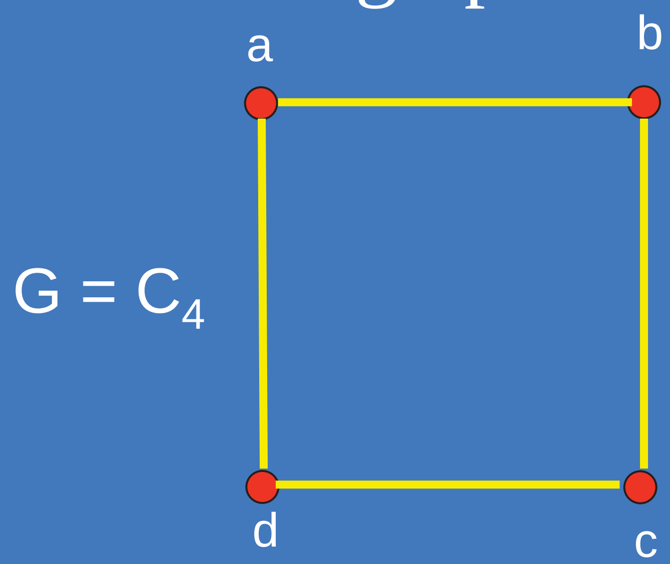




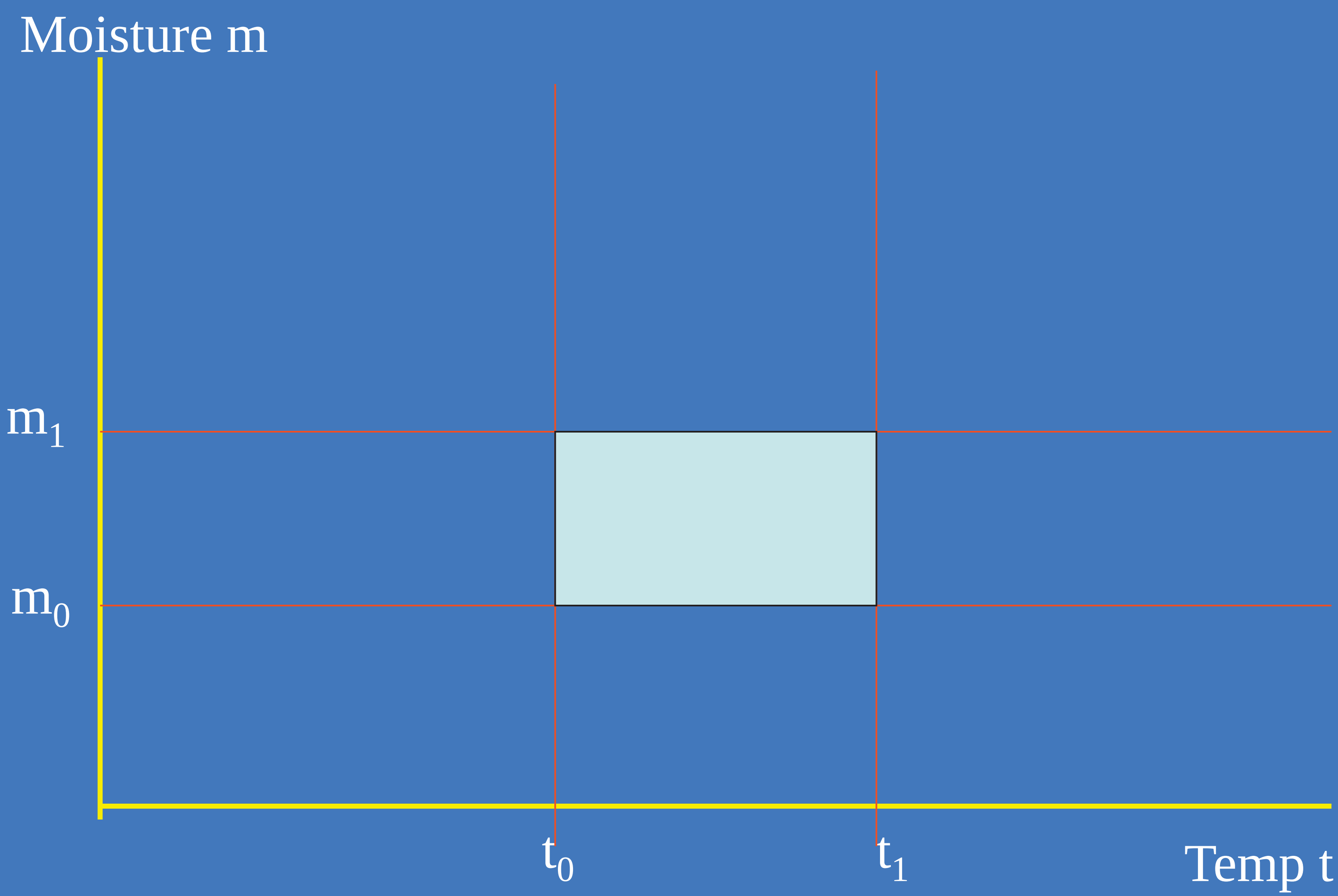
Ecological Niche

- Different factors determine a species' normal healthy environment.
  - –Moisture, Temperature, pH, …

- We can use each such factor as a dimension
- Then the range of acceptable values on each dimension is an interval.
- Each species can be represented as a box in Euclidean space – defined by intervals on each of the dimensions.
- ***The box represents its ecological niche*.**

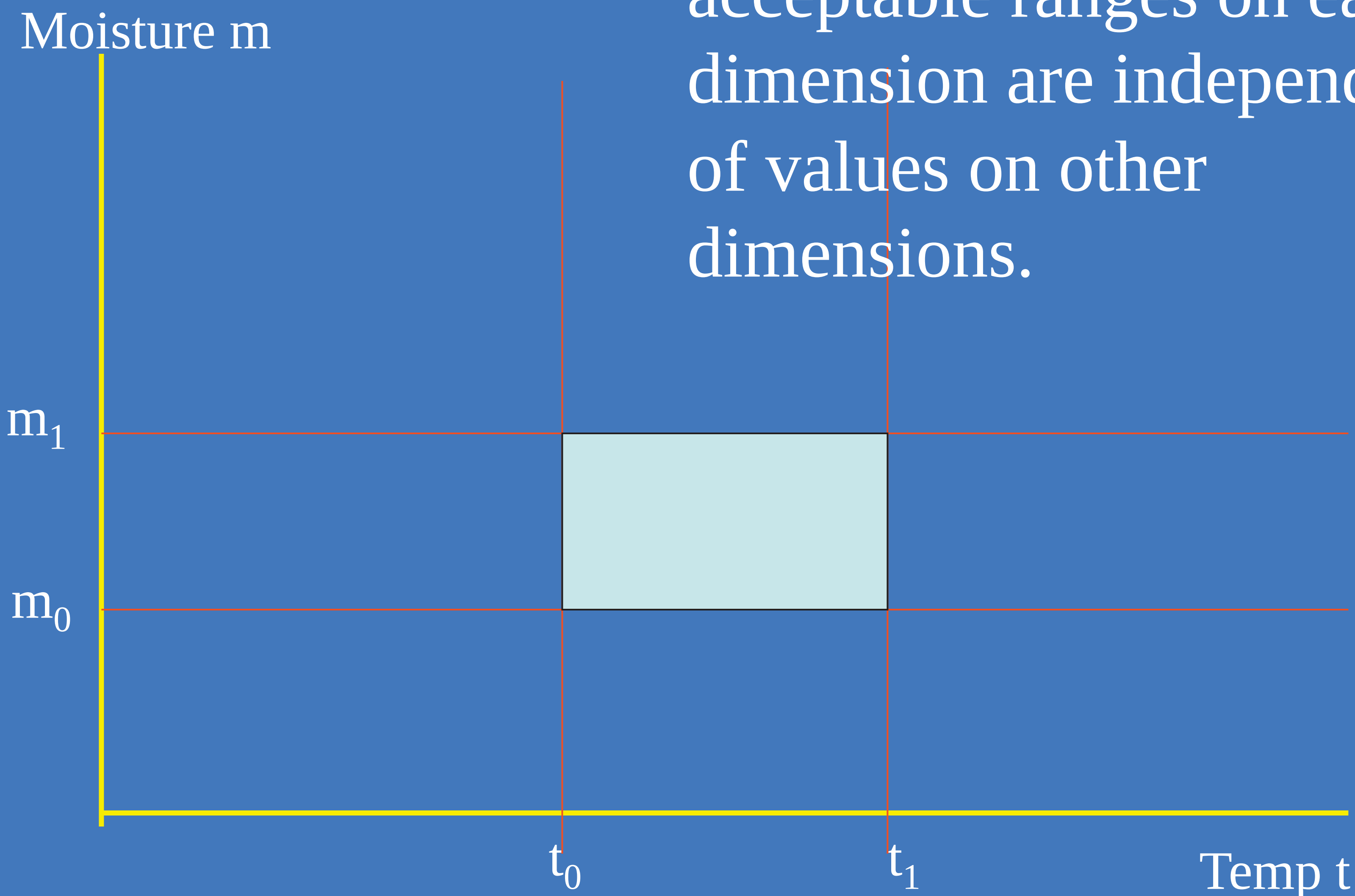
Ecological Niche

- The ecological niche is a box.



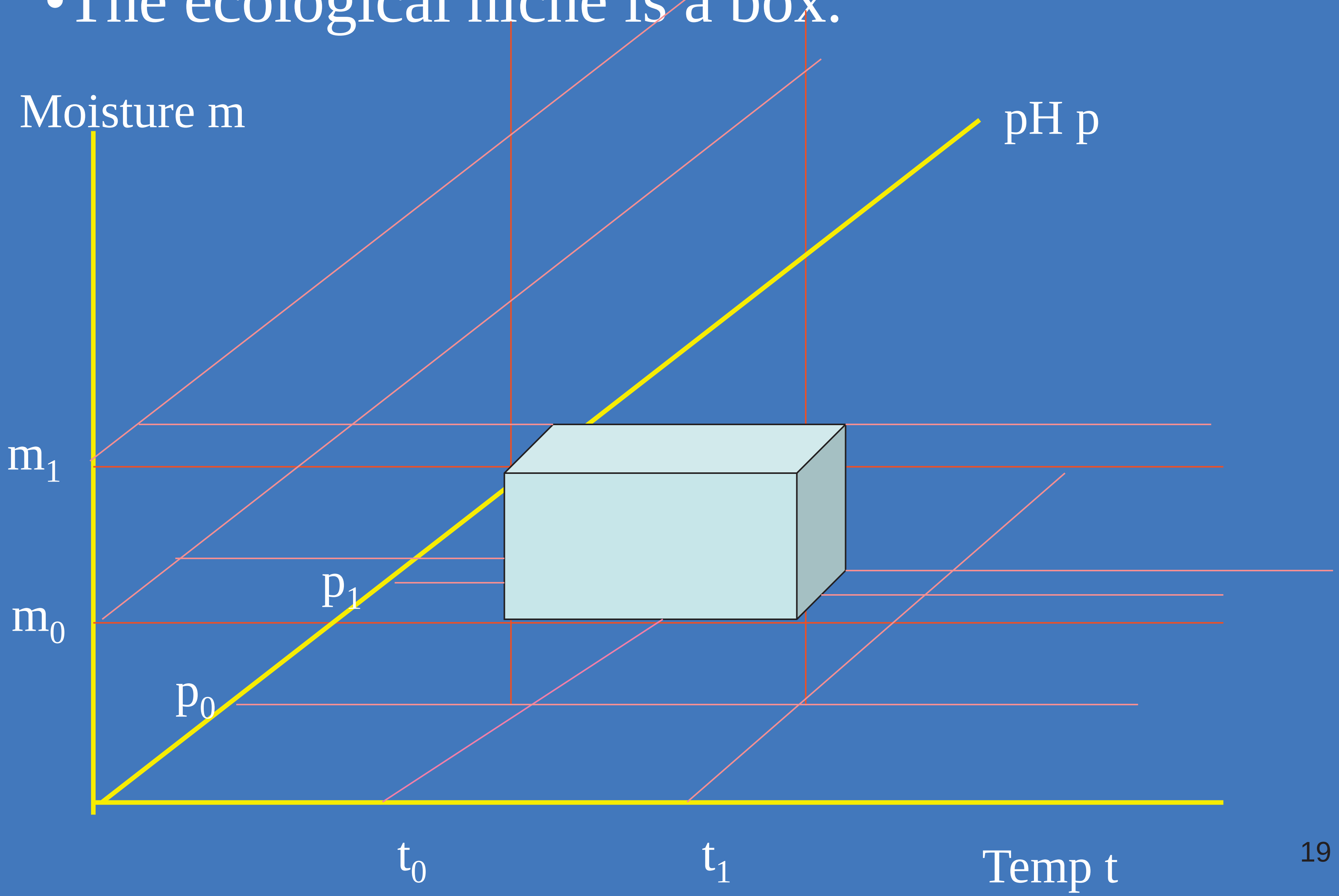
Ecological Niche

- Simplifying assumption: acceptable ranges on each dimension are independent of values on other dimensions.



Ecological Niche

- The ecological niche is a box.



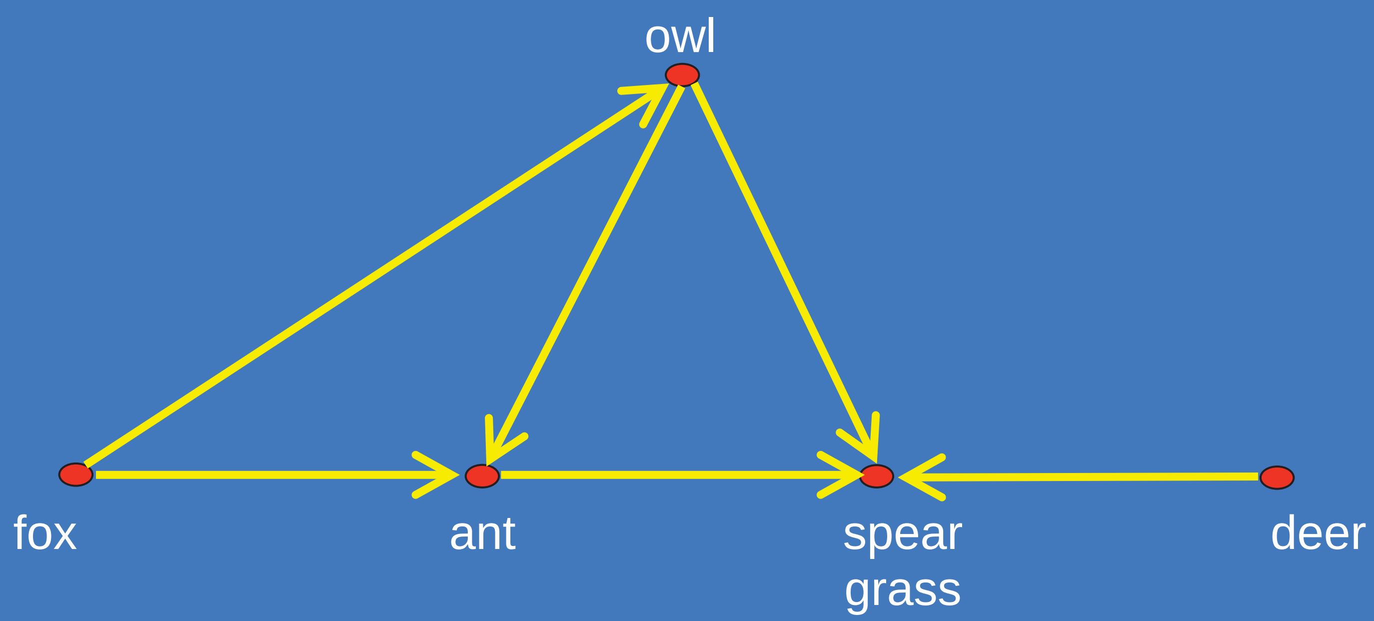
Competition

- ***Old ecological principle: Two species compete if and only if their ecological niches overlap.***

- Joel Cohen (1968):
  - Start with an independent definition of competition
  - Map each species into a box (niche) in k-space so competition corresponds to box overlap (niche overlap)
  - Find smallest k that works.

Competition

- Specifically, Cohen started with the competition graph as defined before.
- The question then becomes: What is the boxicity of the competition graph?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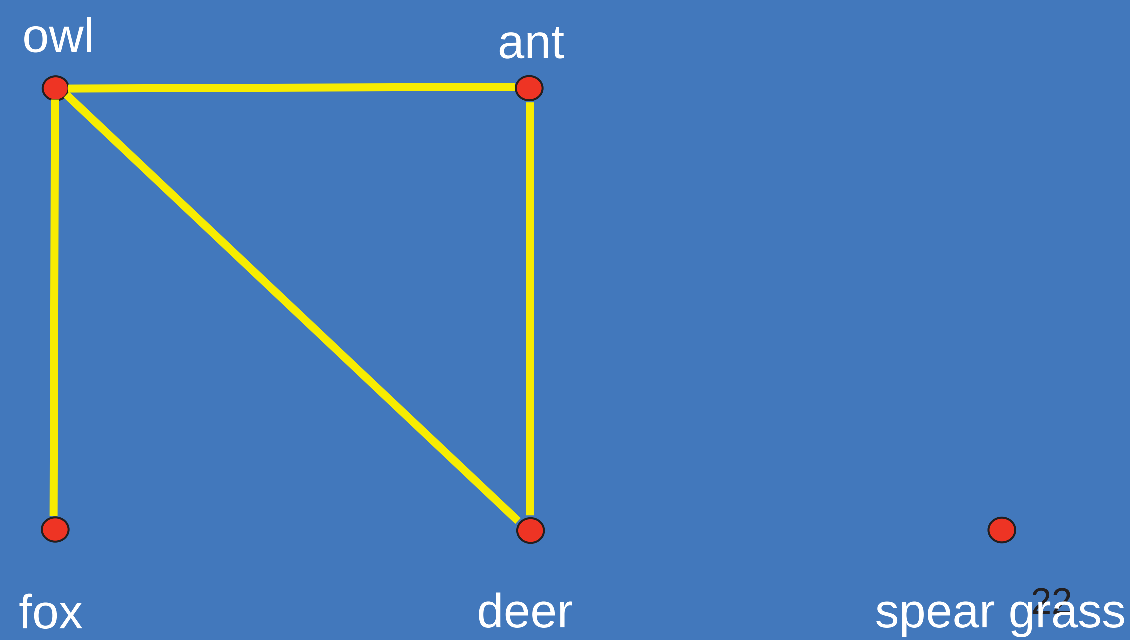
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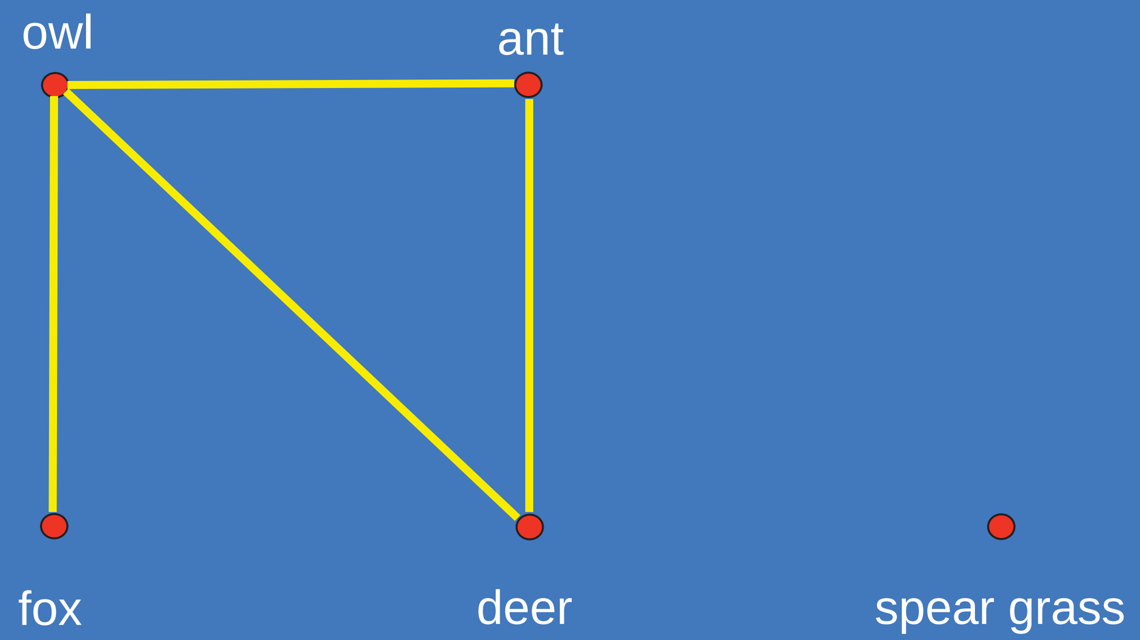
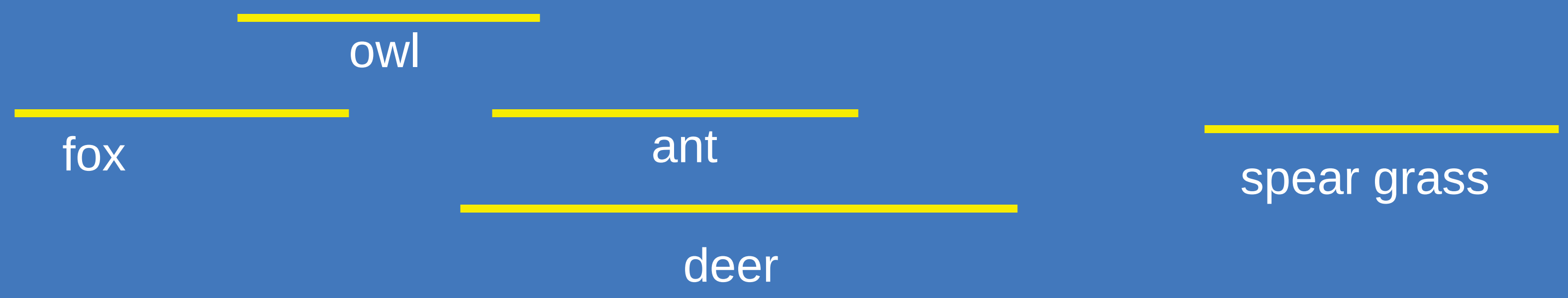
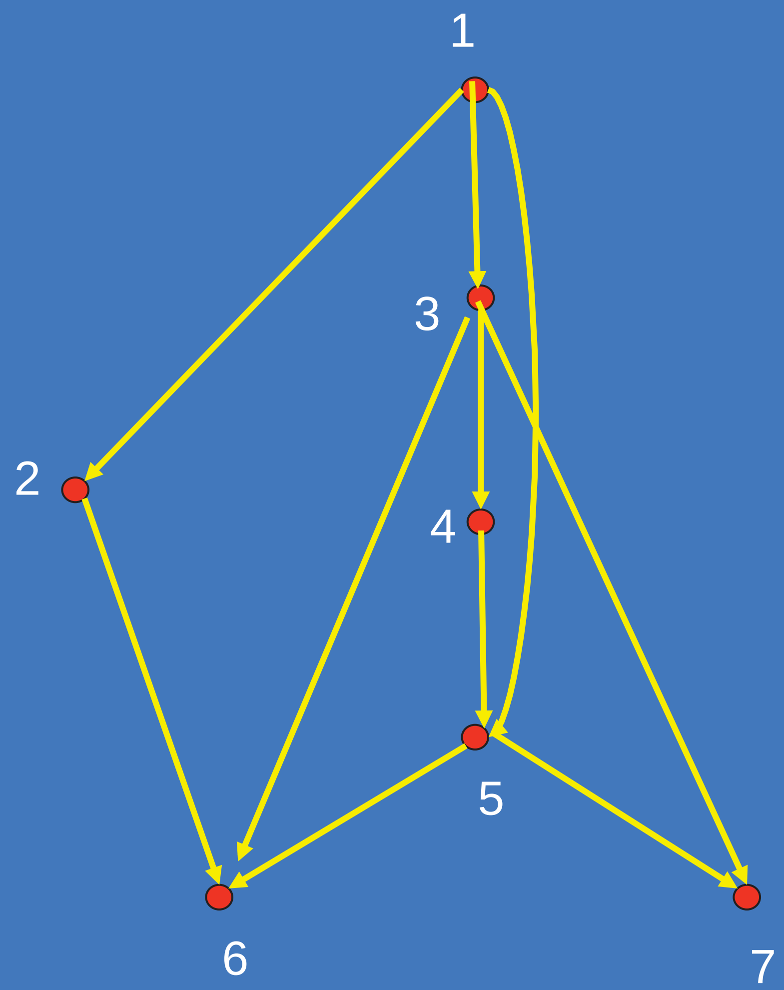


This is an interval graph. Thus, boxicity is 1.





Key:

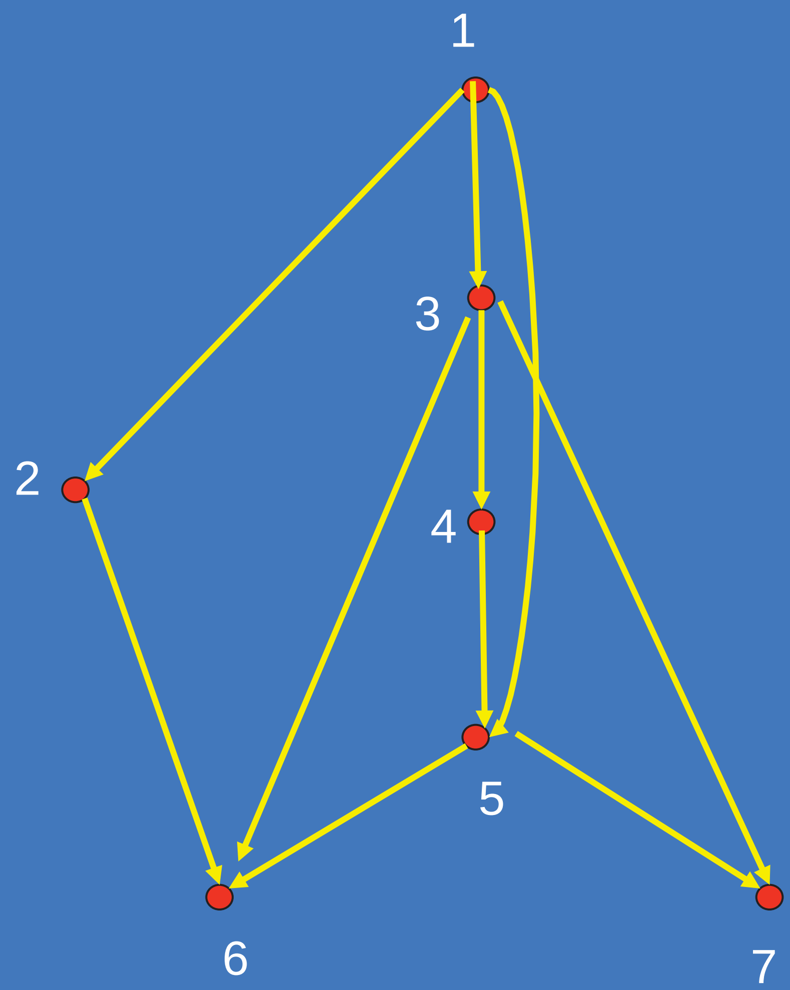
1. Juvenile Pink Salmon
2. P. Minutus
3. Calanus & Euphasiid Barcillia
4. Euphasiid Eggs
5. Euphasiids
6. Chaetoceros Socialis & Debilis
7. Mu-Flagellates

Strait of Georgia, British Columbia, Canada

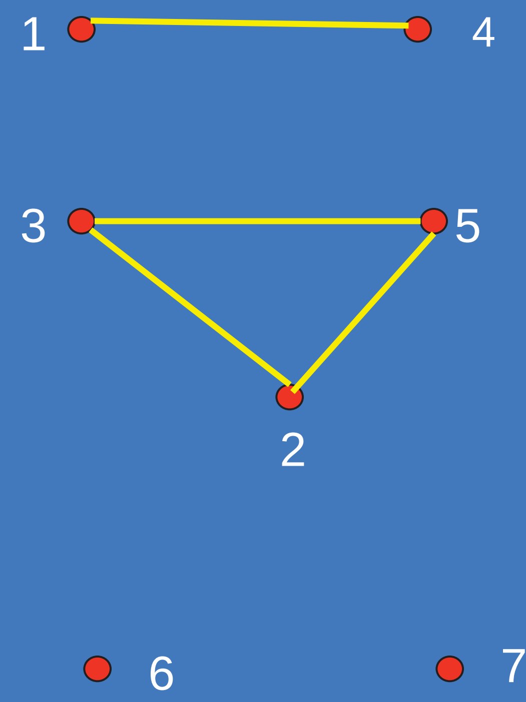
Due to Parsons and LeBrasseur

From Joel Cohen, *Food Webs and Niche Space*

Princeton University Press, 1978



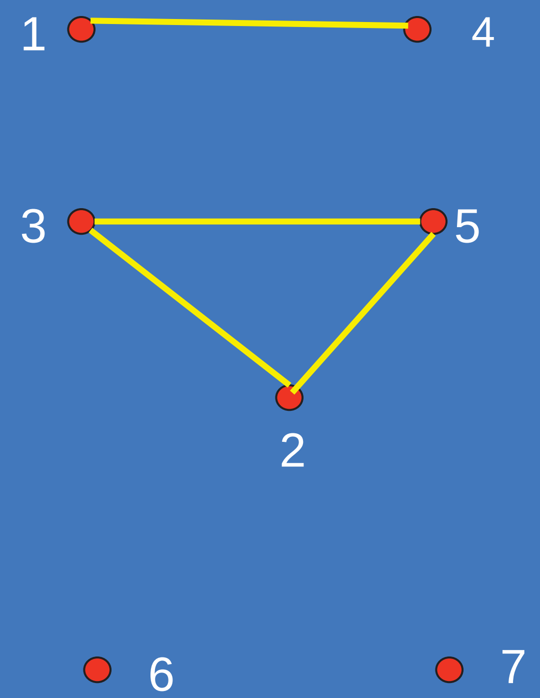
Competition graph



Strait of Georgia, British Columbia, Canada

What is the boxicity of the competition graph?

Competition graph



Strait of Georgia, British Columbia, Canada

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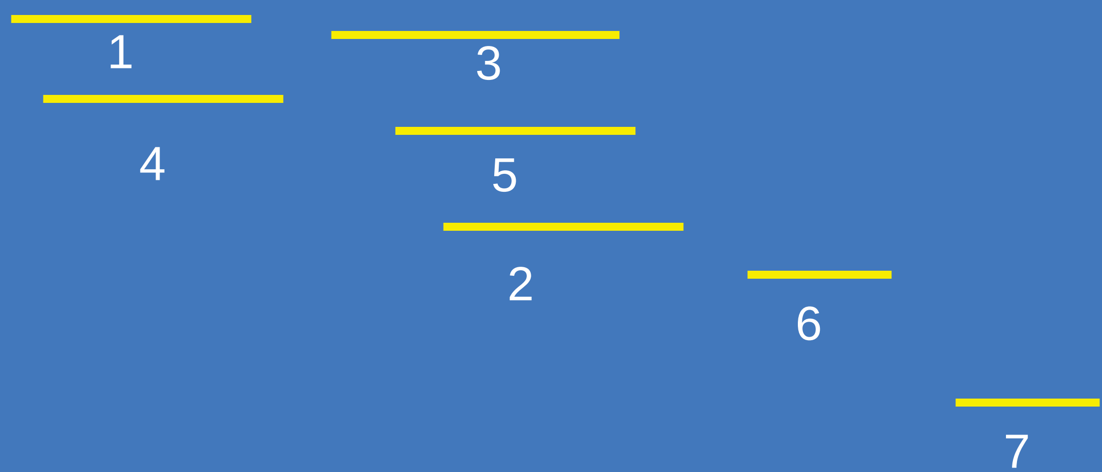
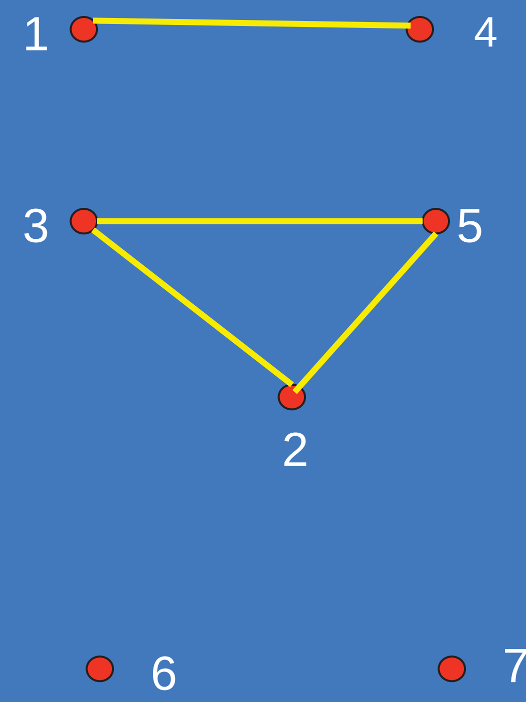
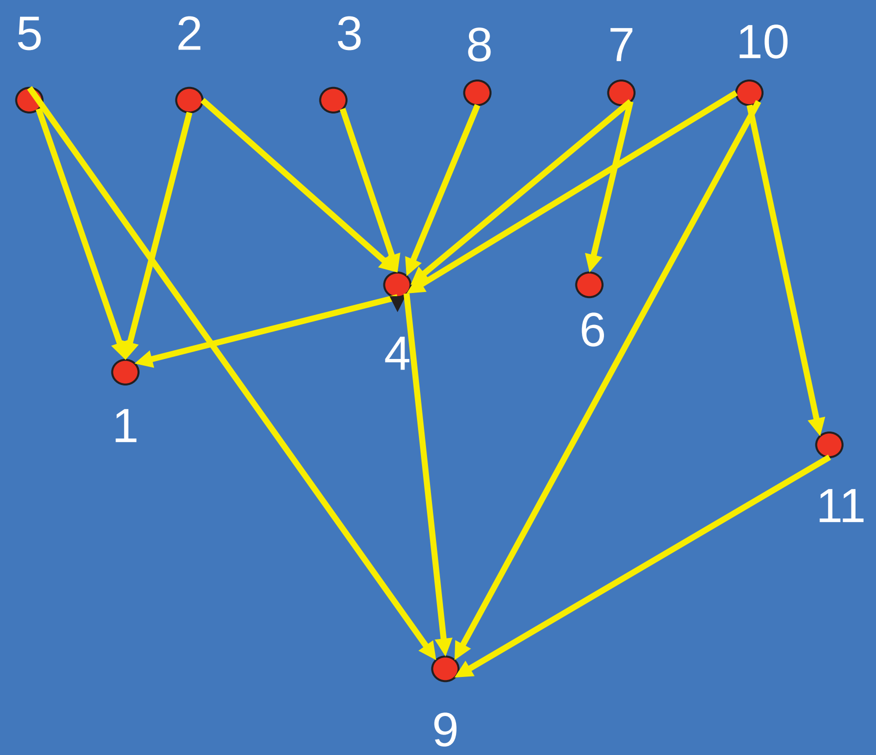


Competition graph



Strait of Georgia, British Columbia, Canada

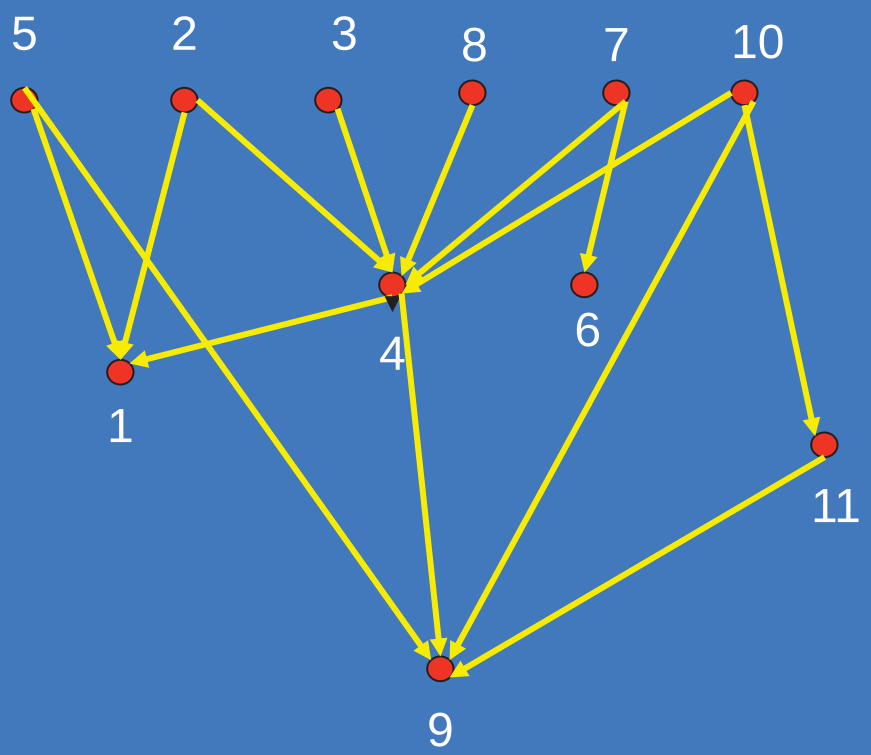


Key
1. Canopy – leaves, fruits, flowers
2. Canopy animals – birds, bats, etc.
3. Upper air animals – insectivores
4. Insects
5. Large ground animals – large mammals & birds
6. Trunk, fruit, flowers
7. Middle-zone scansorial animals
8. Middle-zone flying animals
9. Ground – roots, fallen fruit, leaves
10. Small ground animals
11. Fungi

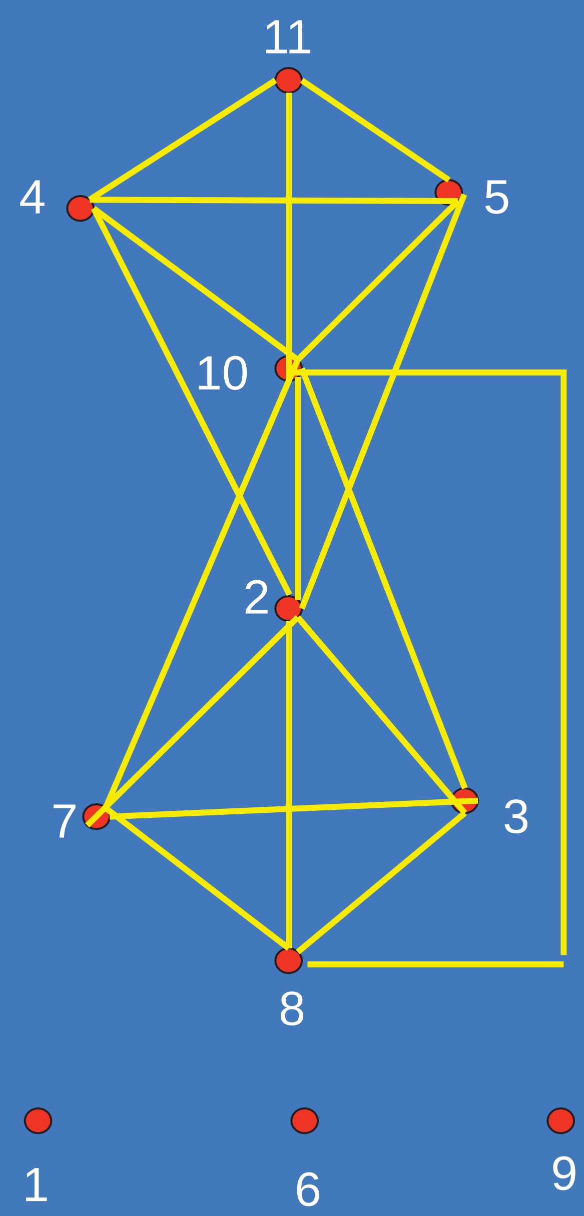
Malaysian Rain Forest

Due to Harrison

From Cohen, *Food Webs and Niche Space*



Competition Graph



Malaysian Rain Forest

Competition Graph

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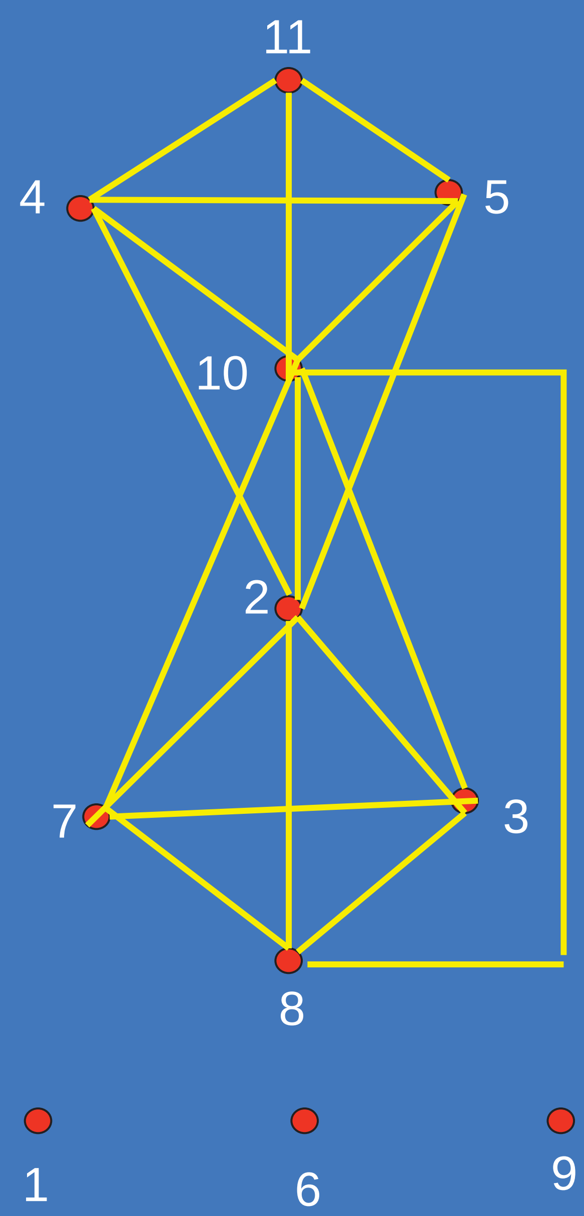

Malaysian Rain Forest

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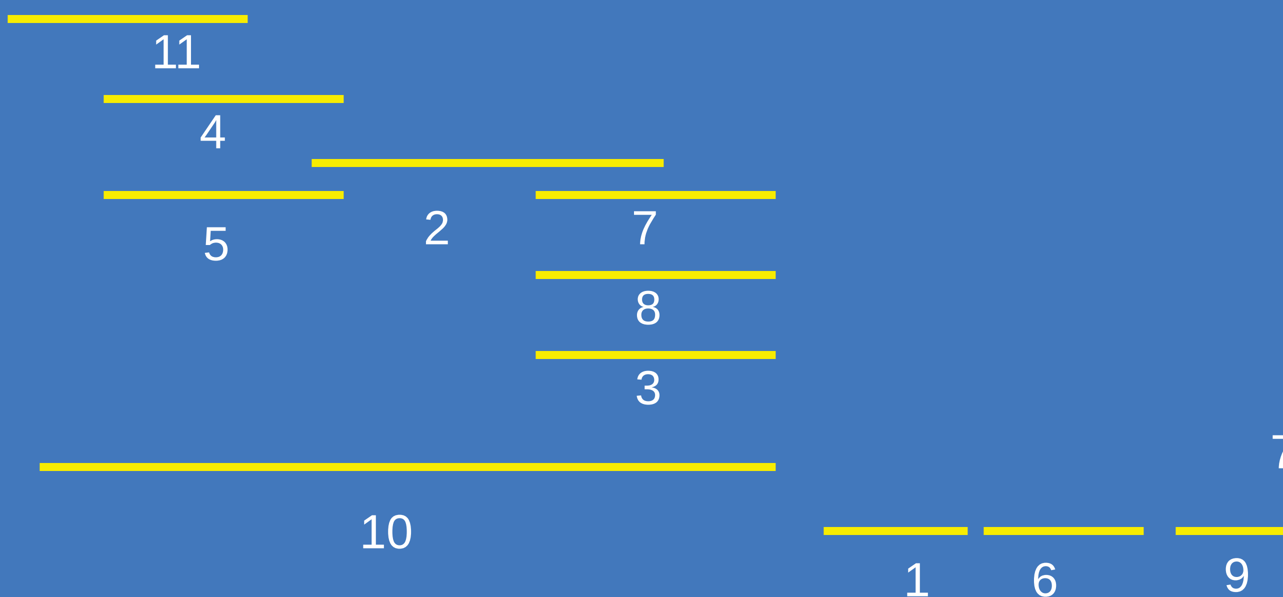
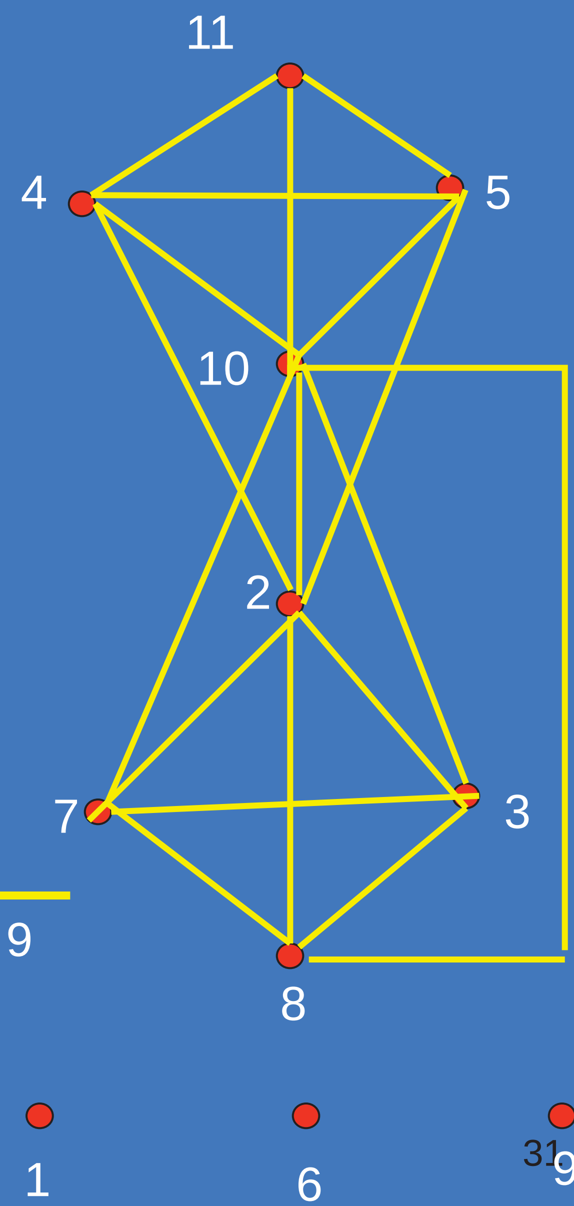




Malaysian Rain Forest

Structure of Competition Graphs

•In the first 8 years after this problem was introduced, every food web studied was found to have a competition graph that was an interval graph.

•In 1976, a Rutgers undergraduate, Gordon Kruse, found the first example of a food web whose competition graph was not an interval graph.

•It arose from a complex set of habitats.

•***Generally since then: Food webs arising from "single habitat ecosystems" (homogeneous ecosystems) have competition graphs that are interval graphs.***

Structure of Competition Graphs

- Thus, for single habitat ecosystems, the competition graphs have boxicity 1.
- One ecological dimension is enough to account for competition.
- Challenges:
  - Explain why?
  - Interpret this single ecological dimension

Structure of Competition Graphs

The remarkable empirical observation of Cohen's that real-world competition graphs are usually interval graphs has led to a great deal of research on the structure of competition graphs and on the relation between the structure of digraphs and their corresponding competition graphs.

Competition graphs of many kinds of digraphs have been studied.

In many of the applications of interest, the digraphs studied are acyclic.

Structure of Competition Graphs

- The explanations for the empirical observation have taken two forms:
  - Statistical
  - Graph-theoretical

Structure of Competition Graphs

•***Statistical Explanations***:

–Develop models for randomly generating food webs

–Calculate probability that the corresponding competition graph is an interval graph

–Much of Cohen’s *Food Webs and Niche Space* takes this approach.

–Later: Cascade model developed by Cohen, Newman, and Briand. But Cohen and Palka showed that under this model, the probability that a competition graph is an interval graph goes to 0 as the number of species increases.

Structure of Competition Graphs

- ***Graph-theoretical Explanations:***
  - –Analyze the properties of competition graphs that arise from different kinds of digraphs.
  - –Characterize the digraphs whose corresponding competition graphs are interval graphs.
  - –Much known about the former problem.
  - ***–Latter problem remains the fundamental open problem in the subject.***

The Competition Number

Suppose D is an acyclic digraph.

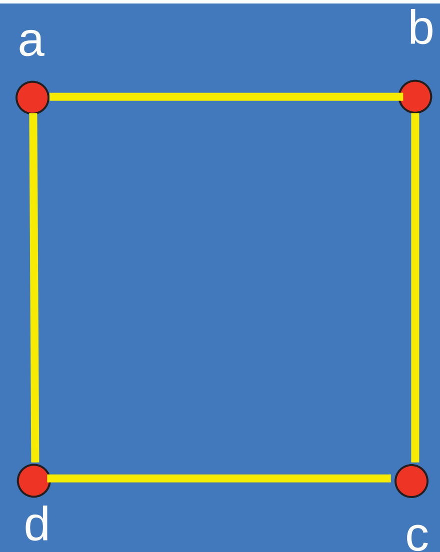
Then its competition graph must have an isolated vertex (a vertex with no neighbors).

Theorem: If G is any graph, adding sufficiently many isolated vertices produces the competition graph of some acyclic digraph.

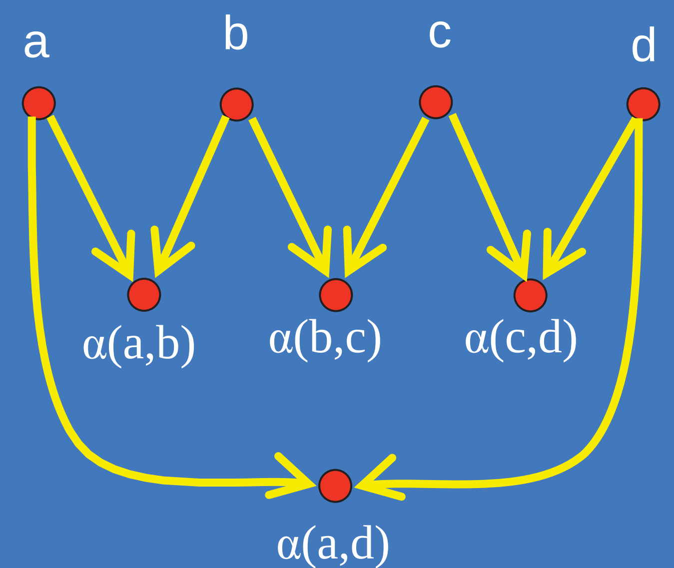
Proof: Construct acyclic digraph D as follows. Start with all vertices of G. For each edge {x,y} in G, add a vertex α(x,y) and arcs from x and y to α(x,y). Then G together with the isolated vertices α(x,y) is the competition graph of D.

The Competition Number

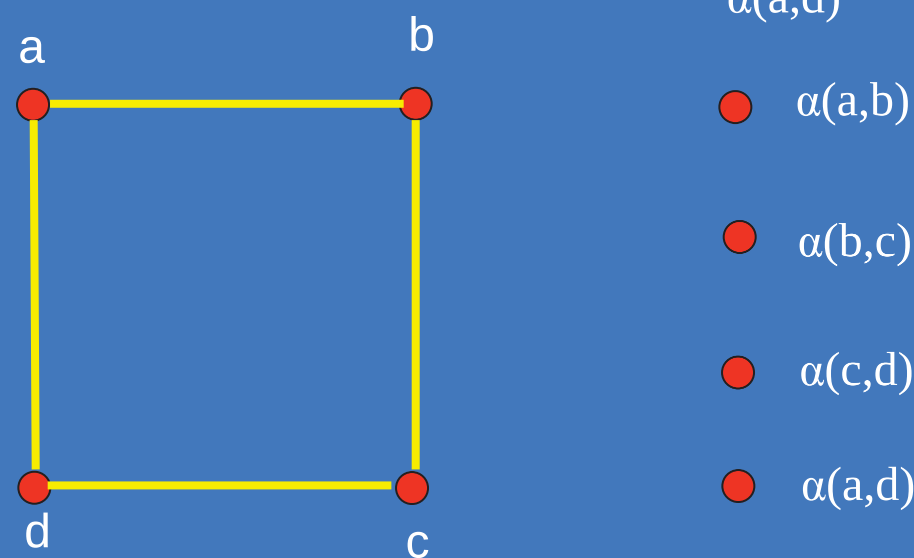
$G = C_4$



D



$C(D) = G \cup I_4$



The Competition Number

- Thus, D as shown in previous slide has a competition graph that is not an interval graph.
- In fact, there are examples of competition graphs of acyclic digraphs that have arbitrarily high boxicity.
  - Just start with a graph of boxicity b.
  - Add sufficiently many isolated vertices to make the graph into a competition graph.
  - Adding isolated vertices does not change the boxicity.
- ***Thus, the empirical observations tracing back to Joel Cohen are truly surprising.***

The Competition Number

If G is any graph, let k be the smallest number so that $G \cup I_k$ is a competition graph of some acyclic digraph.

$k = k(G)$ is well defined.

It is called the ***competition number*** of G.
(Roberts 1978)

The Competition Number

Our previous construction shows that

$k(C_4) \leq 4$.

In fact:

- $C_4 \cup I_2$ is a competition graph
- $C_4 \cup I_1$ is not

- So $k(C_4) = 2$.

The Competition Number

Competition numbers are known for many interesting graphs and classes of graphs.

However:

Theorem (Opsut 1982): It is an NP-complete problem to compute $k(G)$.

Characterization of which graphs arise as competition graphs of acyclic digraphs comes down to the question: Given a graph, how many isolated vertices is it necessary to add to make it into a competition graph? Thus, the characterization problem is NP-complete

The Competition Number

<u>Theorem (Dutton and Brigham 1983)</u>: A graph G with n vertices is the competition graph of an acyclic digraph iff we can find n cliques C_1, C_2, …, C_n that cover all the edges and we can label the vertices v_1, v_2, …, v_n so that if v_i in C_j, then $i > j$.

<u>Theorem (Lundgren and Maybee 1983)</u>: If $m < n$, then a graph G with n vertices has $k(G) \leq m$ iff we can find cliques C_1, C_2, …, C_{n+m-2} that cover all the edges and we can label the vertices v_1, v_2, …, v_n so that if v_i in C_j, then $i \geq j-m+1$.

Opsut's Conjecture

Let $\theta(G)$ = smallest number of cliques covering $V(G)$.

$N(v)$ = open neighborhood of v.

Observation: If G is a line graph, then for all vertices u, $\theta(N(u)) \leq 2$.

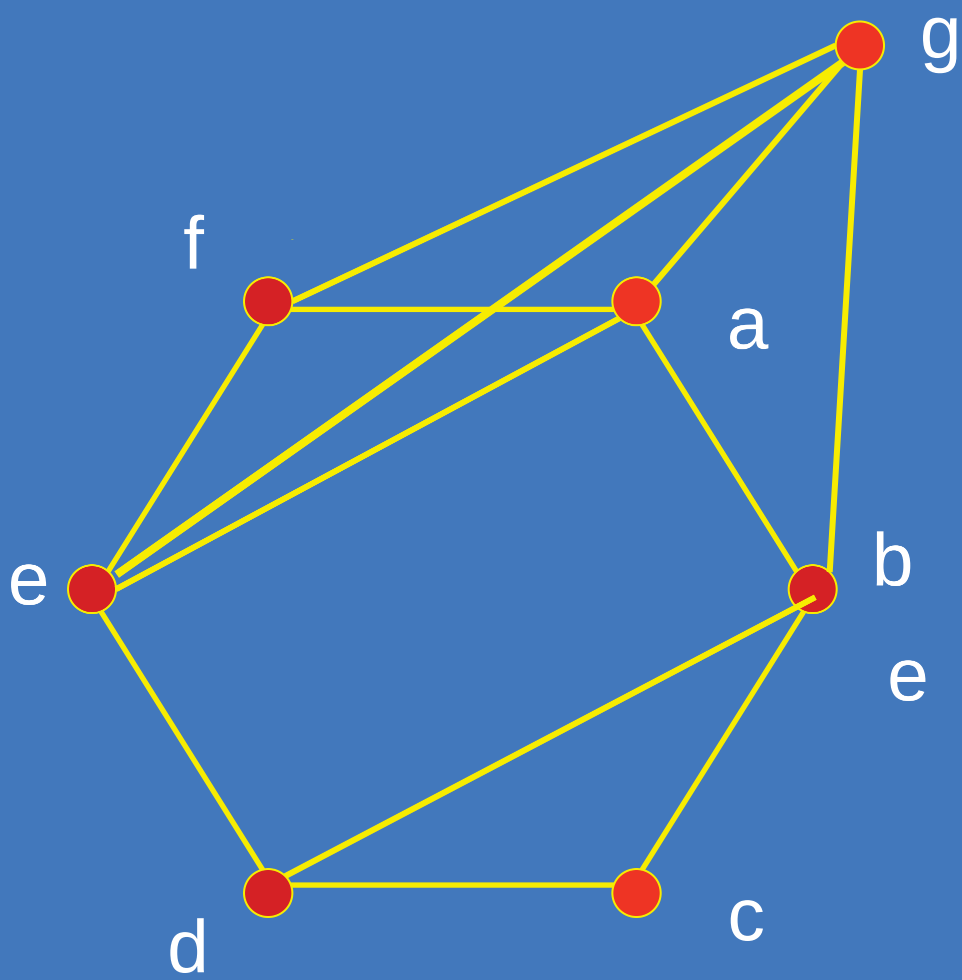
Theorem (Opsut, 1982): If G is a line graph, then $k(G) \leq 2$, with equality iff for every u, $\theta(N(u)) = 2$.

Opsut's Conjecture

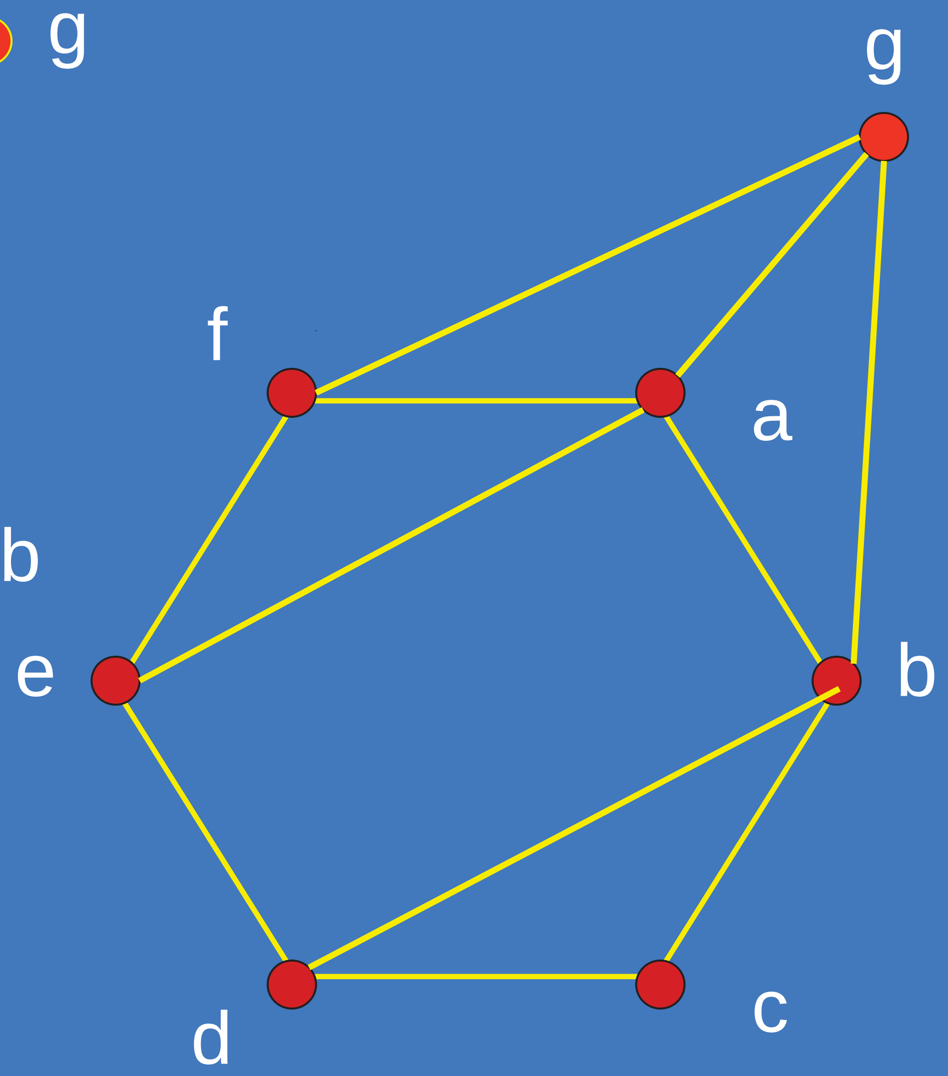
<u>**Opsut's Conjecture** (1982)</u>: Suppose G is any graph in which $\theta(N(u)) \leq 2$ for all u. Then $k(G) \leq 2$, with equality iff for every u, $\theta(N(u)) = 2$.

Note: graphs with $\theta(N(u)) \leq 2$ are sometimes called ***quasi-line graphs*** or ***locally co-bipartite graphs.***

Quasi-line Graphs



Quasi-line graph



Not a quasi-line graph: $\theta(N(a)) = 3$

Opsut's Conjecture

Hard problem.

<u>Sample Theorem (Wang 1991)</u>: Opsut's Conjecture holds for all K_4-free graphs.

G is ***critical*** if $\theta(N(u)) \leq 2$ for all u and for every (not necessarily maximal) clique K, there is a vertex u in K such that $\theta(N(u)-K) = 2$.

<u>Sample Theorem (Wang 1991)</u>: Opsut's Conjecture holds for all non-critical graphs.

Opsut's Conjecture

Theorem (McKay, Schweitzer, Schweitzer 2011): Opsut's Conjecture is true.

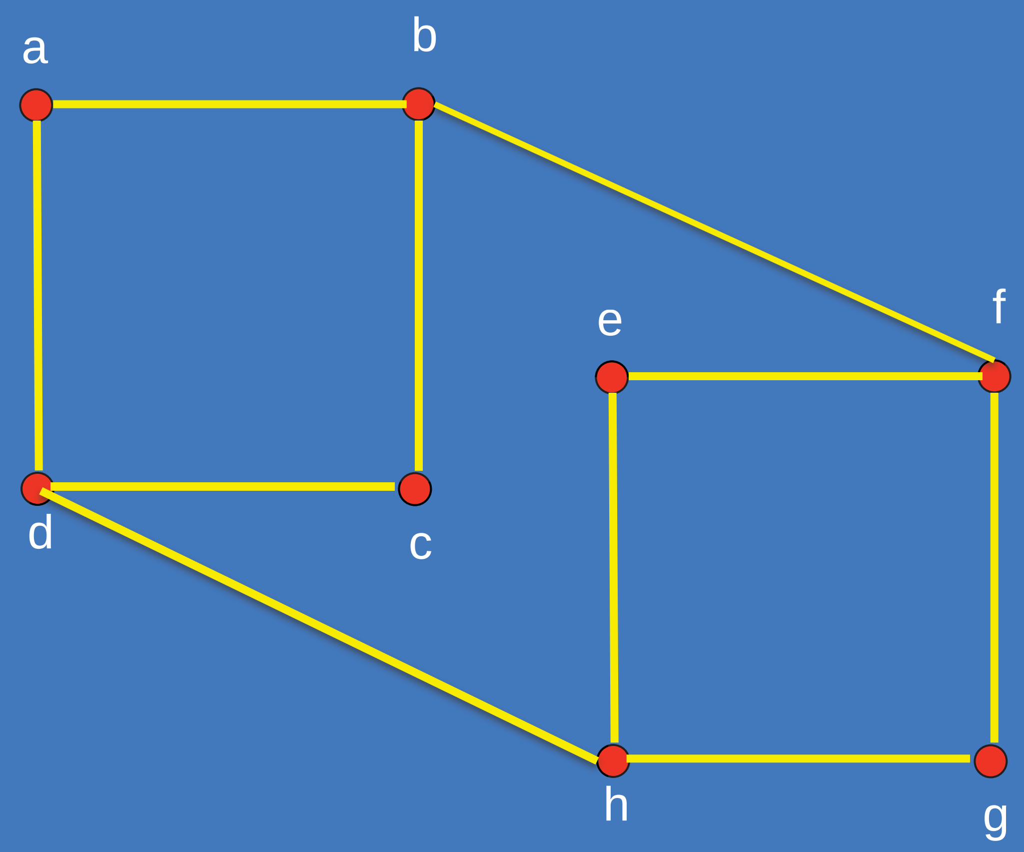
Opsut's Conjecture

Comment on the Proof:

- A key part of the proof is to prove a variant of a characterization of quasi-line graphs, graphs in which $\theta(N(u)) \leq 2$ for all u.
- Originally characterized by Chudnovsky and Seymour 2005.

Holes in Graphs

A ***hole*** in a graph is an induced cycle C_n with $n > 3$.



Holes in Graphs

A ***chordal graph*** is a graph with no holes.

Theorem (Roberts 1978): If G is chordal, then $k(G) \leq 1$.

Theorem (Cho & Kim 2005): If G has exactly one hole, $k(G) \leq 2$.

Theorem (Lee, Kim, Kim, Sano 2010): If G has exactly two holes, $k(G) \leq 3$.

Conjecture (Kim 2005): $k(G) \leq$ number of holes $+ 1$.

Holes in Graphs

Theorem (McKay, Schweitzer, Schweitzer 2011): Kim's conjecture is true: $k(G) \leq$ number of holes + 1.

McKay, et al. also proved a generalization of this result.

Holes in Graphs

Consider the subspace of the cycle space of a graph that is spanned by the holes.

Cycle space: represent each cycle by a 0-1 vector with each entry corresponding to an edge and entry corresponding to edge e being 1 iff e is on the cycle.

Hole Space $\mathcal{H}$(G): subspace of cycle space spanned by vectors corresponding to holes.

Holes in Graphs

<u>Conjecture (Kim, Lee, Park, Sano 2011)</u>:
$k(G) \leq \dim \mathcal{H}(G) + 1$

<u>Theorem (McKay, Schweitzer, Schweitzer 2011)</u>: This conjecture is also true.

<u>Theorem (Lee, et al 2011)</u>: If all holes are pairwise edge-disjoint, then $k(G) \leq \dim \mathcal{H}(G) - \omega(G) + 3$

$\omega(G)$ = size of the largest clique.

Data Gathering: Community Food Webs, Sink Food Webs, Source Food Webs

- Interesting observation that how one gathers data about food webs can influence your conclusions about competition graphs.
- A ***community food web*** includes all predation relations among species.
- In practice, we don't get all this data.
- We might start with some species, look for species they prey on, look for species they prey on, etc.

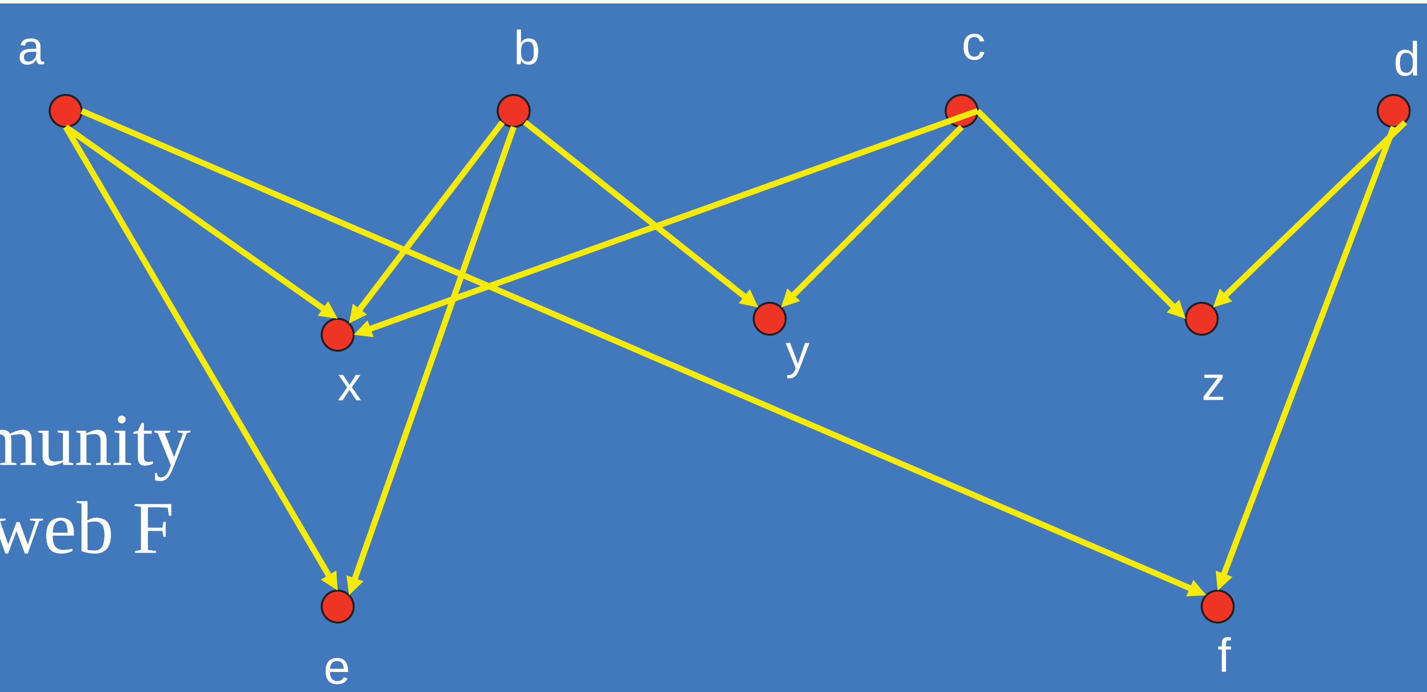
Data Gathering: Community Food Webs, Sink Food Webs, Source Food Webs

- Suppose F is a community food web.
- Let W be a set of species in F (ones we start with).
- Let X be the set of all species that are reachable by a path in F from vertices in W.
  - So, we start with vertex of W, find its prey, find prey of the prey, etc.
- Let Y be the set of all species that reach vertices of W by a path in F.
  - So we start with vertex of W, find its predators, find predators of those predators, etc.

Data Gathering: Community Food Webs, Sink Food Webs, Source Food Webs

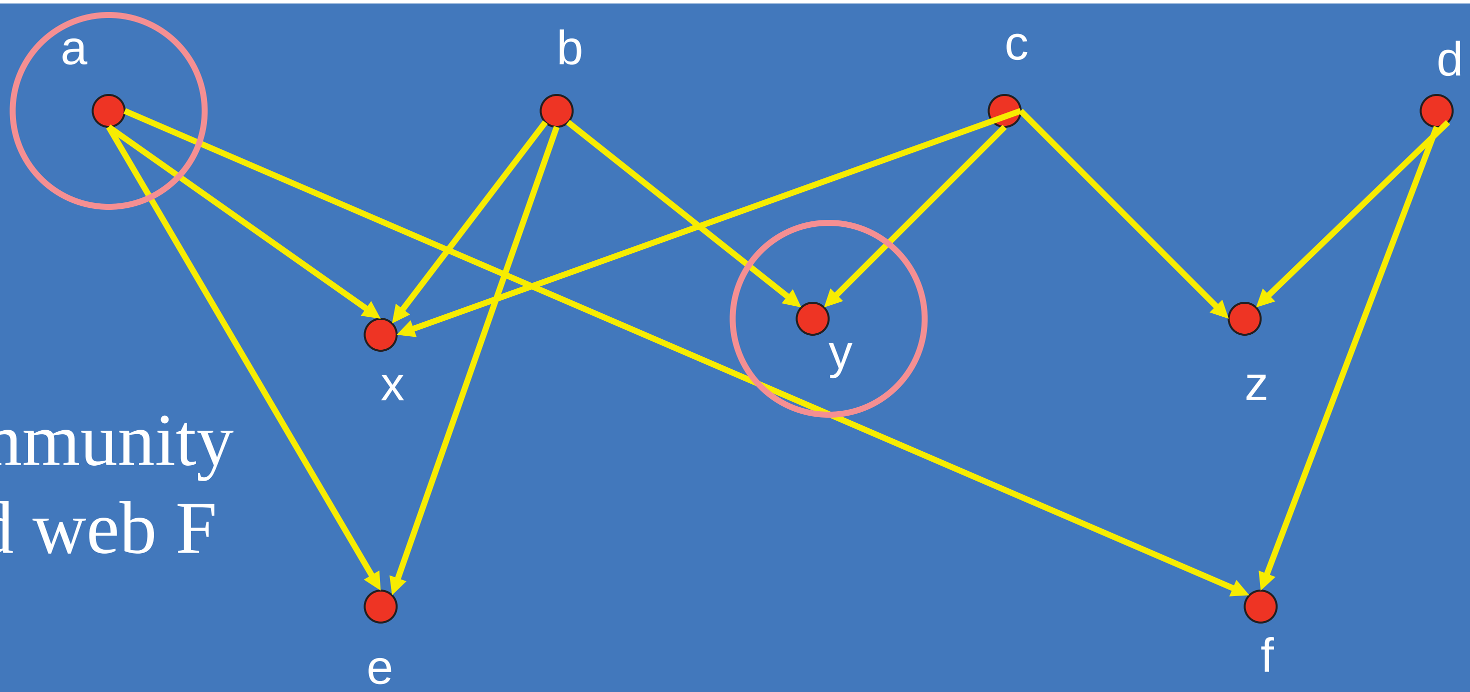
- Suppose F is a community food web.
- Let W be a set of species in F (ones we start with).
- Let X be the set of all species that are reachable by a path in F from vertices in W.
  - The subgraph induced by vertices of X is called the ***sink food web*** corresponding to W.
- Let Y be the set of all species that reach vertices of W by a path in F.
  - The subgraph induced by vertices of Y is called the ***source food web*** corresponding to W.

Data Gathering



Community food web F

Data Gathering



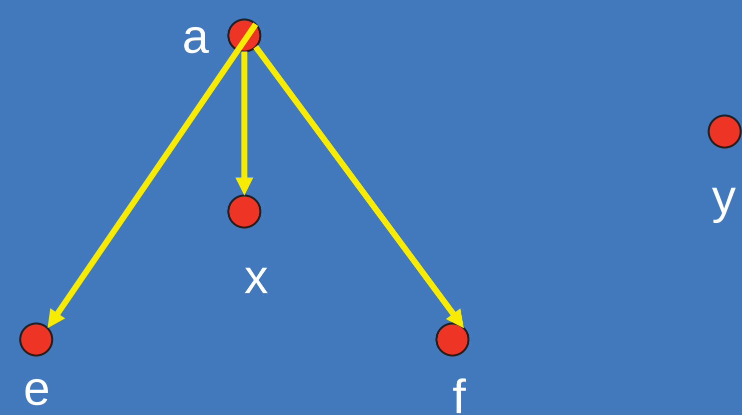
Community food web F

W = {a,y}

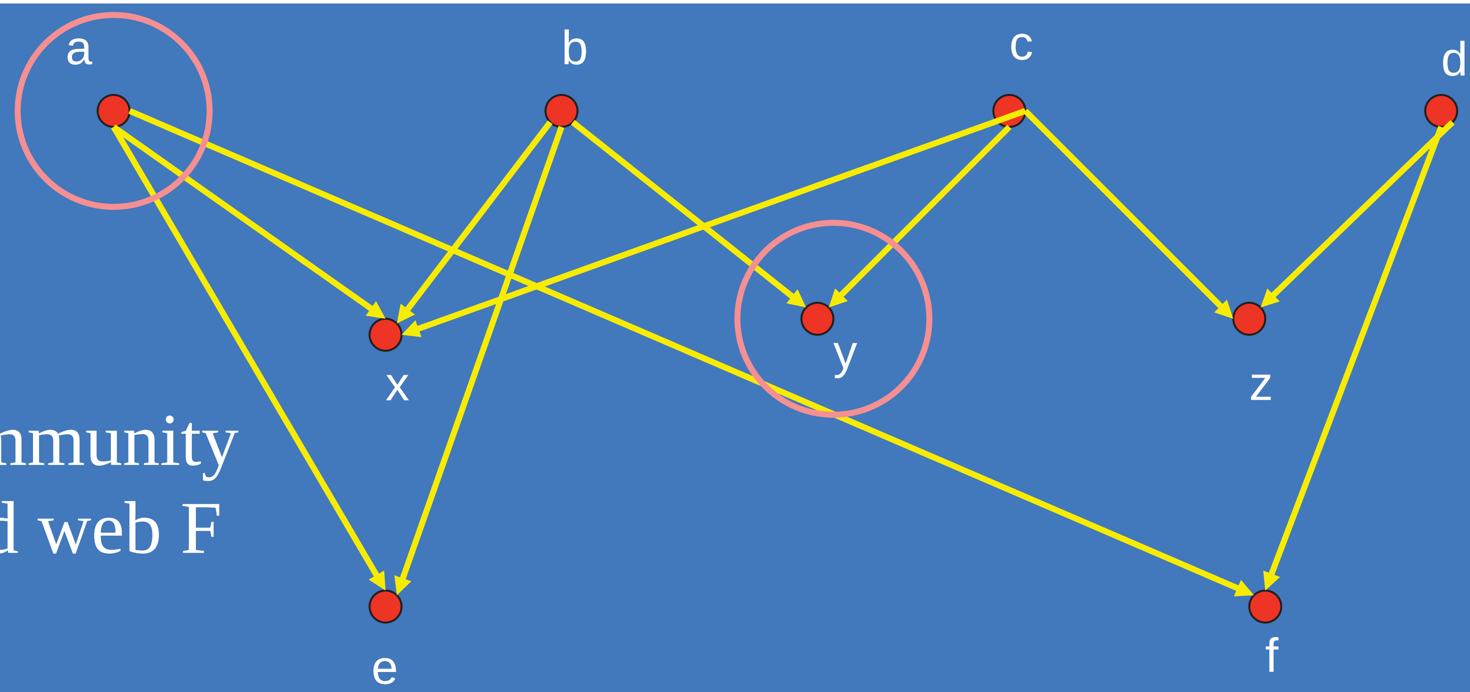
What is the sink food web?

X = {a,x,e,f,y}

Sink food web from W



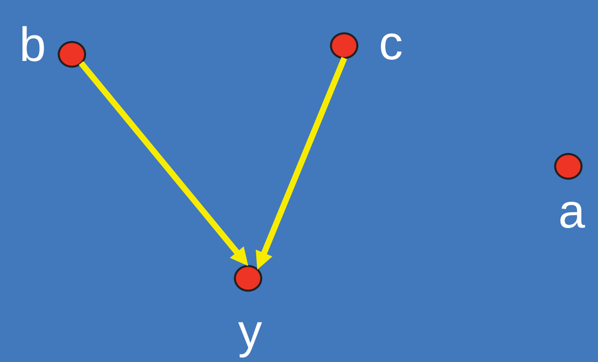
Data Gathering



Community
food web F

W = {a,y}
What is the source
food web?
Y = {a,b,c,y}

Source food web from W

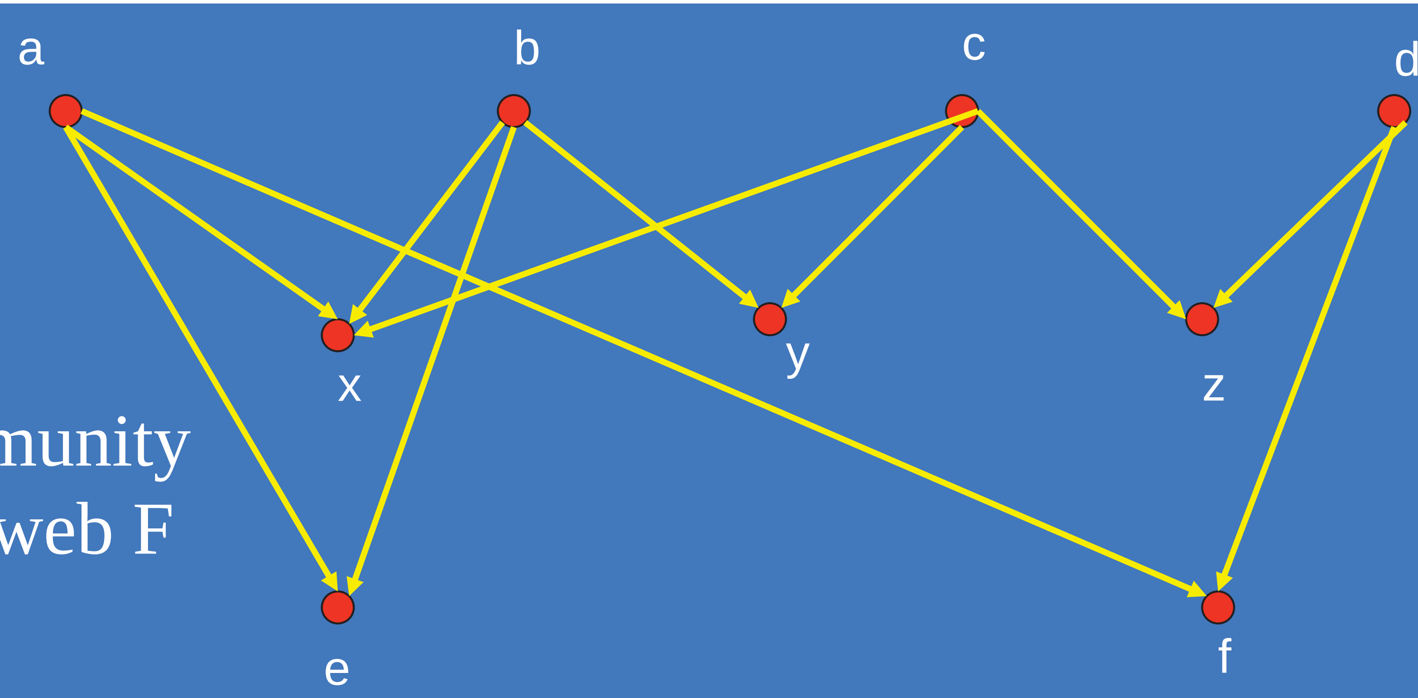


Data Gathering: Community Food Webs, Sink Food Webs, Source Food Webs

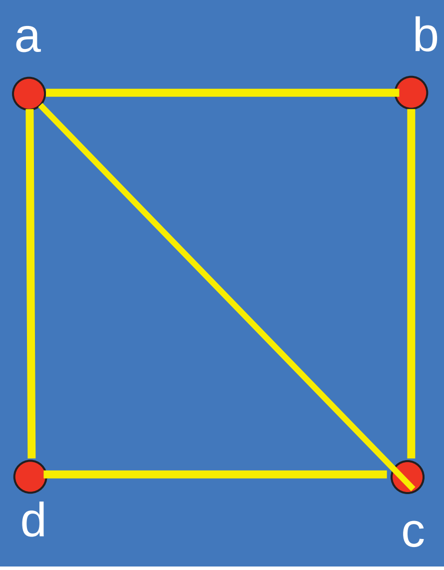
- Theorem (Cohen): A community food web has a competition graph that is an interval graph if and only if every sink food web contained in it does.

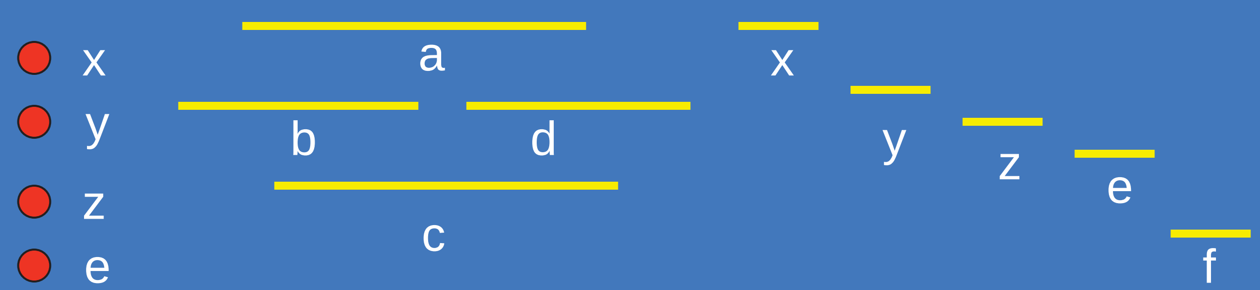
- However: A community food web can have a competition graph that is an interval graph while some source food web contained in it has a competition graph that is not an interval graph.

Data Gathering



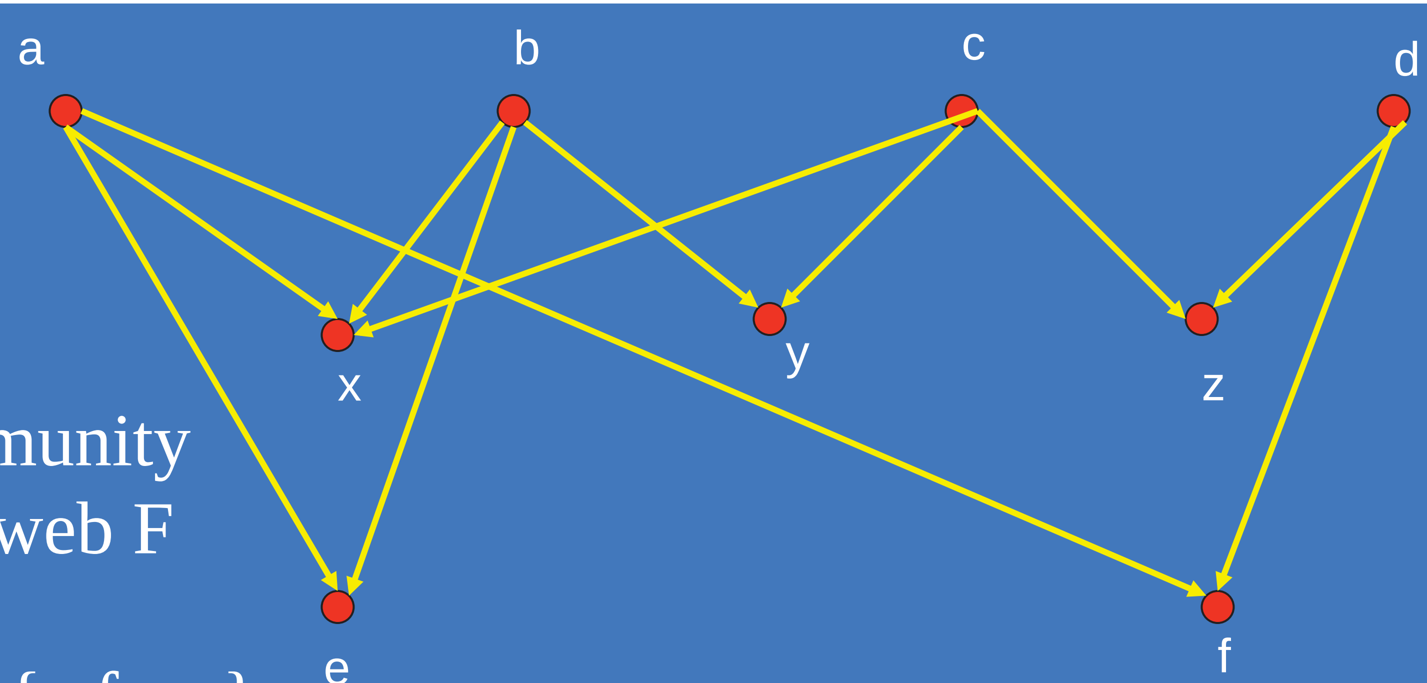
Community food web F





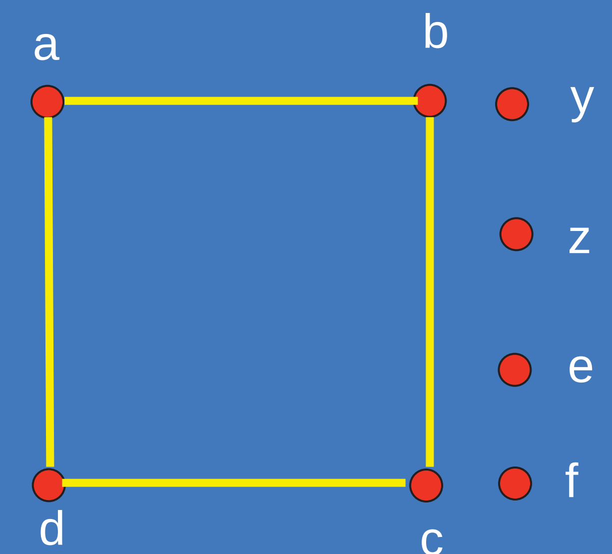
The competition graph of F is an interval graph.

Data Gathering



Community food web F

W = {e,f,y,z}
What is the competition graph of the source food web of W?
Y = {a,b,c,d,e,f,y,z}



Competition graph of the source food web from W
This is not an interval graph.

Data Gathering: Community Food Webs, Sink Food Webs, Source Food Webs

- This surprising result points up some of the difficulties involved in understanding the structure of competition graphs.
- It also leads to interesting caveats about general conclusions using models that are tested with data.

The Interval Graph Competition Graph Problem

- It remains a challenge (dating back to 1968) to understand what properties of food webs give rise to competition graphs of boxicity 1, i.e., interval graphs.
- In a computational sense this is easy to answer:
  - Given a digraph, compute its competition graph (easy)
  - Determine if this is an interval graph (well known to be solvable in linear time)

The Interval Graph Competition Graph Problem

•More useful would be results that explain the structural properties of acyclic digraphs that give rise to interval graph competition graphs.
•However, such results might be difficult to find:

•Theorem (Steif 1982): There is no list L (finite or infinite) of digraphs such that an acyclic digraph D has an interval graph competition graph if and only if it does not have an induced subgraph in the list L.

The Interval Graph Competition Graph Problem

- There are, however, results with extra assumptions about the acyclic digraph D.
- Example: It is useful is to place limitations on the indegree and outdegree of vertices (the maximum number of predator species and maximum number of prey species for any given species in the food web).
- Then there are some results with forbidden lists L. (e.g., Hefner, et al., 1991).

Variants of Competition Graphs

•Many variants of competition graphs have been studied in the literature:

- Common enemy graphs (Lundgren/Maybee)
- Competition common enemy graphs (Scott)
- Niche graphs (Cable, et al.)
- Phylogeny graphs (Roberts and Sheng)
- Competition hypergraphs (Sonntag & Teichert)
- p-competition graphs (Kim, et al.)
- Tolerance competition graphs (Brigham, et al.)
- m-step competition graphs (Cho, et al.)

Concluding Comments

There is much left to do in the study of competition graphs and their ecological and other applications.

Cicada images courtesy of Nina Fefferman