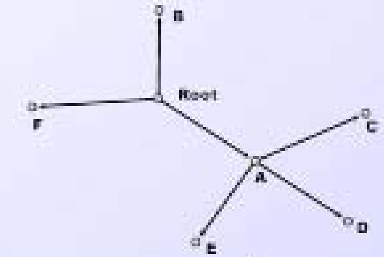
Secondary extinctions in ecological networks: Bottlenecks unveiled



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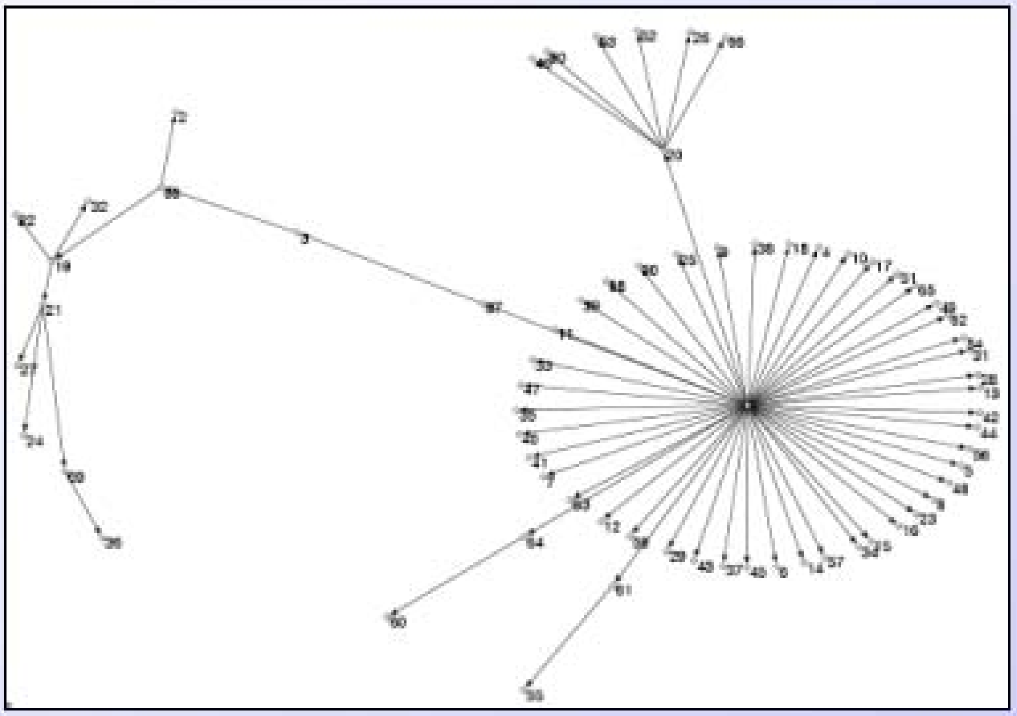

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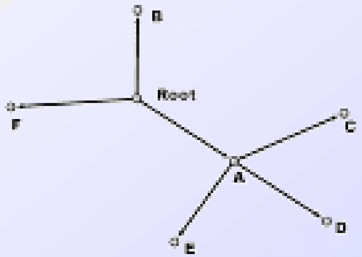
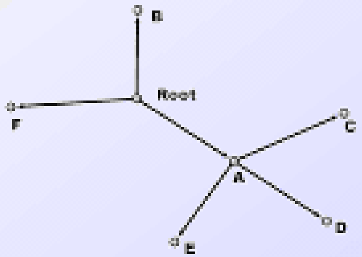
Secondary Extinction



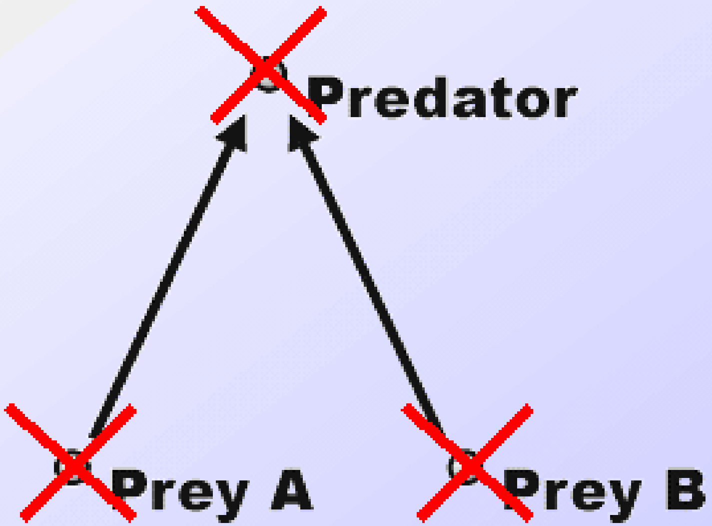
Because of complex relations between species in ecosystems, a **single extinction** event could precipitate into **cascading extinction** (secondary extinction) of other species.

This is an important issue for conservation biology and has been approached using various techniques. Depending on the modeling context, one can evaluate different aspects of the problem.

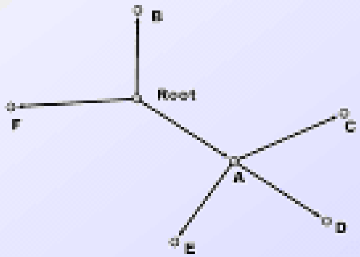
Secondary extinction: lack of nutrients



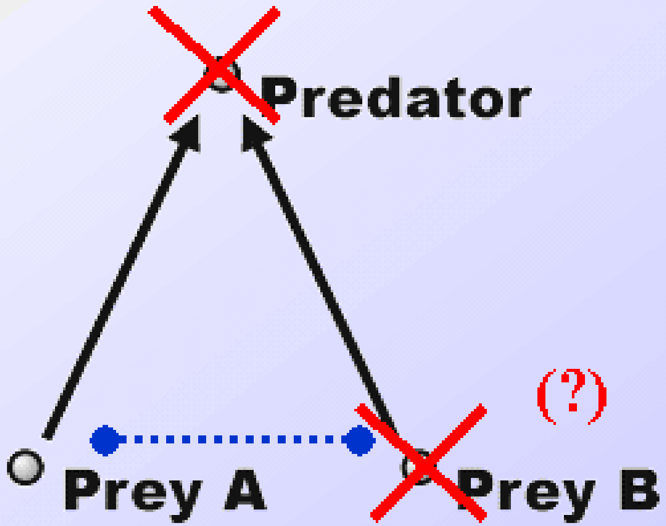
When all **prey** of a given predator go extinct, the predator will starve as well.



Secondary extinction: lack of control

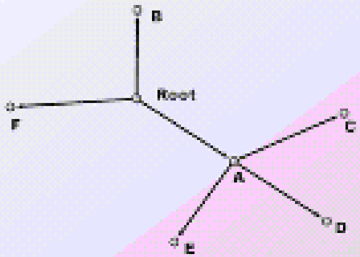


The extinction of a **top predator** could enhance **competition** between prey, leading to **extinction** of one or more of them.

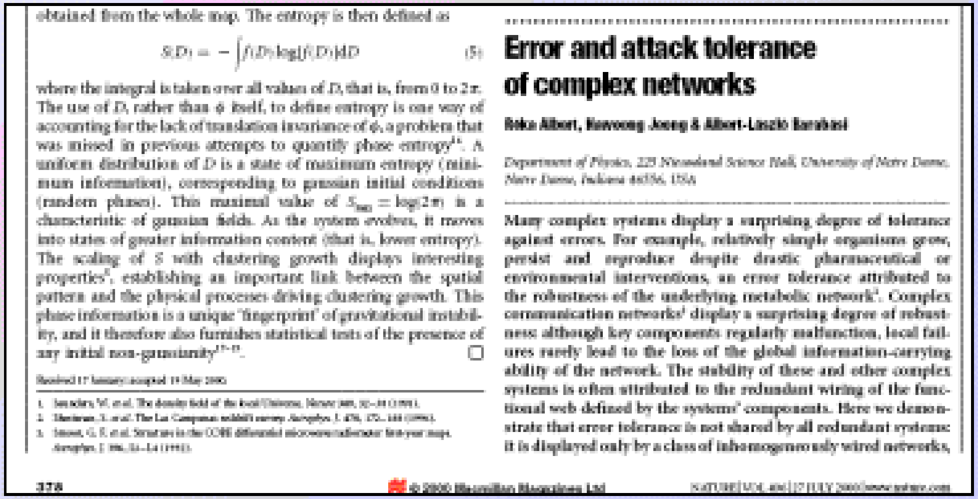


We will concentrate on the former cause of secondary extinction because it's the simplest one, and can be applied to statical (who eats whom) descriptions of ecosystems

Species removal and the Internet



A great input came from statistical mechanics of networks: Albert et al. Studied the effects of "extinction" of servers on the Internet (and other networks) structure



obtained from the whole map. The entropy is then defined as

$$S(D) = -\int f(D) \log[f(D)] dD \quad (5)$$

where the integral is taken over all values of D, that is, from 0 to 2π. The use of D, rather than ϕ itself, to define entropy is one way of accounting for the lack of translation invariance of ϕ, a problem that was missed in previous attempts to quantify phase entropy[4]. A uniform distribution of D is a state of maximum entropy (minimum information), corresponding to gaussian initial conditions (random phases). This maximal value of $S_{max} = \log(2\pi)$ is a characteristic of gaussian fields. As the system evolves, it moves into states of greater information content (that is, lower entropy). The scaling of S with clustering growth displays interesting properties[5], establishing an important link between the spatial pattern and the physical processes driving clustering growth. This phase information is a unique 'fingerprint' of gravitational instability, and it therefore also furnishes statistical tests of the presence of any initial non-gaussianity.

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Error and attack tolerance of complex networks

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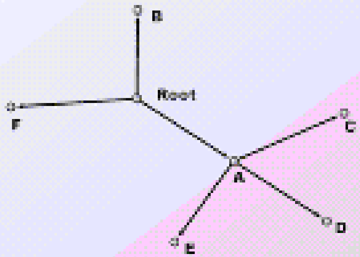
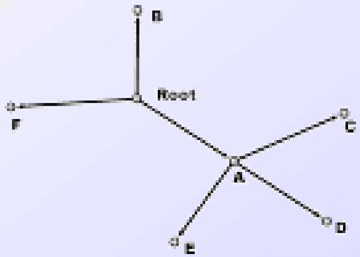
Many complex systems display a surprising degree of tolerance against errors. For example, relatively simple organisms grow, persist and reproduce despite drastic pharmaceutical or environmental interventions, an error tolerance attributed to the robustness of the underlying metabolic network[1]. Complex communication networks[2] display a surprising degree of robustness: although key components regularly malfunction, local failures rarely lead to the loss of the global information-carrying ability of the network. The stability of these and other complex systems is often attributed to the redundant wiring of the functional web defined by the systems' components. Here we demonstrate that error tolerance is not shared by all redundant systems: it is displayed only by a class of inhomogeneously wired networks,

Scale Free networks



- Albert and colleagues studied the effects of node removal in scale-free networks
- In such networks the majority of nodes are poorly connected, while a few of them (hubs) hold most of the connections

Errors and Attacks

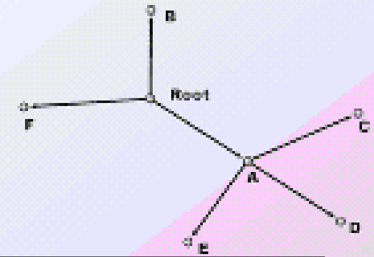


Applying nodes “extinction” to scale-free networks they discriminate between two cases:

- Error → Random removal of nodes
- Attack → Targeted removal of nodes

This is important because the removal of a few hubs could damage the network structure dramatically, while the removal of other nodes could poorly affect it.

Errors and Attacks in biological networks



Montoya & Solé (2002) and Dunne et al. (2002), applied the same experiment to **food webs**.

They started removing the **most connected node** and removed all nodes with no incoming arcs (secondary extinctions). They plotted extinction curves for **most connected removal** vs. **random removal**.

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Small World Patterns in Food Webs

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REPORT

Network structure and biodiversity loss in food webs: robustness increases with connectance

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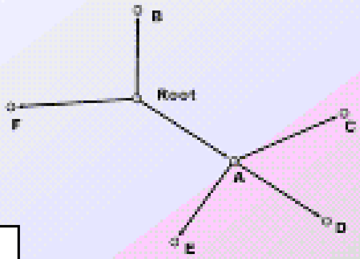
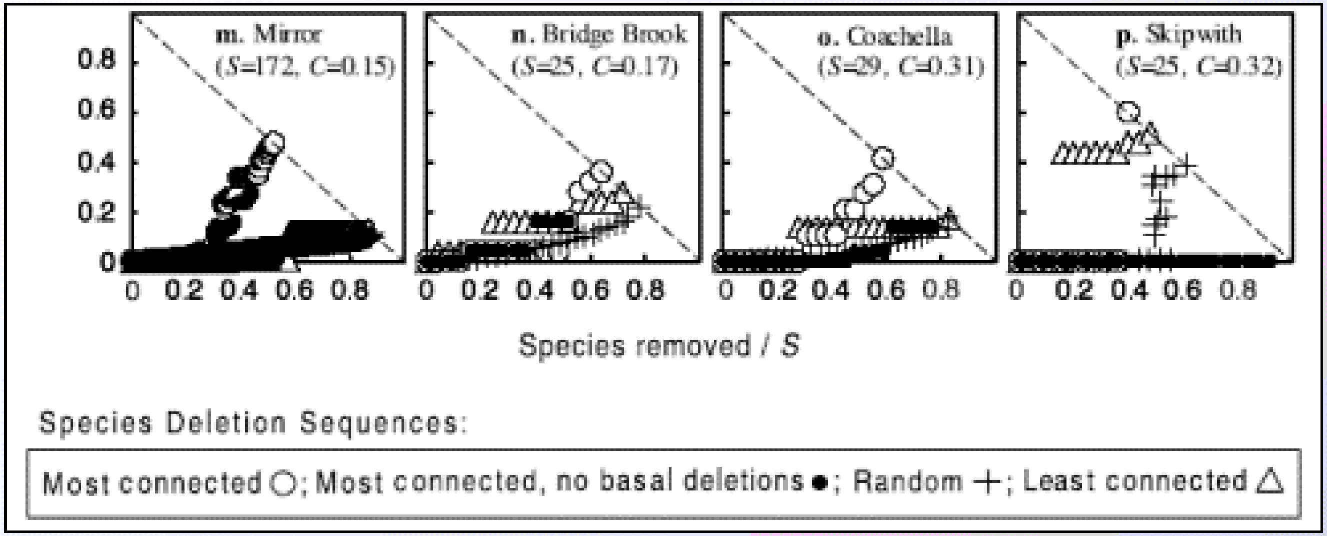
Abstract

Food-web structure mediates dramatic effects of biodiversity loss including secondary and 'cascading' extinctions. We studied these effects by simulating primary species loss in 16 food webs from terrestrial and aquatic ecosystems and measuring robustness in terms of the secondary extinctions that followed. As observed in other networks, food webs are more robust to random removal of species than to selective removal of species with the most trophic links to other species. More surprisingly, robustness increases with food-web connectance but appears independent of species richness and omnivory. In particular, food webs experience 'rivet-like' thresholds past which they display extreme sensitivity to removal of highly connected species. Higher connectance delays the onset of this threshold. Removing species with few trophic connections generally has little effect though there are several striking exceptions. These findings emphasize how the number of species removed affects ecosystems differently depending on the trophic *function* of species removed.

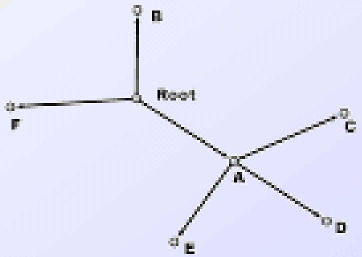


Extinction curves

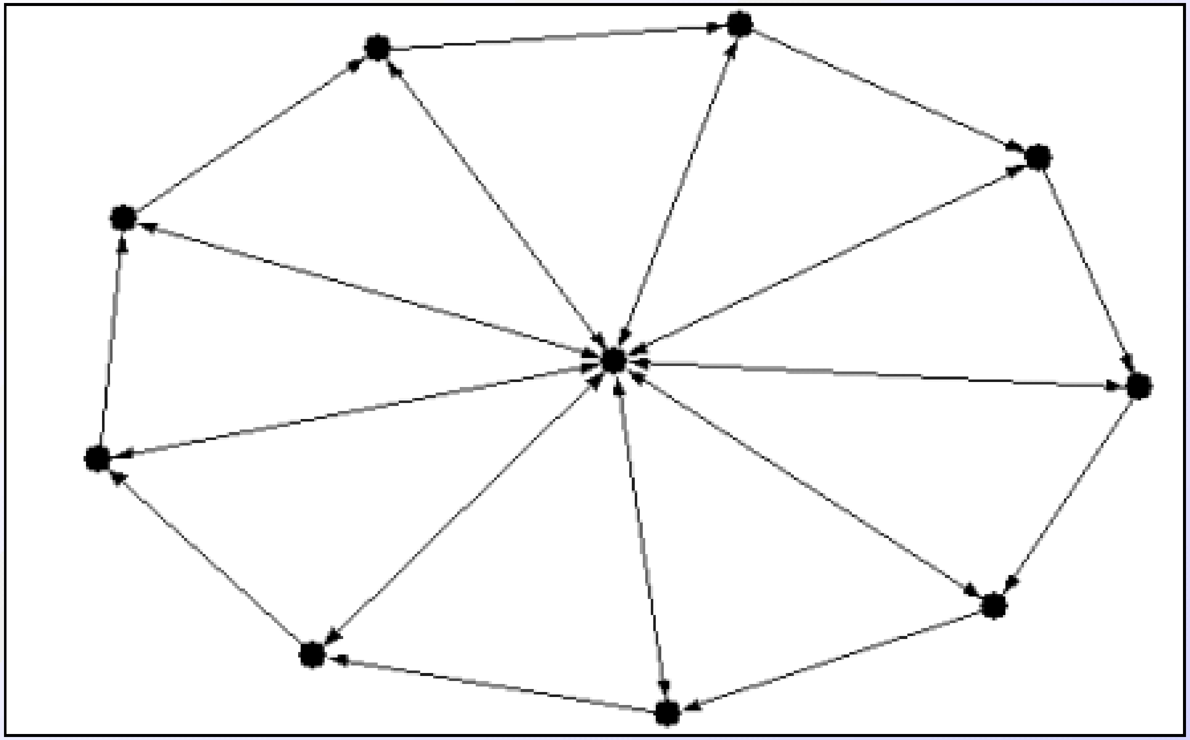


Sequential removal of nodes; simulation; emphasis on node's connectance.

But is connectance the most important factor for assessing species importance in maintaining the food web connected?

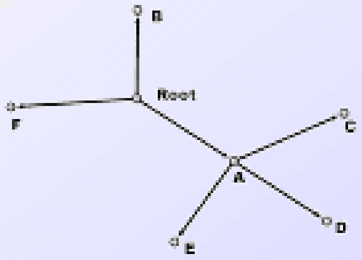


A Counterexample

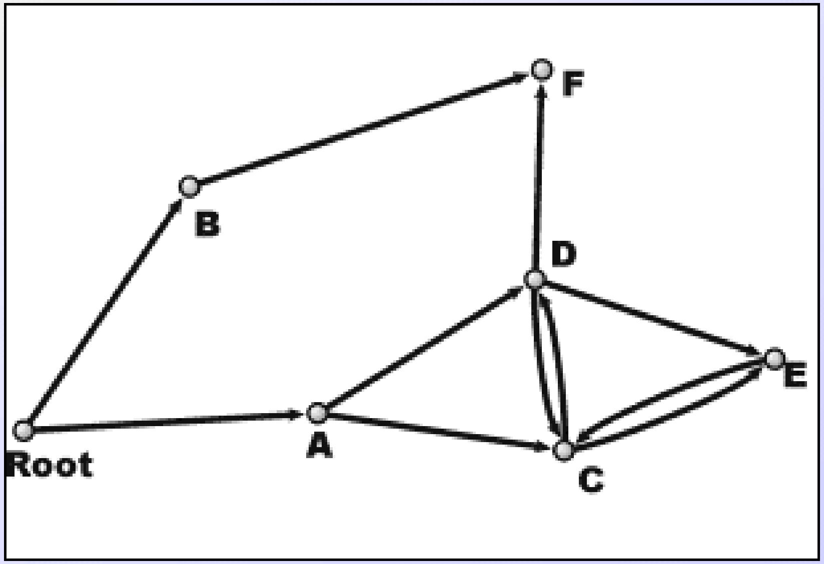


In this case removing the node with the **highest connectance** would produce **no** secondary **effects**

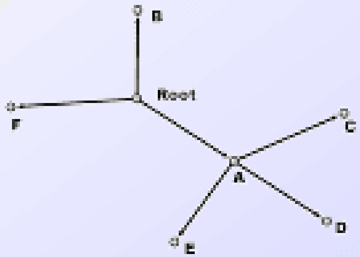
Rooted networks



- While the Internet can be seen as an undirected graph, food webs representing transfers of matter are always directed (*a* → *b* means "b eats a")
- All the energy comes from outside the system (Root)

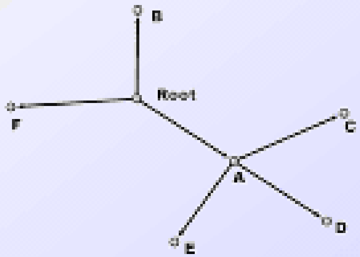


Dominators

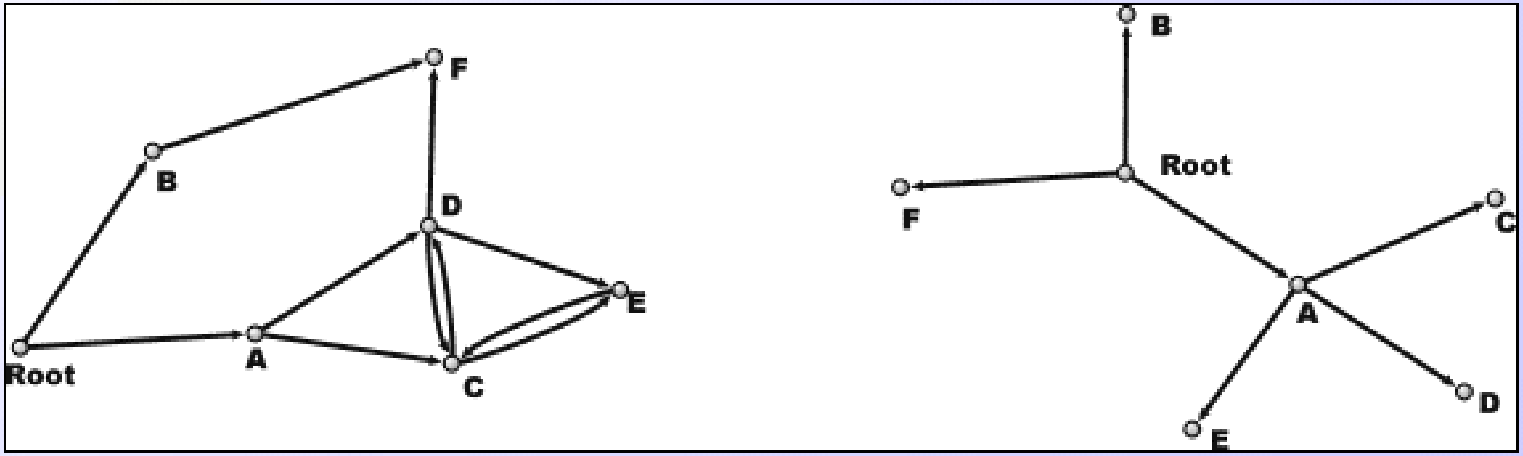


- We say that node *A* dominates *B* iff every path going from *Root* to *B* contains *A*
- *A* is the immediate dominator of *B* if *A* =*dom(B)* and every dominator of *A* is a dominator of *B* as well.
- The removal of a node will extinguish all the nodes it dominates
- Connecting every node to its immediate dominator yields to the so-called dominator tree.

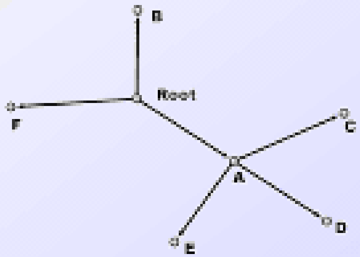
Dominator Trees



We can associate to any Directed Graph rooted in R another connected graph, containing N-1 arcs, called the Dominator Tree: the removal of a node in the original Graph will extinguish all the nodes that belong to its branch in the Dominator Tree.



Dominators & Pathways



e.g.

Paths connecting R to A

R→**B**→C→D→A

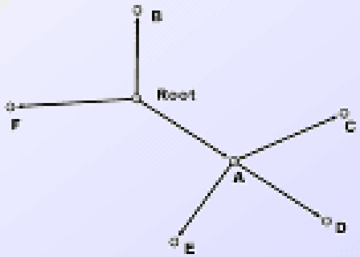
R→**B**→E→D→A

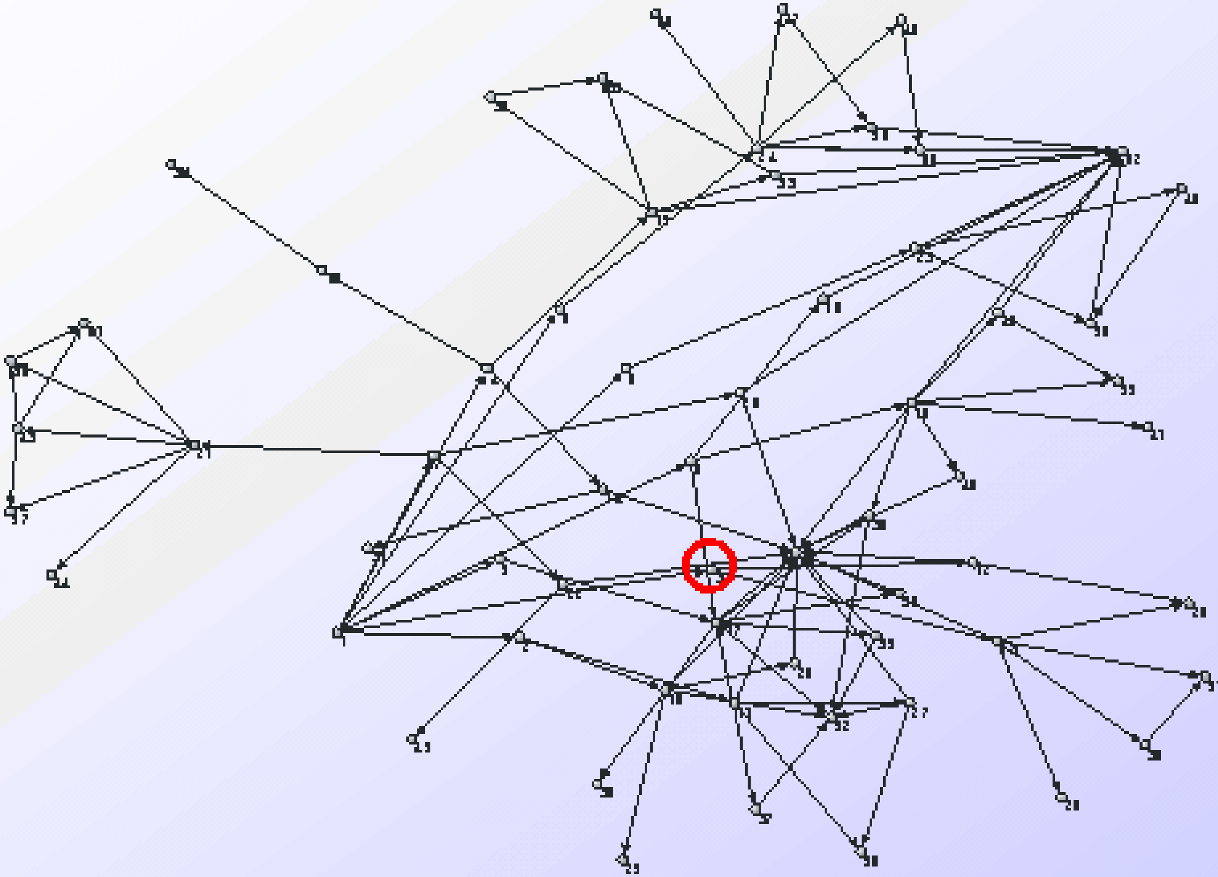
R→**B**→C→A

R→**B**→C→B→C→B→…→A

Only the nodes R,B,A belongs to all paths, therefore the branch of the dominator tree would look like R→B→A

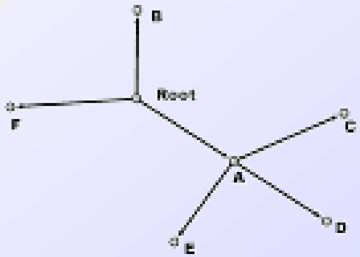
Grassland Foodweb

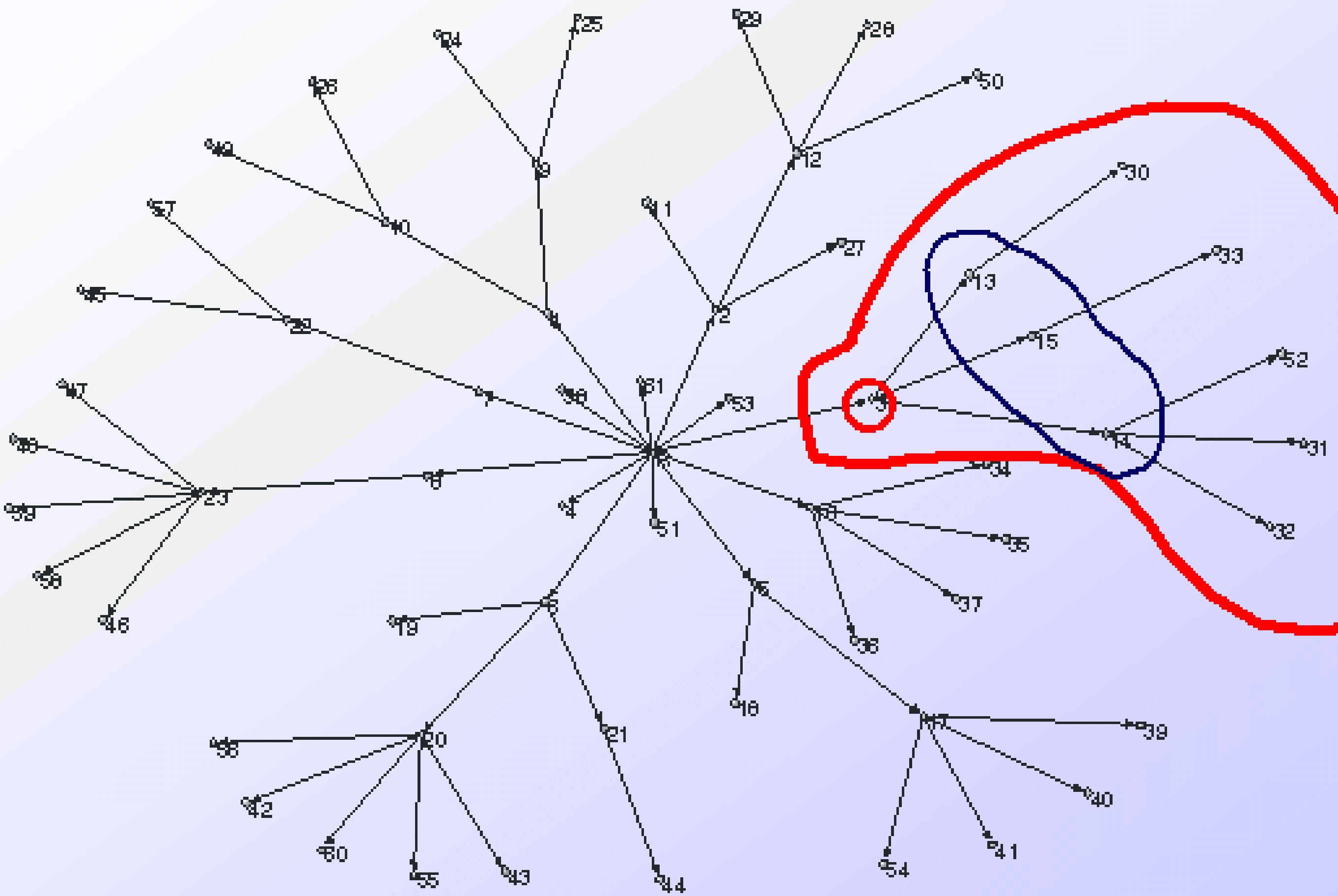


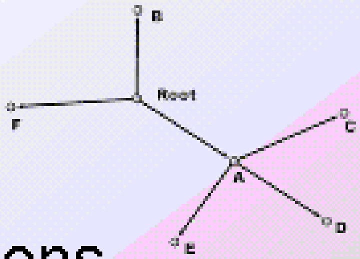


Martinez, N.D., Hawkins, B.A., Dawah, H.A. and Feifarek, B.P., 1999. Effect of sampling effort on characterization of food-web structure. Ecology, 80, 1044-1055

Grassland Dominator Tree







Attacks & Errors Redefined

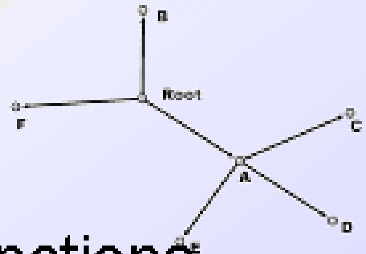
Error Sensitivity (**ES**): average number of extinctions due to **random** removal

Max:

$$ES = \sum_{i \neq r} \frac{|dom(i)| - 1}{(N-1)^2} = \frac{1}{(N-1)^2} + \frac{2}{(N-1)^2} + \ldots + \frac{N-1}{(N-1)^2}$$
$$= \frac{N(N-1)}{2(N-1)^2} = \frac{N}{2(N-1)} \approx \frac{1}{2}$$

Min:

$$ES = \sum_{i \neq r} \frac{|dom(i)| - 1}{(N-1)^2} = \frac{1}{(N-1)^2} + \frac{1}{(N-1)^2} + \ldots + \frac{1}{(N-1)^2}$$
$$= \frac{(N-1)}{(N-1)^2} = \frac{1}{(N-1)}$$



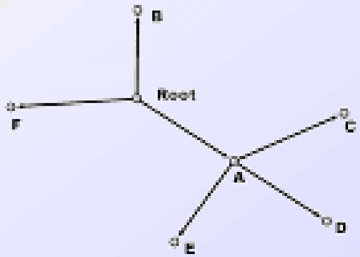
Attacks & Errors Redefined/2

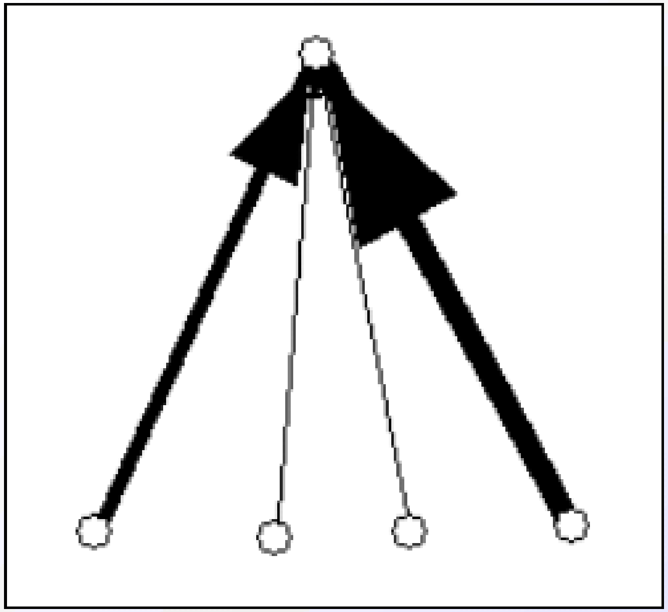
Attack Sensitivity (**AS**): maximum number of extinctions one can cause with a single removal

$$AS = max\left\{\frac{|dom(i)| - 1}{(N-1)}\right\}$$

AS ranges from 1/(N-1) (no secondary extinction) to 1 (complete extinction of the network).

Quantitative extension





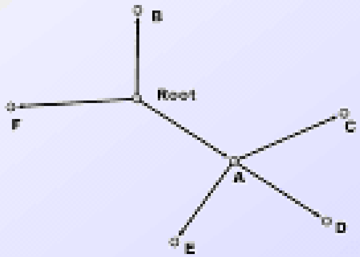
The dominator's algorithm is strictly qualitative (presence-absence).

In real ecosystems the different arcs (relations) have different importance (values).

In ecological networks arcs represent flux of matter.

If one removes a node that furnishes the majority of energy/matter the remaining fluxes could not be sufficient to mantain the population.

Quantitative extension/2

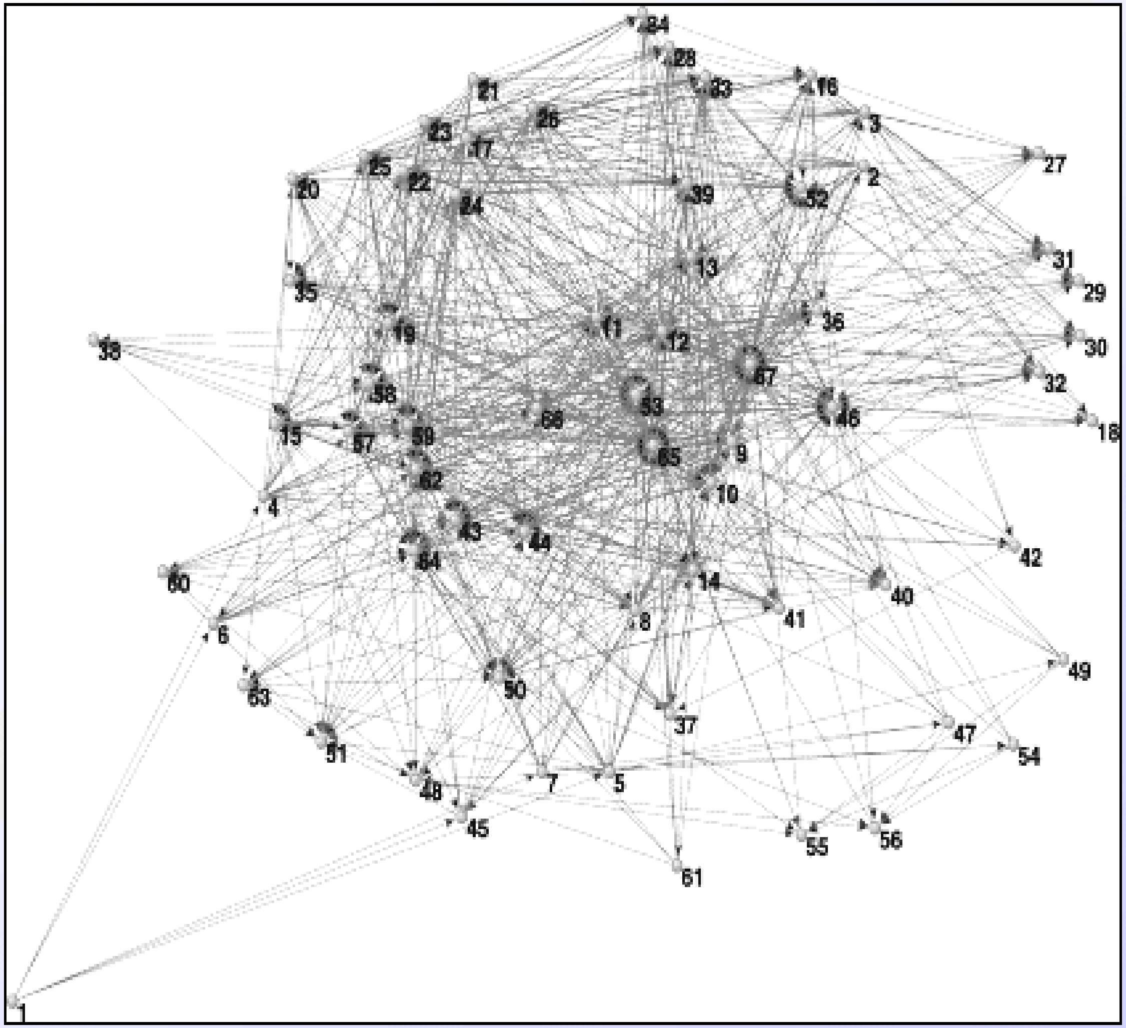


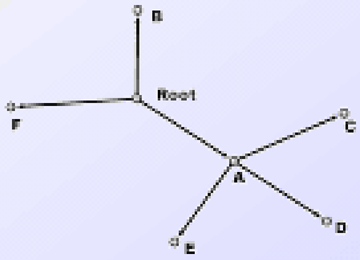
We plotted the behavior of ES and AS when only the strongest arcs were retained.

For each node we kept only the fluxes that contribute to each node's diet for a fraction greater than a given threshold *t*.

Diet's fraction = (Entering Flux)/(Sum of Entering Fluxes)

Results example

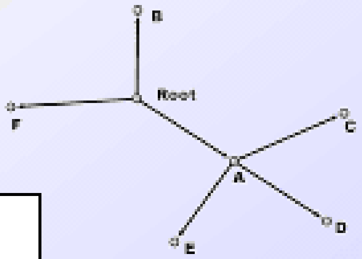




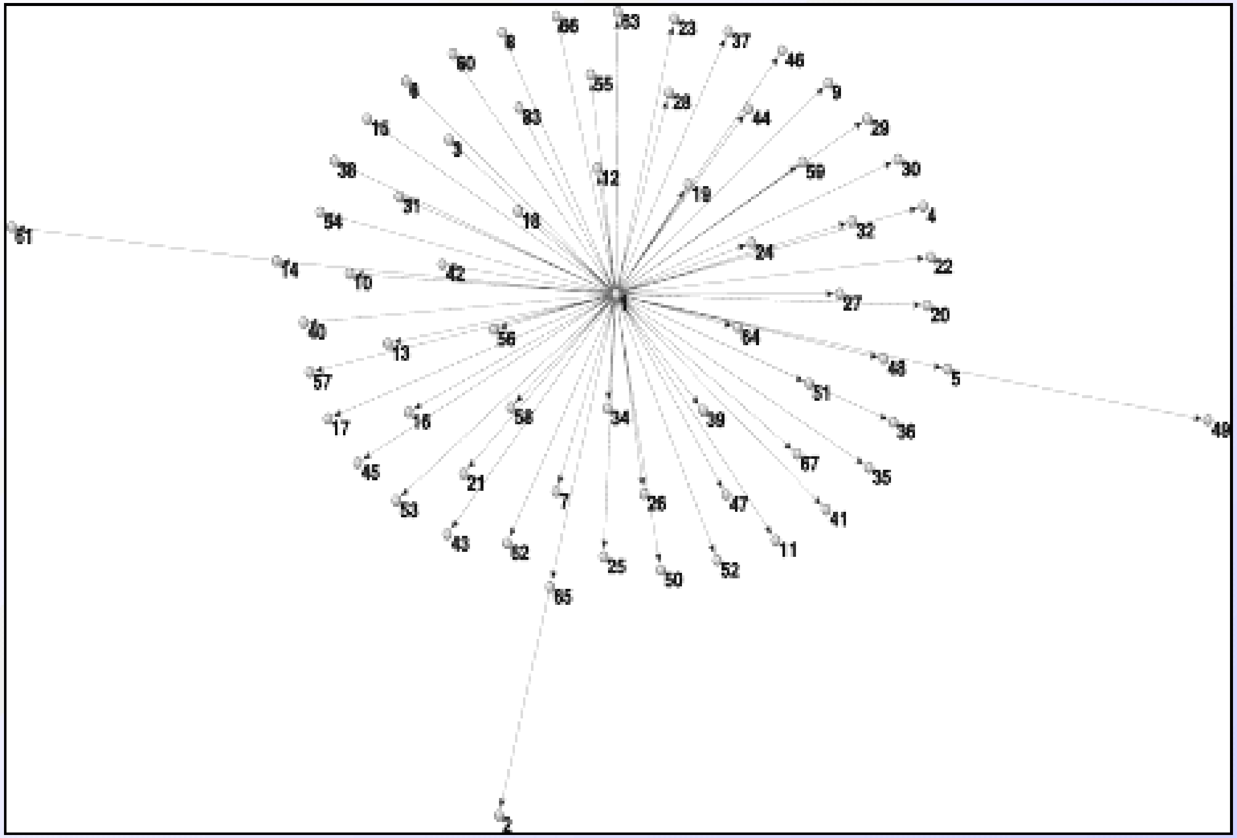
Gramminoid Marshes:

67 Nodes

798 arcs



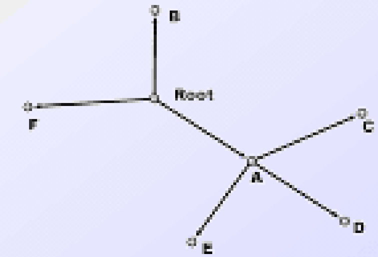
Results example - DT

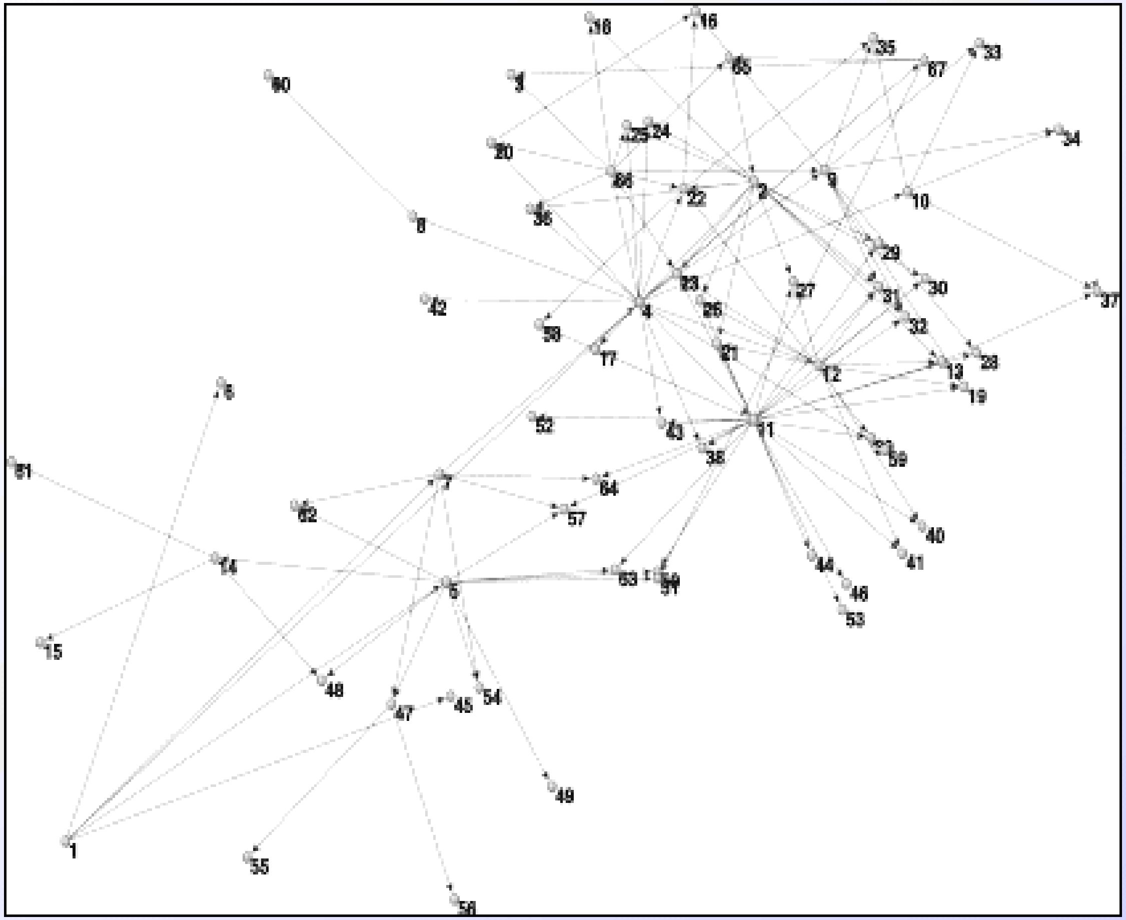


Gramminoid Marshes:

ES = 0.016 (1.056 nodes) AS=0.03 (2 nodes)

Results example - 2





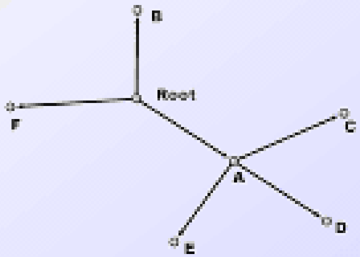
Gramminoid Marshes:

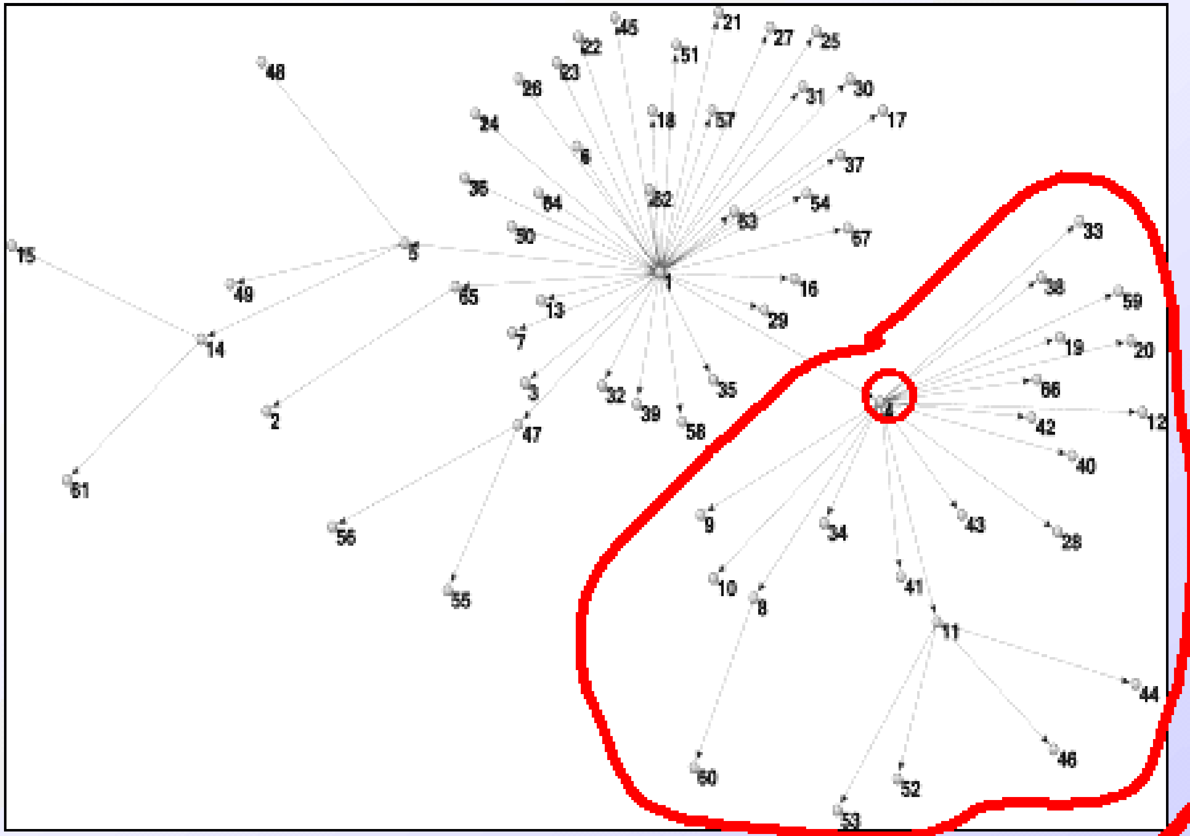
Setting Threshold 15%

→127 arcs

Only 16% of arcs are retained!

Results example – 2 DT

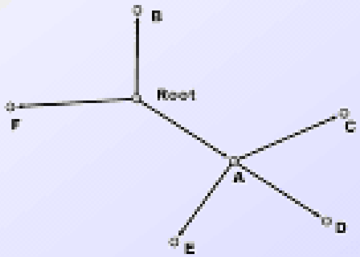




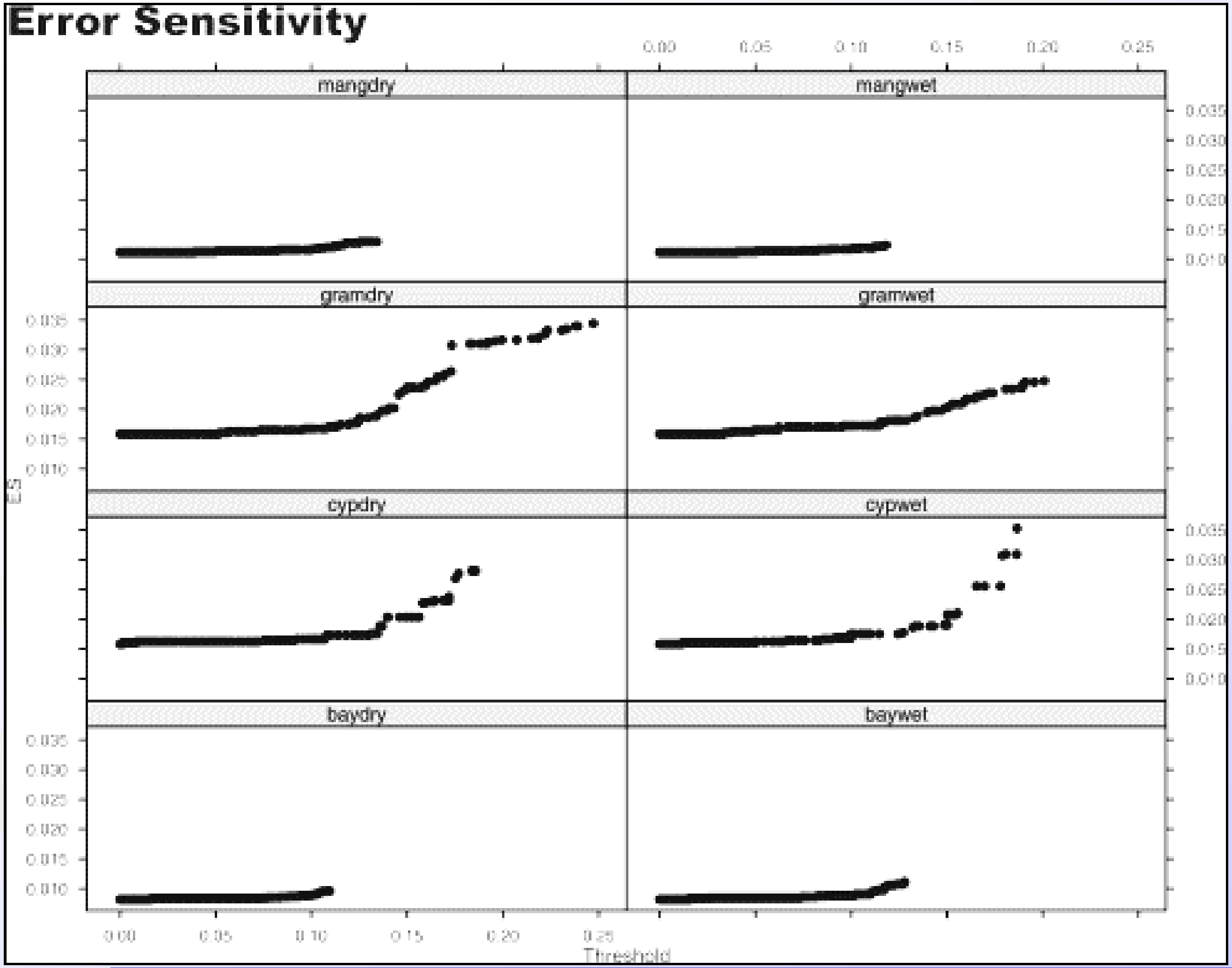
34% of species would go extinct with a single node removal!

Gramminoid Marshes:

ES = 0.024 AS=0.34



Errors in Big Networks



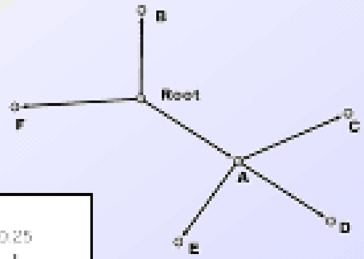
8 well-studied ecosystems

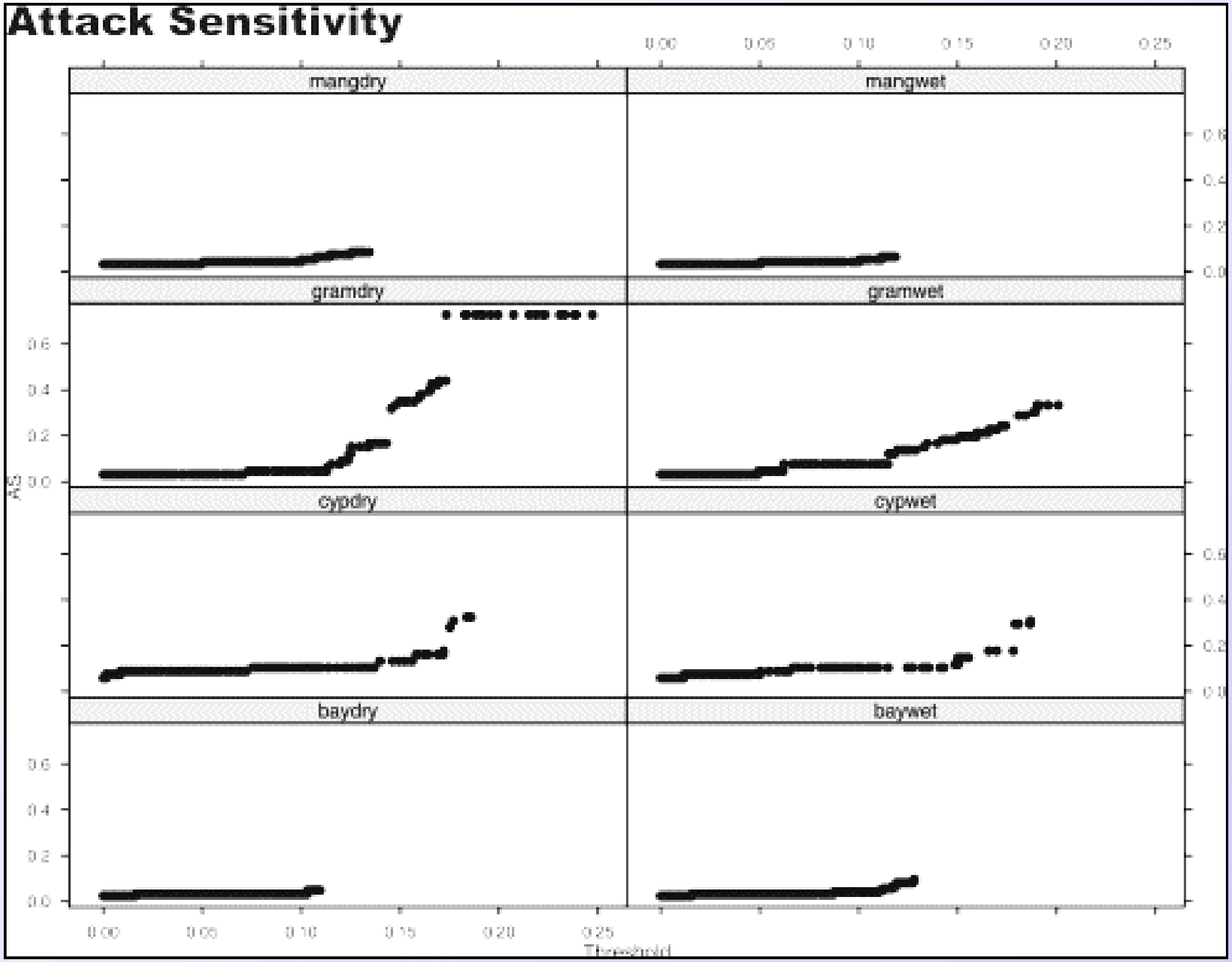
Big networks

(67-126 nodes)

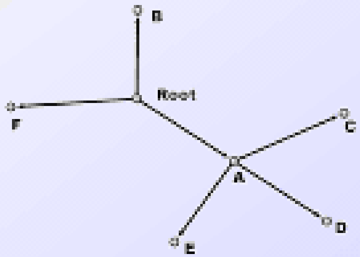
Threshold ranges from 0% to 25%

Attacks in Big Networks



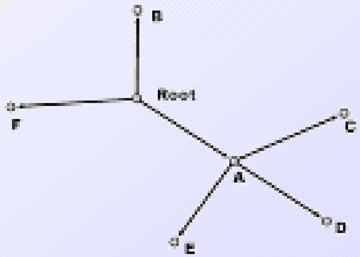


Conclusions



- Dominator Trees are elegant structures that forecast the effects of node removal
- DTs can be studied using graph-theory techniques
- DT approach has still several limitations, that can be solved taking into account quantitative data
- DT is based on static description and has to be rebuilt in order to assess sequential extinctions

Further readings



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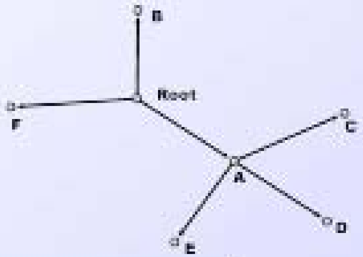
Secondary extinctions in ecological networks: Bottlenecks unveiled



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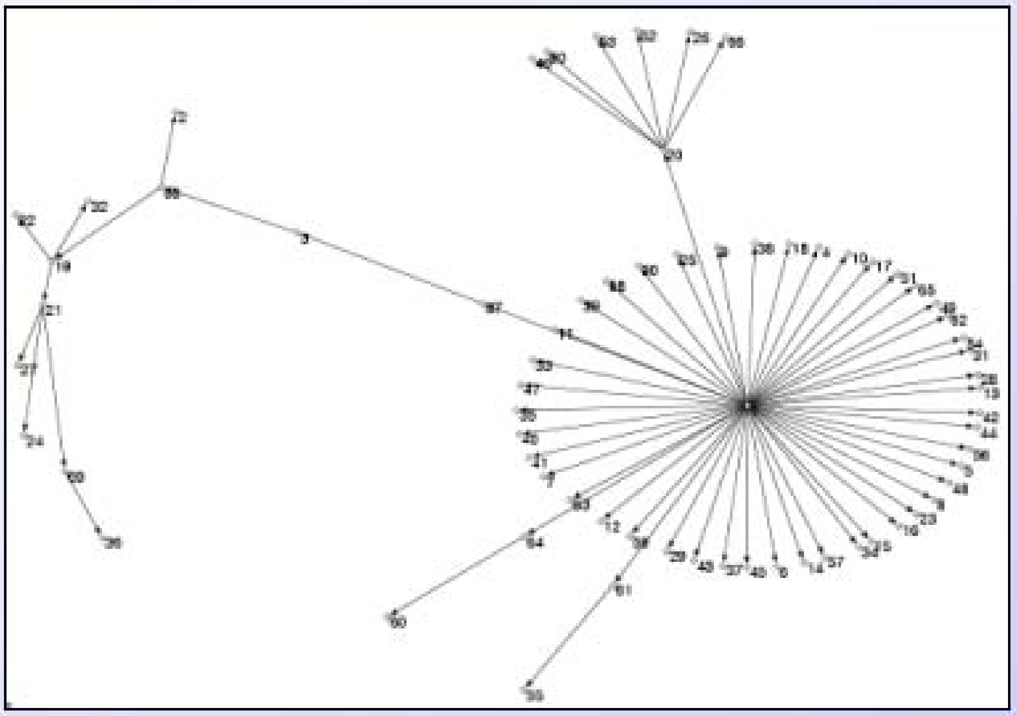

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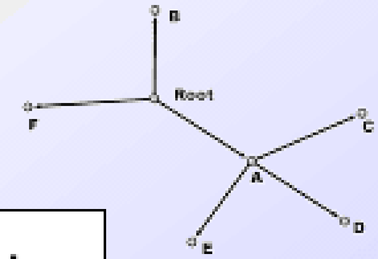
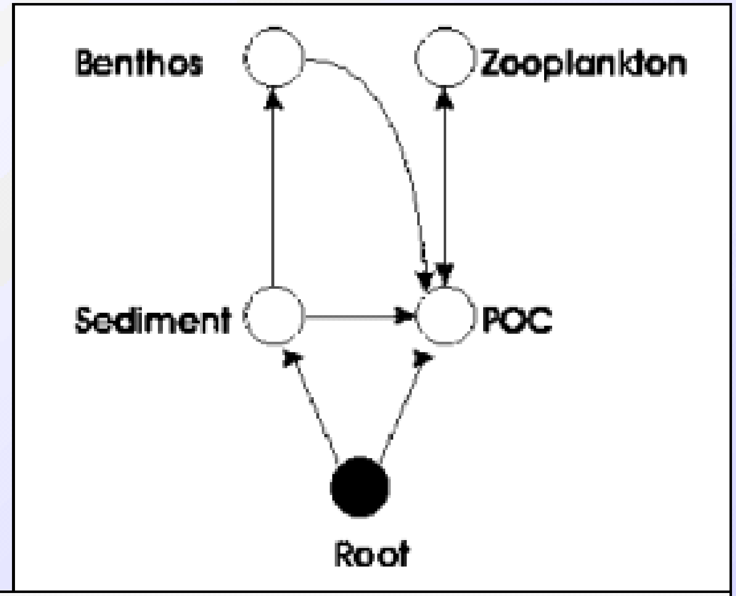


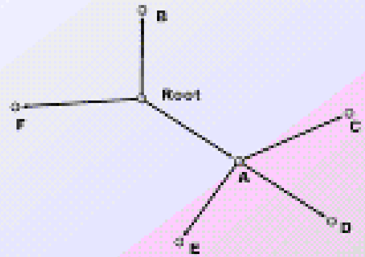
Dominators Algorithm - 1

- We present the implementation of Aho et al. Because it's the simplest one.
- This algorithm runs in **n**^{3} in the worst case.

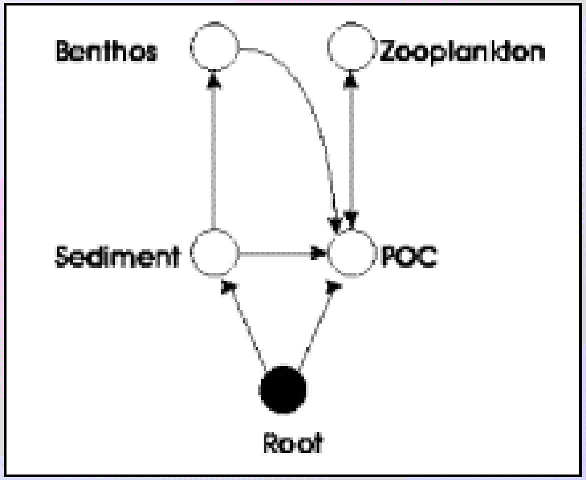


	R	Sediment	POC	Benthos	Zooplankton
R	0	1	1	0	0
Sediment	0	0	0	1	0
POC	0	1	0	0	1
Benthos	0	1	0	0	0
Zooplankton	0	1	0	0	0

Dominators Algorithm - 2



R	1	0	0	0	0
Sediment	1	1	1	1	1
POC	1	1	1	1	1
Benthos	1	1	1	1	1
Zooplankton	1	1	1	1	1



For each node x excluding root we rewrite the x^{th} row as:

$dom(x)=x\cup(dom(i_1)\cap dom(i_2)\cap\ldots\cap dom(i_k))$

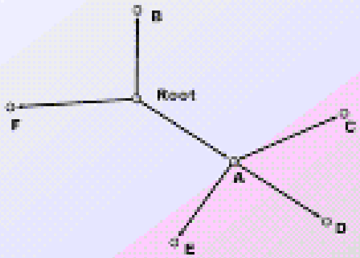
Where i_1, i_2,…,i_k are the nodes that point to x

e.g.: dom(Sediment)= Sediment ∪(dom(R)∩dom(POC)∩ dom(Zoopl.)∩dom(Benthos))

```
  0 1 0 0 0 OR
{ 1 0 0 0 0 AND
  1 1 1 1 1 AND
  1 1 1 1 1 AND
  1 1 1 1 1 }
```

That becomes: dom(Sediment) =

0 1 0 0 0 OR {1 0 0 0 0} = 1 1 0 0 0



Dominators Algorithm - 3

We reiterate the procedure for every row, and then restart until no changes are made

The final Dominator Matrix is utilized for building the Dominator Tree

R	1	0	0	0	0
Sediment	1	1	0	0	0
POC	1	0	1	0	0
Benthos	1	1	0	1	0
Zooplankton	1	0	1	0	1