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Robustness of Food Webs: Effects of Species' Extinction on Networks Structure

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Robustness of Food Webs

Effects of Species' Extinction on Networks Structure

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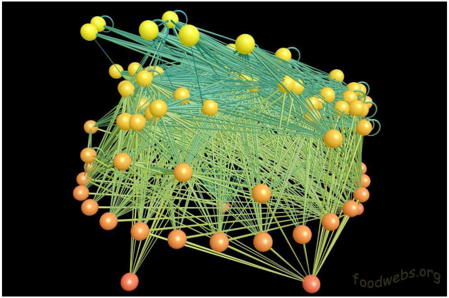
Outline

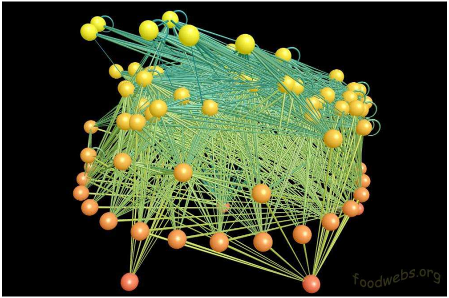
Food webs: "Who eats whom?"



Caribbean Reef Trophic Web

50 Nodes (groups of species)
556 Directed Edges (feeding relations)

Food webs: "Who eats whom?"



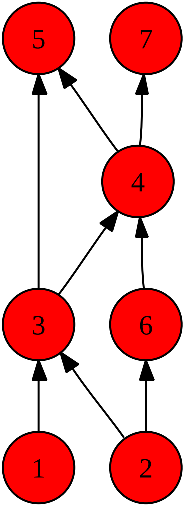
Caribbean Reef Trophic Web

50 Nodes (groups of species)
556 Directed Edges (feeding relations)

Topology of networks

The structure of the food web is going to influence its dynamics and ultimately the ways in which it responds to human disturbance.

Notation



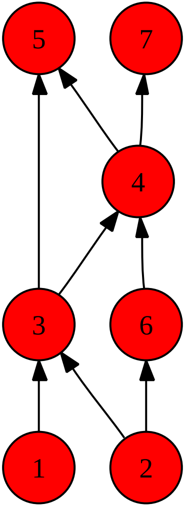
Typically, a food web is constituted by:

- Nodes → species or trophic species.
- Edges (Arcs, Links) → feeding relations among species.

Example

7 nodes. (S)
8 edges. (E)
Connectance $= E/S^2 = 0.16$.

Adjacency Matrix

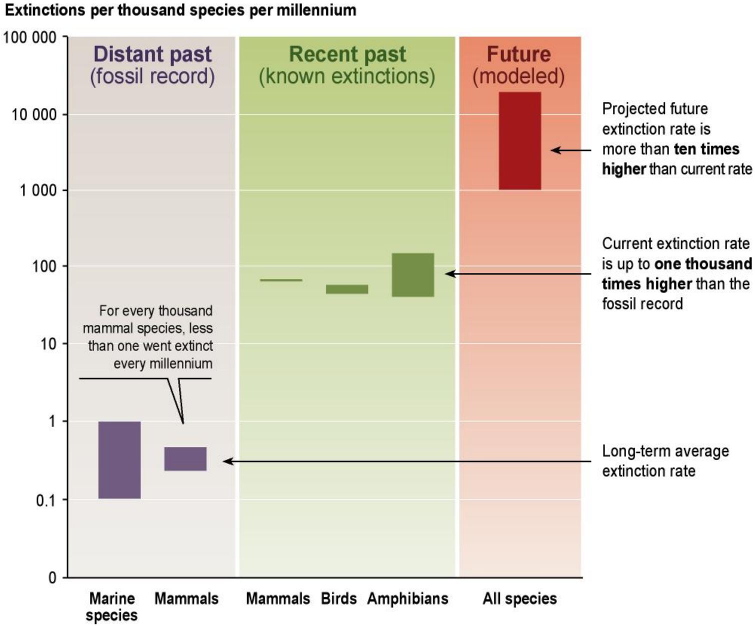


This graph can be associated with a matrix:

$$A = \begin{bmatrix} 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

Adjacency Matrix

$a_{ij} = 0 \longrightarrow$ species i and j do not interact directly.
$a_{ij} = 1 \longrightarrow$ species i is a prey of j.



Source: Millennium Ecosystem Assessment

Causes of Extinction

- Habitat destruction/degradation
- Alien species invasion
- Pollution
- Overexploitation
- Diseases




Mechanism of Extinction

Mortality/Fecundity

- Increase in mortality or removal rate; decrease in reproduction rate
- Fishing; Disease; Pollution

Competitive Exclusion

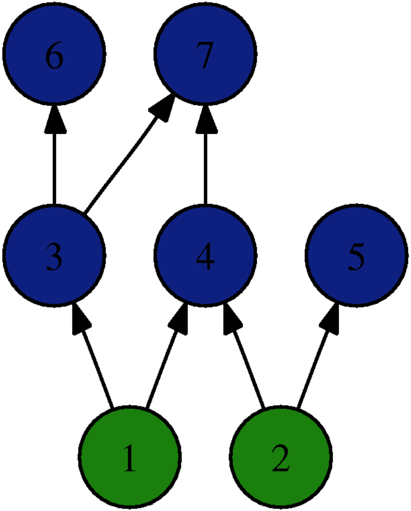
- Presence of better competitors
- Invasive species; Extinction of predators or other species that regulate competition

Lack of resources

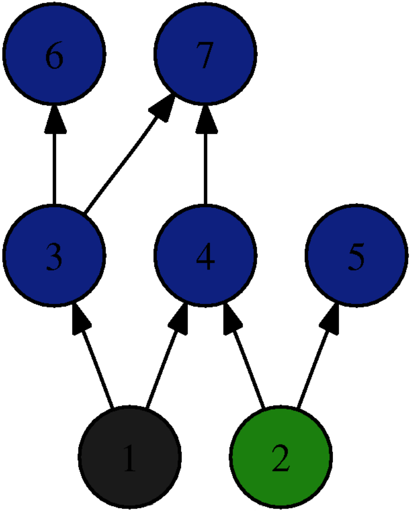
- Decrease in growth rate
- Habitat destruction; Overexploitation of prey

The last mechanism is connected to network structure

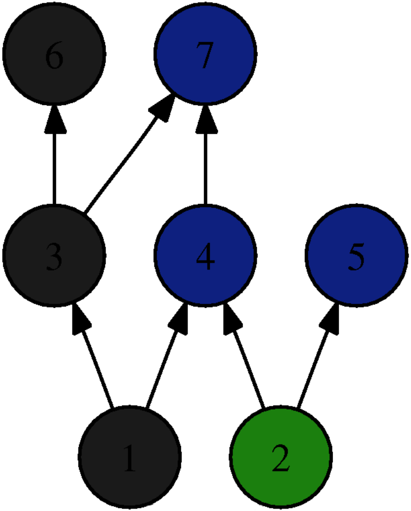
Secondary Extinctions



Secondary Extinctions



Secondary Extinctions



Best Case Scenario

Other mechanisms can add to, but not subtract from, these "bottom-up" extinctions.

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,

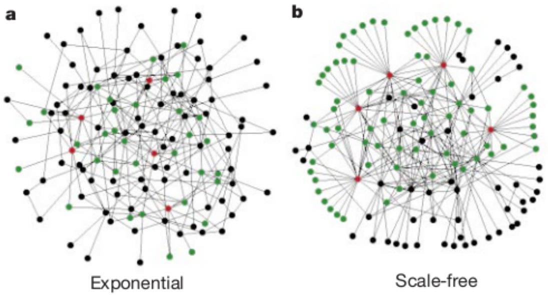

Figure 1 Visual illustration of the difference between an exponential and a scale-free network. **a**, The exponential network is homogeneous: most nodes have approximately the same number of links. **b**, The scale-free network is inhomogeneous: the majority of the nodes have one or two links but a few nodes have a large number of links, guaranteeing that the system is fully connected. Red, the five nodes with the highest number of links; green, their first neighbours. Although in the exponential network only 27% of the nodes are reached by the five most connected nodes, in the scale-free network more than 60% are reached, demonstrating the importance of the connected nodes in the scale-free network Both networks contain 130 nodes and 215 links ($\langle k \rangle = 3.3$). The network visualization was done using the Pajek program for large network analysis: ⟨http://vlado.fmf.uni-lj.si/pub/networks/pajek/pajekman.htm⟩.

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Complexity and fragility in ecological networks

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A detailed analysis of three species-rich ecosystem food webs has shown that they display skewed distributions of connections. Such graphs of interaction are, in fact, shared by a number of biological and technological networks, which have been shown to display a very high homeostasis against random removals of nodes. Here, we analyse the responses of these ecological graphs to both random and selective perturbations (directed against the most-connected species). Our results suggest that ecological networks are very robust against random removals but can be extremely fragile when selective attacks are used. These observations have important consequences for biodiversity dynamics and conservation issues, current estimations of extinction rates and the relevance and definition of keystone species.

Ecology Letters, (2002) **5**: 558–567

REPORT

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

Jennifer A. Dunne,[1,2]* Richard J. Williams[1] and Neo D. Martinez[1]
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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 *functions* of species removed.

Food-web structure and network theory: The role of connectance and size

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Edited by Burton H. Singer, Princeton University, Princeton, NJ, and approved July 25, 2002 (received for review July 9, 2002)

... although some food webs have small-world and scale-free structure, most do not if they exceed a relatively low level of connectance. Although food-web degree distributions do not display a universal functional form, observed distributions are systematically related to network connectance and size. Also, although food webs often lack small-world structure because of low clustering, we identify a continuum of real-world networks including food webs whose ratios of observed to random clustering coefficients increase as a powerlaw function of network size over 7 orders of magnitude. Although food webs are generally not small-world, scale-free networks, food-web topology is consistent with patterns found within those classes of networks.

Vol. 273: 291–302, 2004 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published June 8

Network structure and robustness of marine food webs

Jennifer A. Dunne[1,4,*], Richard J. Williams[2,4], Neo D. Martinez[3,4]

damental structural and ordering characteristics. Analyses of potential secondary extinctions resulting from species loss show that the structural robustness of marine food webs is also consistent with trends from other food webs. As expected, given their relatively high connectance, marine food webs appear fairly robust to loss of most-connected taxa as well as random taxa. Still, the short average path length between marine taxa (1.6 links) suggests that effects from perturbations, such as overfishing, can be transmitted more widely throughout marine ecosystems than previously appreciated.

Control Flow Graphs

T. Lengauer and R. E. Tarjan

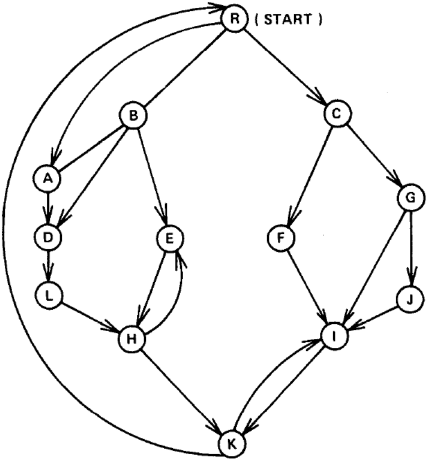


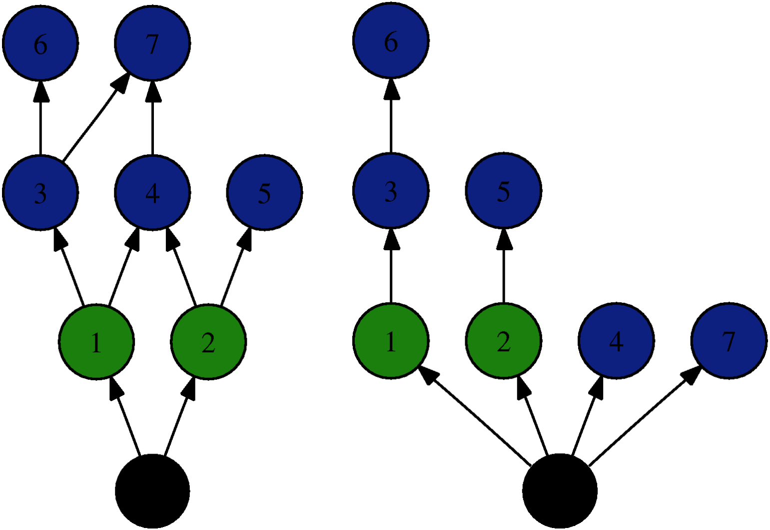
Fig. 1. A flowgraph

Dominators

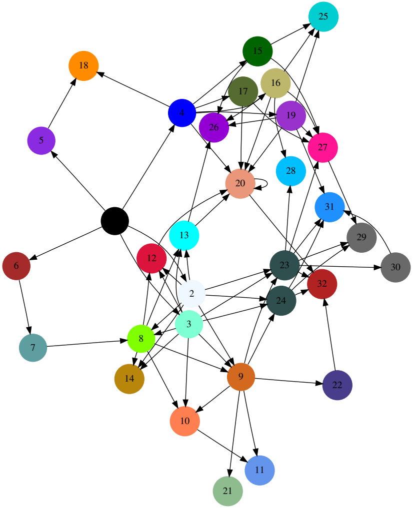
- A control flow graph $G(V, E, r)$ has V nodes, E edges and starts in r.
- A node v dominates $w \neq v$ if every path from r to w contains v.
- v is the immediate dominator of w ($v = imdom(w)$) if v dominates w and every other dominator of w dominates v.
- Connecting each node with its immediate dominator yields the Dominator Tree.

In food webs the r is the external environment, that provides energy to primary producers (plants).

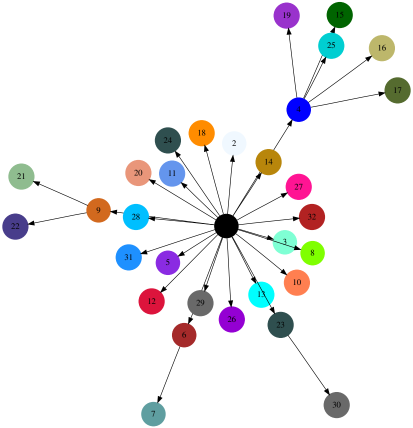
Dominator Tree



Chesapeake Bay: Who Eats Whom?



Chesapeake Bay: Who Dominates Whom?



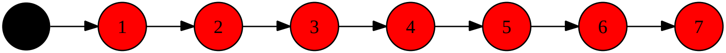
Errors & Attacks

Borrowing notation from studies on the Internet structure we call:

- Error Sensitivity the average effect of random extinction of one species.
- Attack Sensitivity the effect of the disconnection of the most "critical" species (i.e. the one that causes the maximum damage in terms of secondary extinctions).
- $ES = \sum_{i \neq R} \frac{dom(i)-1}{(N-1)^2}$
- $AS = MAX_{i \neq R} \frac{dom(i)-1}{(N-1)}$

where $dom(i)$ is the number of species the species i dominates and N is the size of the system.

Extreme cases: Chain



Chain-like Dominator Tree

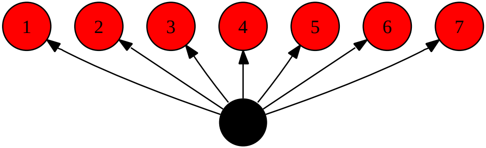
Error Sensitivity

$$ES = \sum_{i \neq R} \frac{dom(i) - 1}{(N-1)^2} = \frac{N(N-1)}{2(N-1)^2} \simeq \frac{1}{2}$$

Attack Sensitivity

$$AS = MAX_{i \neq R} \frac{dom(i) - 1}{(N-1)} = \frac{N-1}{N-1} = 1$$

Extreme cases: Star



Star-like Dominator Tree

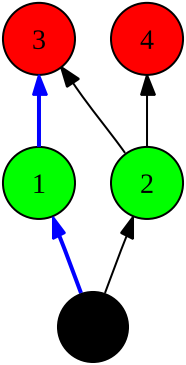
Error Sensitivity

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

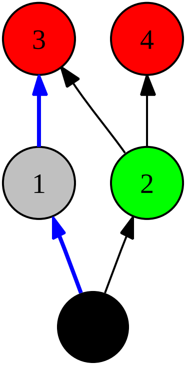
Attack Sensitivity

$$AS = MAX_{i \neq R} \frac{dom(i) - 1}{(N-1)} = \frac{1}{N-1}$$

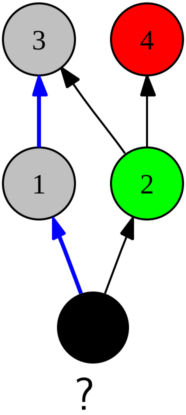
Different Flows



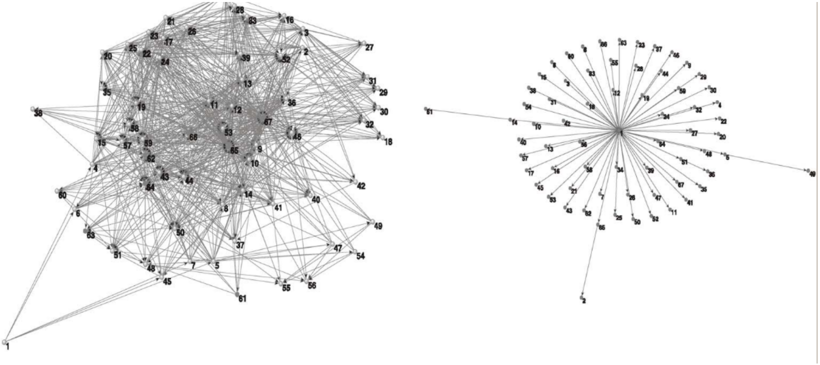
Different Flows



Different Flows



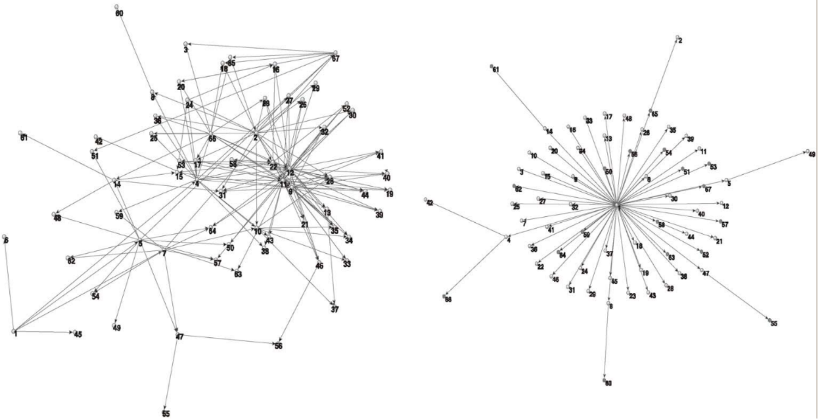
Example with Flows



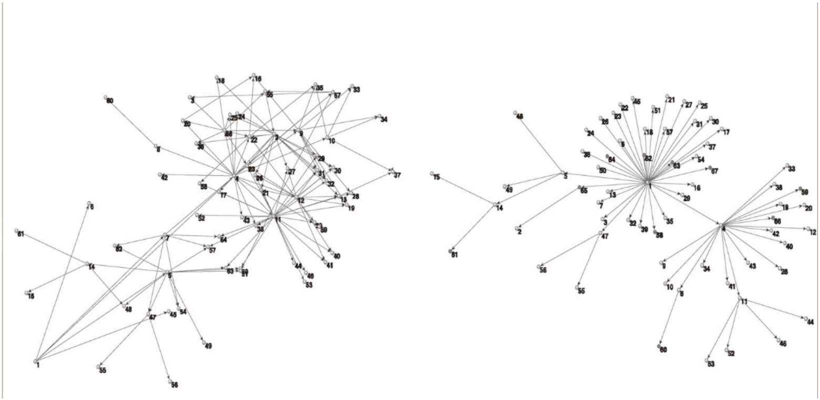
Gramminoid Marshes

67 Nodes, 798 Links Bondavalli et al. 2000.

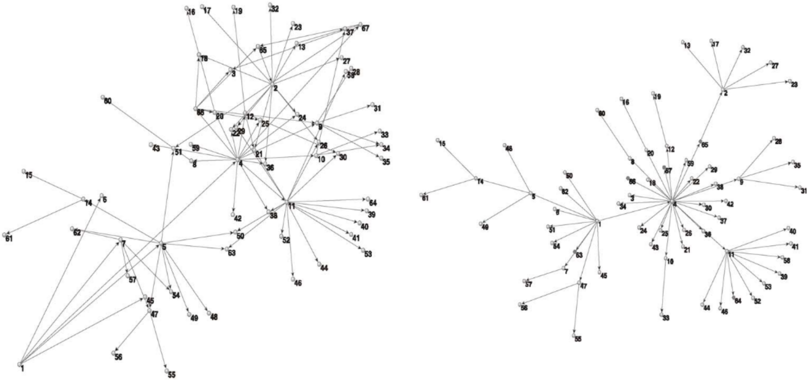
Example with Flows



Example with Flows



Example with Flows



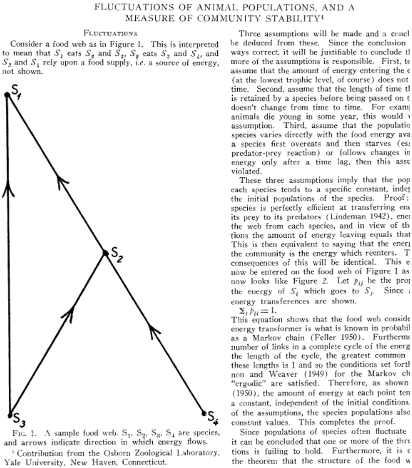
Dominators Analysis

- Dominator trees are compact, elegant tools for studying the effects of extinctions in food webs.
- This method represents a more systematic approach to the study of food web robustness.
- Extension to quantitative flows is promising for applications to the "real world".
- Dominators also illustrate which species are key players in mantaining the flow of energy. Surprisingly, they are not trivially the most connected species.

Allesina & Bodini, Journal of Theoretical Biology, 2004.

Allesina et. al., Ecological Modelling, 2006

MacArthur 1954



FLUCTUATIONS OF ANIMAL POPULATIONS, AND A MEASURE OF COMMUNITY STABILITY[1]

FLUCTUATIONS

Consider a food web as in Figure 1. This is interpreted to mean that S_1 eats S_2 and S_3, S_2 eats S_3 and S_4, and S_3 and S_4 rely upon a food supply, *i.e.* a source of energy, not shown.

FIG. 1. A sample food web. S_1, S_2, S_3, S_4 are species, and arrows indicate direction in which energy flows.

[1] Contribution from the Osborn Zoological Laboratory, Yale University, New Haven, Connecticut.

Three assumptions will be made and a concl
be deduced from these. Since the conclusion
ways correct, it will be justifiable to conclude tl
more of the assumptions is responsible. First, te
assume that the amount of energy entering the c
(at the lowest trophic level, of course) does not
time. Second, assume that the length of time tl
is retained by a species before being passed on t
doesn't change from time to time. For exam
animals die young in some year, this would
assumption. Third, assume that the populatio
species varies directly with the food energy ava
a species first overeats and then starves (es
predator-prey reaction) or follows changes in
energy only after a time lag, then this assu
violated.

These three assumptions imply that the pop
each species tends to a specific constant, inde
the initial populations of the species. Proof:
species is perfectly efficient at transferring en
its prey to its predators (Lindeman 1942), ene
the web from each species, and in view of th
tions the amount of energy leaving equals that
This is then equivalent to saying that the ener
the community is the energy which reenters. T
consequences of this will be identical. This e
now be entered on the food web of Figure 1 as
now looks like Figure 2. Let p_{ij} be the pro
the energy of S_i which goes to S_j. Since
energy transferences are shown.

$\Sigma_j p_{ij} = 1.$

This equation shows that the food web conside
energy transformer is what is known in probabil
as a Markov chain (Feller 1950). Furtherm
number of links in a complete cycle of the energ
the length of the cycle, the greatest common
these lengths is 1 and so the conditions set fort
non and Weaver (1949) for the Markov ch
"ergodic" are satisfied. Therefore, as shown
(1950), the amount of energy at each point ten
a constant, independent of the initial conditions.
of the assumptions, the species populations also
constant values. This completes the proof.

Since populations of species often fluctuate
it can be concluded that one or more of the thr
tions is failing to hold. Furthermore, it is
the theorem that the structure of the food w

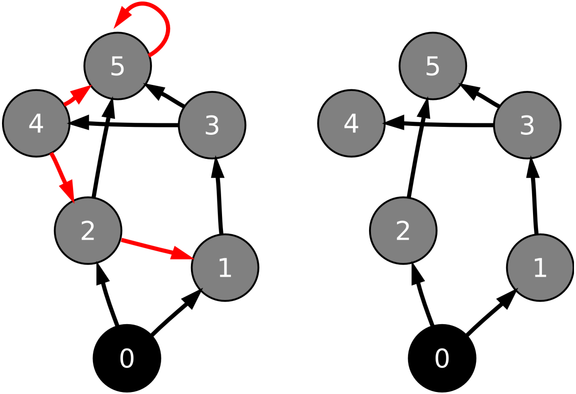
- High Complexity
- Multiple Paths
- Decrease effect of prey fluctuation on predators
- More Complex = More Stable

Are all links contributing to robustness?

Generalized Dominators

Using a generalization of dominators we can divide links into functional & redundant.

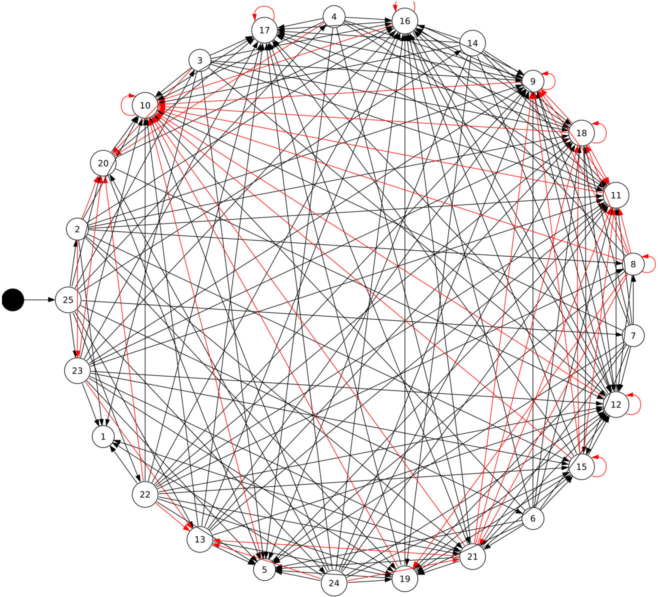
Functional and Redundant Connections



Functional-Redundant

- Functional connections contribute to robustness to extinctions.
- Redundant connections can be removed without altering extinction patterns.

Skipwith Pond



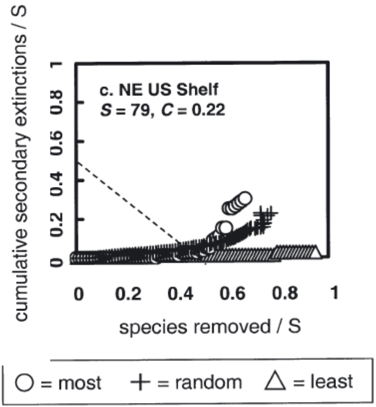
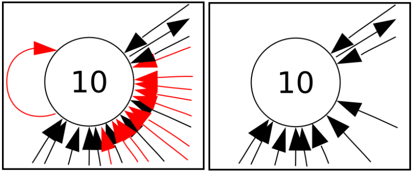


Fig. 2. Secondary extinctions resulting from 3 types of primary species removal in 3 marine food webs. 95% error bars for random species removals fall within the size of the symbols and are not shown. Dashed line shows the points at which there is ≥50% total species loss (primary species removals plus secondary extinctions) in a food web for each type of species removal. Proportion of species that must be removed to reach that point is referred to as 'structural robustness'. S: species richness; C: connectance (links per species^2, L/S^2)

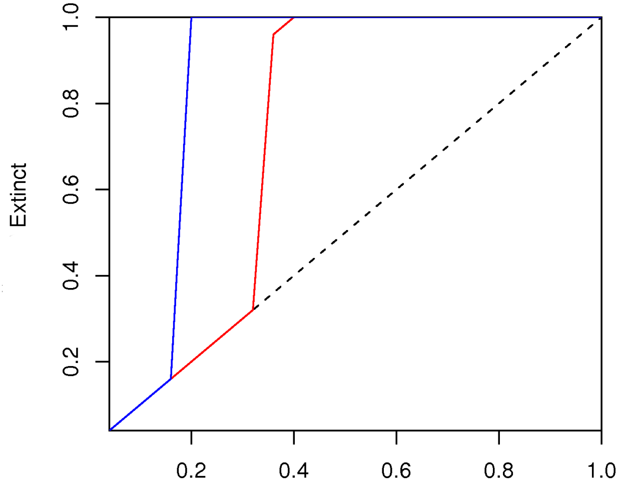
Change in Degree



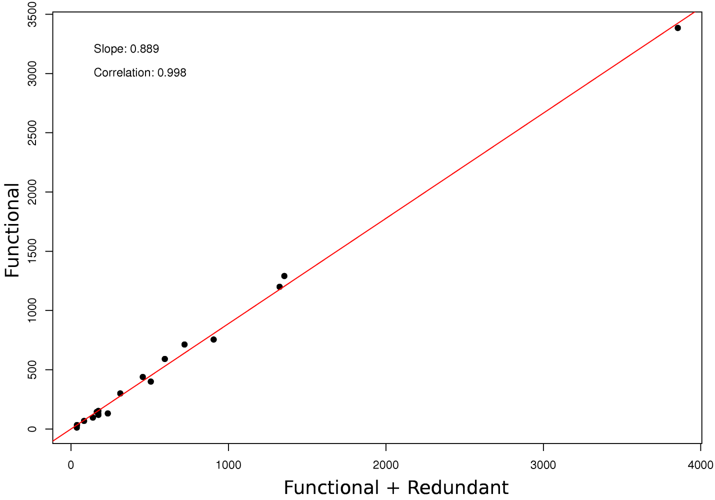
Hubs

Are the “hubs” conserved?

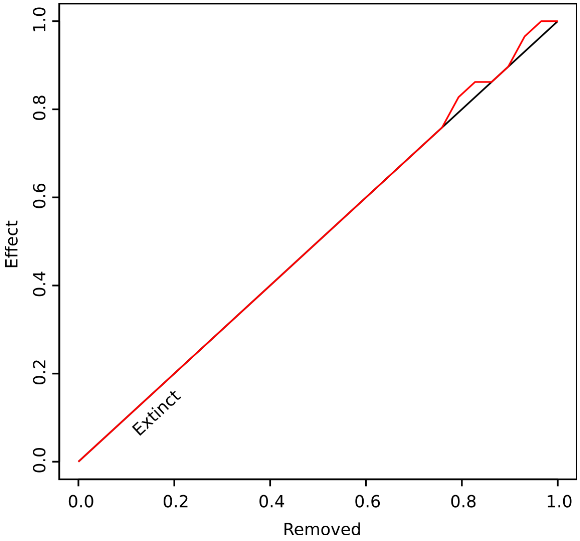
Change in Degree



Empirical Data



Fragility

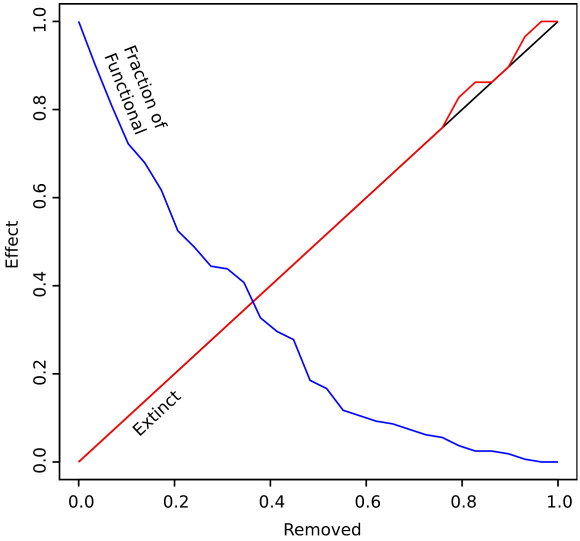


Red Curve

Effect of removing species in random order

No secondary extinctions up to 75% removal

Fragility

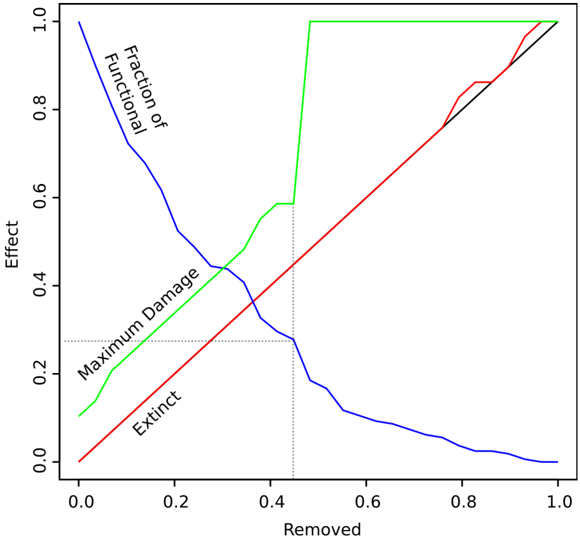


Blue Curve

Fraction of the original functional connections remaining after removal

After 20% removal 50% of functional connections are lost

Fragility



Green Curve

After each removal we compute the max damage we can make removing the most critical species

After less than 50% removal we can find a species that if removed makes the whole web collapse

Patterns

- the presence of multiple independent pathways from primary producers to top predators enhances food web resistance to species extinction.
- The fraction of functional links in empirical food webs is high ($> 90\%$) and is invariant for size and complexity.

Consequences

- Most connected species are not necessarily the most important species for food web robustness.
- Even when secondary extinctions are not observed, the loss of species will make ecosystems more fragile to further extinctions.
- This sobering message underscores the possibility of surprises and tipping points in the collapse of ecological network.

Allesina et al., Phil. Trans. Roy. Soc. B, 2009

Challenges: Realistic extinctions

Ecology, 88(3), 2007, pp. 671–682

RESPONSE OF COMPLEX FOOD WEBS TO REALISTIC EXTINCTION SEQUENCES

U. THARA SRINIVASAN,[1,6] JENNIFER A. DUNNE,[2,3] JOHN HARTE,[1,4] AND NEO D. MARTINEZ[2,5]

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[2]*Pacific Ecoinformatics and Computational Ecology Lab, Berkeley, California 94703 USA*
[3]*Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501 USA*
[4]*Department of Environmental Science, Policy and Management, University of California, Berkeley, California 94702 USA*
[5]*National Center for Ecological Analysis and Synthesis, 735 State Street, Santa Barbara, California 93101 USA*

Plausible Scenarios

- Input: a priori extinction risks
- Output: a posteriori extinction risk

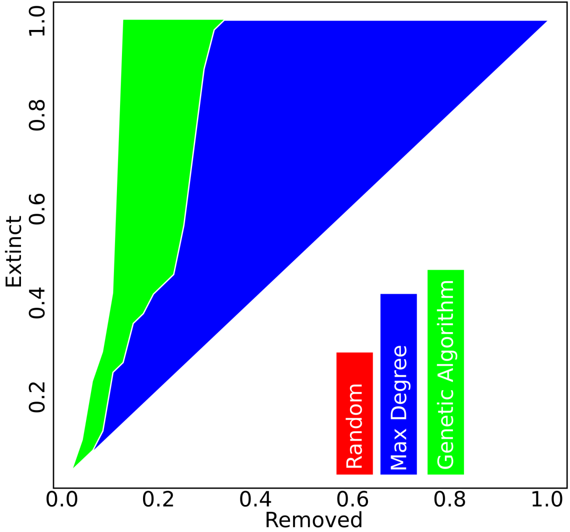
Challenges: Charachterizing species at risk

VOL. 171, NO. 5 THE AMERICAN NATURALIST MAY 2008

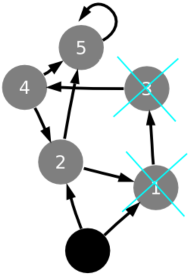
Trophically Unique Species Are Vulnerable to Cascading Extinction

Owen L Petchey,[1,*] Anna Eklöf,[2,†] Charlotte Borrvall,[2,‡] and Bo Ebenman[2,§]

Challenges: Sequential extinctions



Challenges: Predator switching



Possible solution

- Consider a "potential" food web that draws potential prey

Challenges: Top-down extinctions

Considering dynamics

- Human pressure is skewed toward higher trophic levels (esp. marine systems)
- Top-down effects are known and important (e.g. trophic cascades)

Caveat

- To exactly predict top-down extinctions one needs a complete description of the system and its dynamics.
- Initial conditions
- Functional responses
- Interaction strengths
- Allometric relationships could simplify the problem

Challenges: Top-down extinctions

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LETTER

Early onset of secondary extinctions in ecological communities following the loss of top predators

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Abstract

The large vulnerability of top predators to human-induced disturbances on ecosystems is a matter of growing concern. Because top predators often exert strong influence on their prey populations their extinction can have far-reaching consequences for the structure and functioning of ecosystems. It has, for example, been observed that the local loss of a predator can trigger a cascade of secondary extinctions. However, the time lags involved in such secondary extinctions remain unexplored. Here we show that the loss of a top predator leads to a significantly earlier onset of secondary extinctions in model communities than does the loss of a species from other trophic levels. Moreover, in most cases time to secondary extinction increases with increasing species richness. If local secondary extinctions occur early they are less likely to be balanced by immigration of species from local communities nearby. The implications of these results for community persistence and conservation priorities are discussed.

Robustness of Food Webs

Effects of Species' Extinction on Networks Structure

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