Robustness and stability

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Analysis of Biological-Ecological Networks 2026

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Structural vs dynamical stability

Structural Stability - Can the network stay connected if we remove a node?

- **Focus:** Changes to the network layout itself (adding or removing nodes and links).
- **Biological Context:** Habitat loss, overfishing, or the extinction of a keystone species.

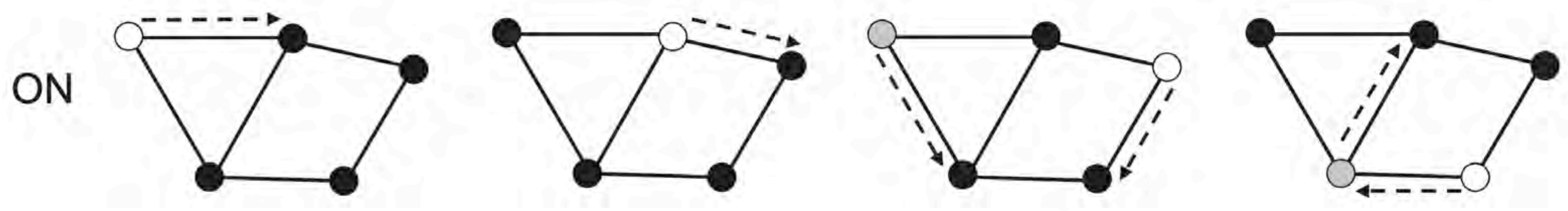
Dynamical stability - If a population crashes will it return to its original size?

- **Focus**: Changes in node states (e.g., population sizes) while the network layout stays exactly the same.
- The Question: "?"
- **Biological Context**: A sudden disease outbreak, a temporary heatwave, or a seasonal change in resource availability.

Dynamics **on** networks

- Biomass flow
- Disease dynamics
- Information flow
- Stability

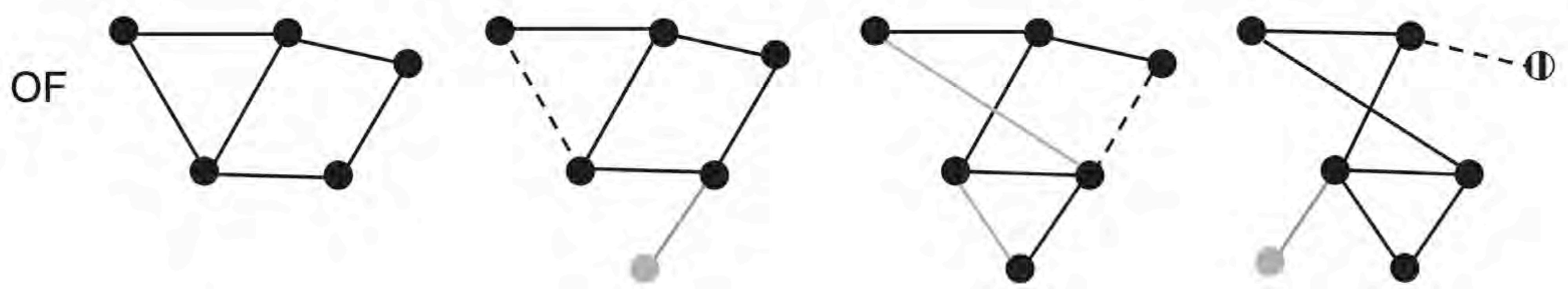
Structure is given,
dynamics are overlaid.



Dynamics **of** networks

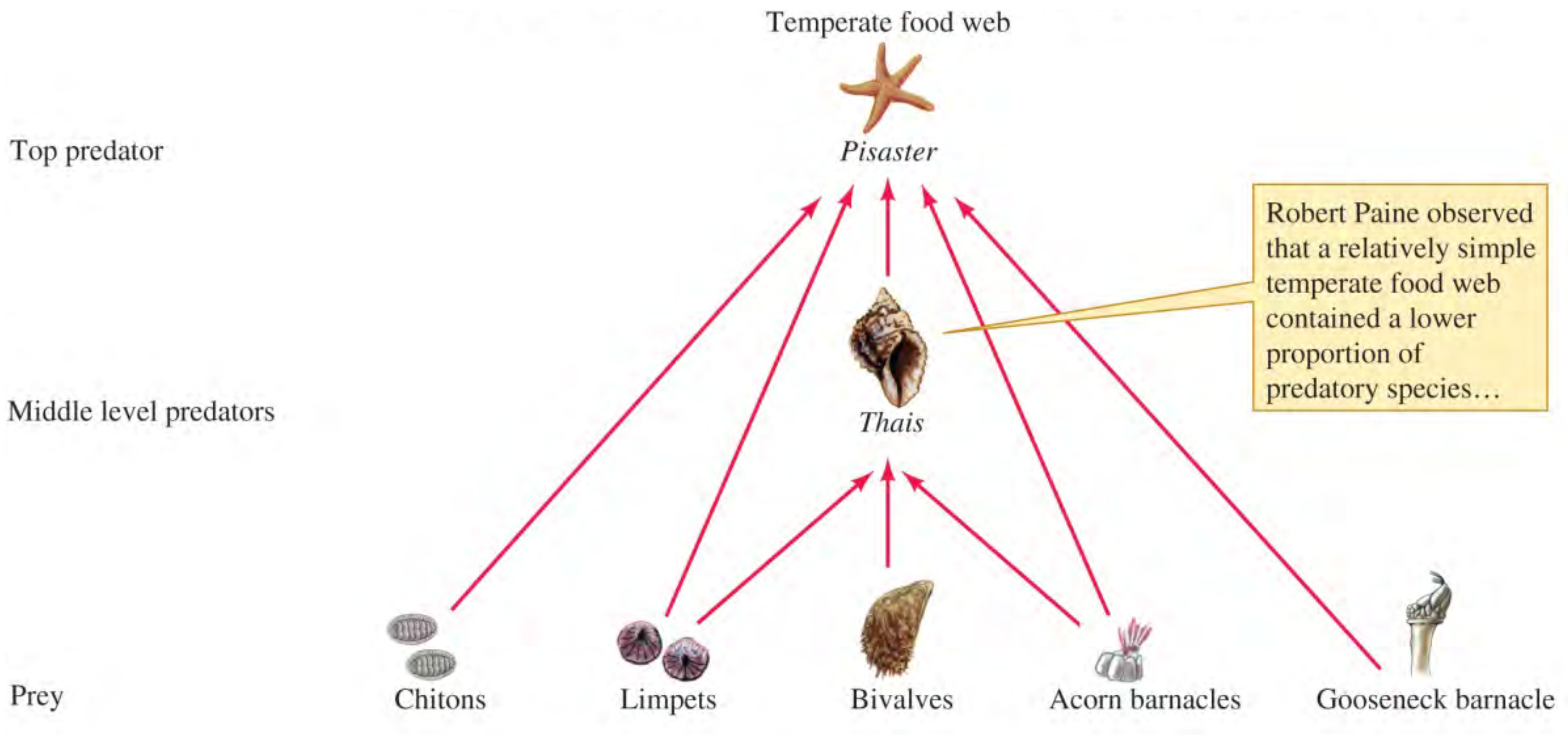
- Assembly, eco/evolutionary dynamics
- Variation across space and time
- Node behavior and rewiring
- Stability

Structure itself is dynamic.
Microscopic rules drive
emerging patterns.



Keystones species

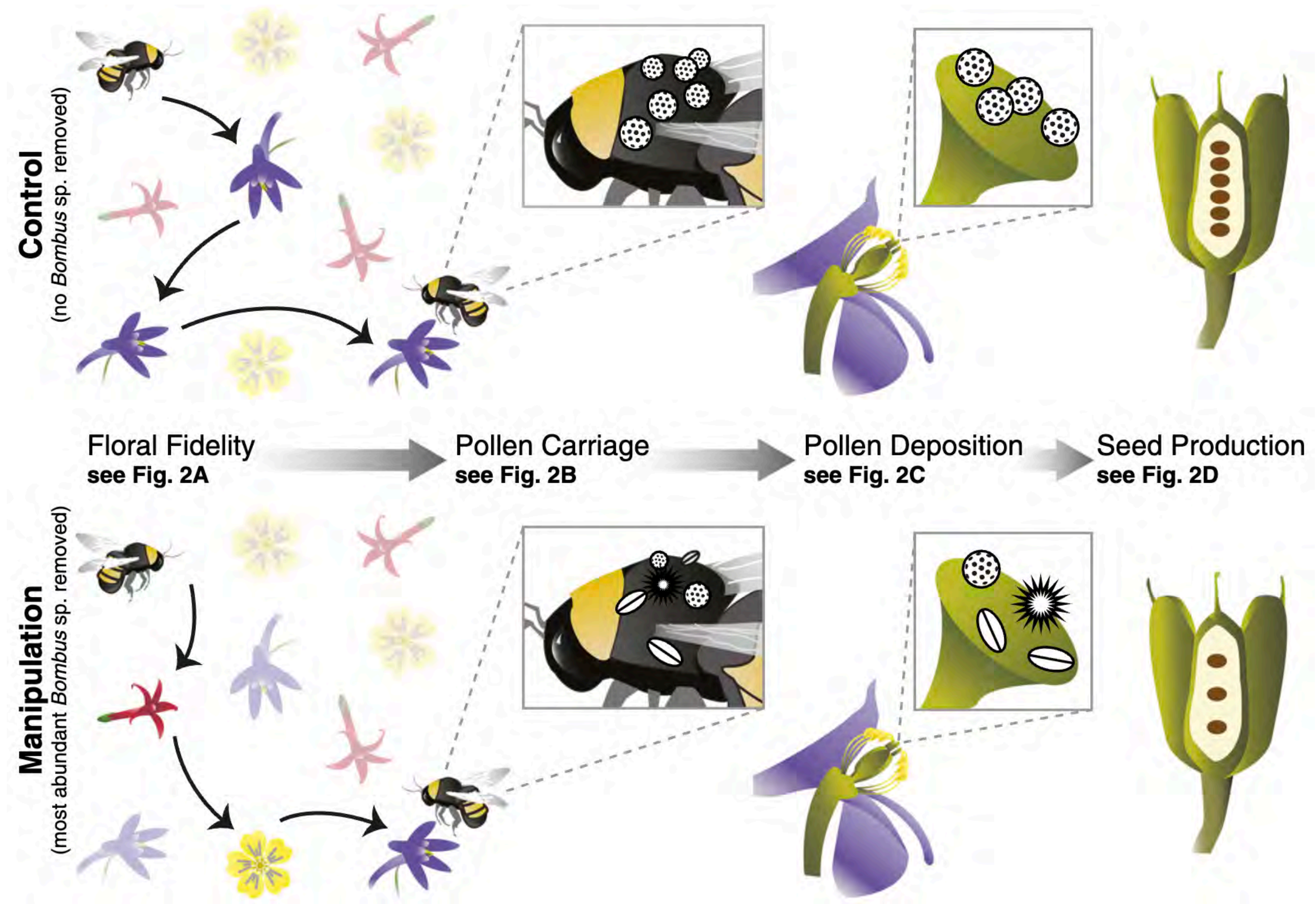
Predation by Pisaster star fish increases species diversity by preventing the monopolization of space by Acorn barnacles.



Robert T. Paine

Paine 1966, American Naturalist.
"Food Web Complexity and Species Diversity"

Node removal has percolating effects



Brosi and Briggs 2013, PNAS

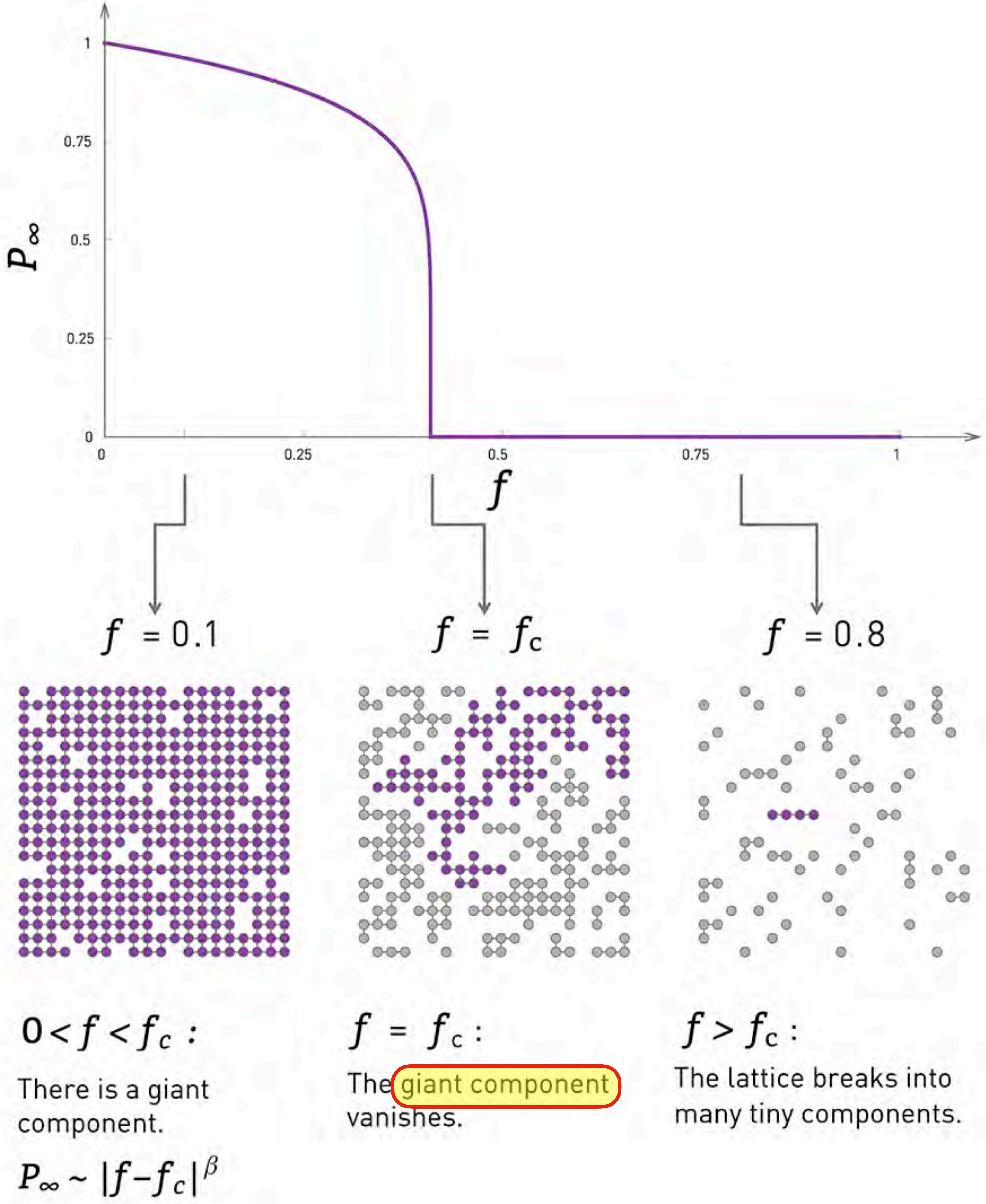
Robustness

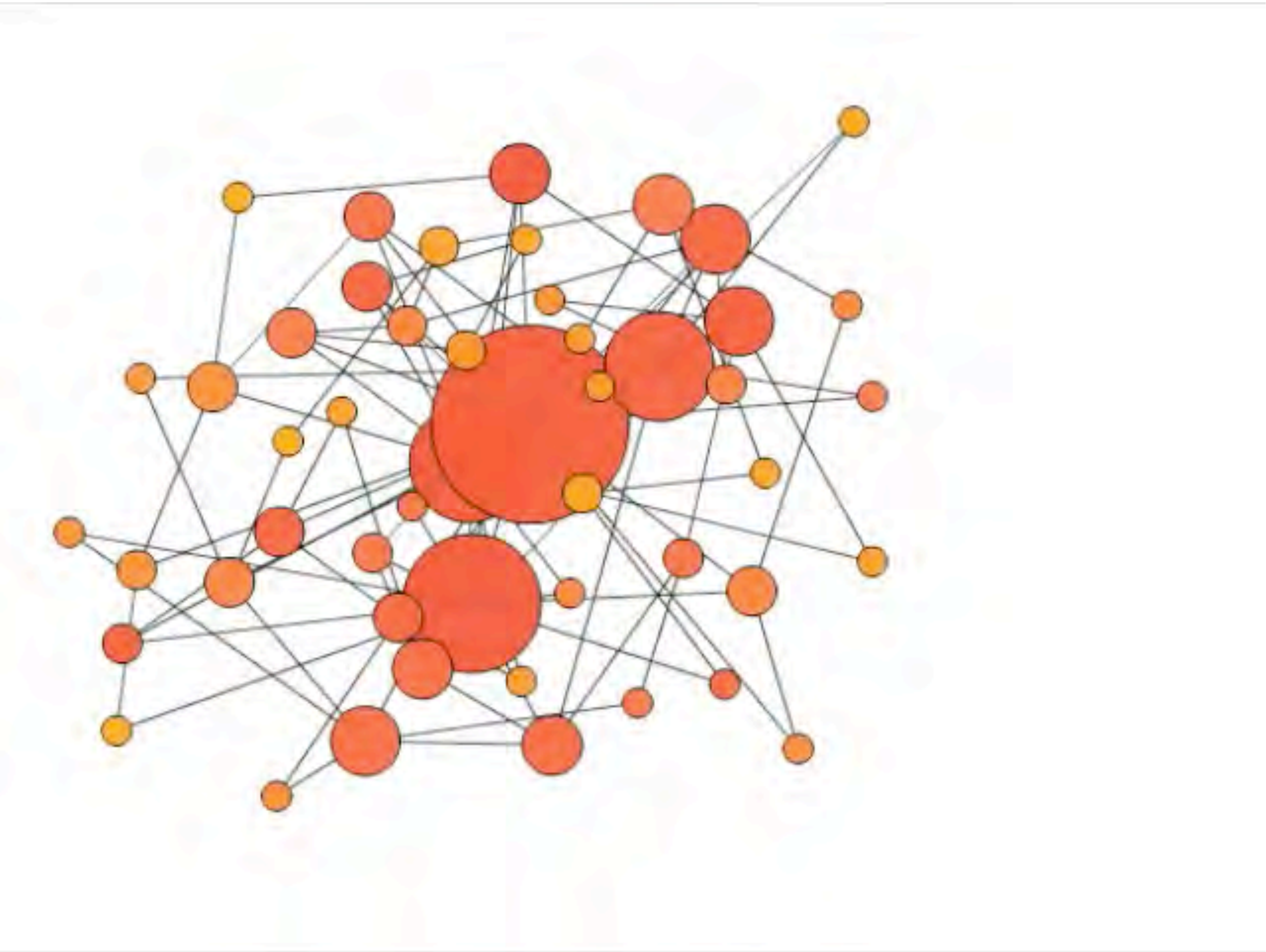
- Loosely: The ability of the system to maintain its function despite node failure.
- Central to biological systems: gene regulation, protein folding, species loss.
- Determined by network structure.

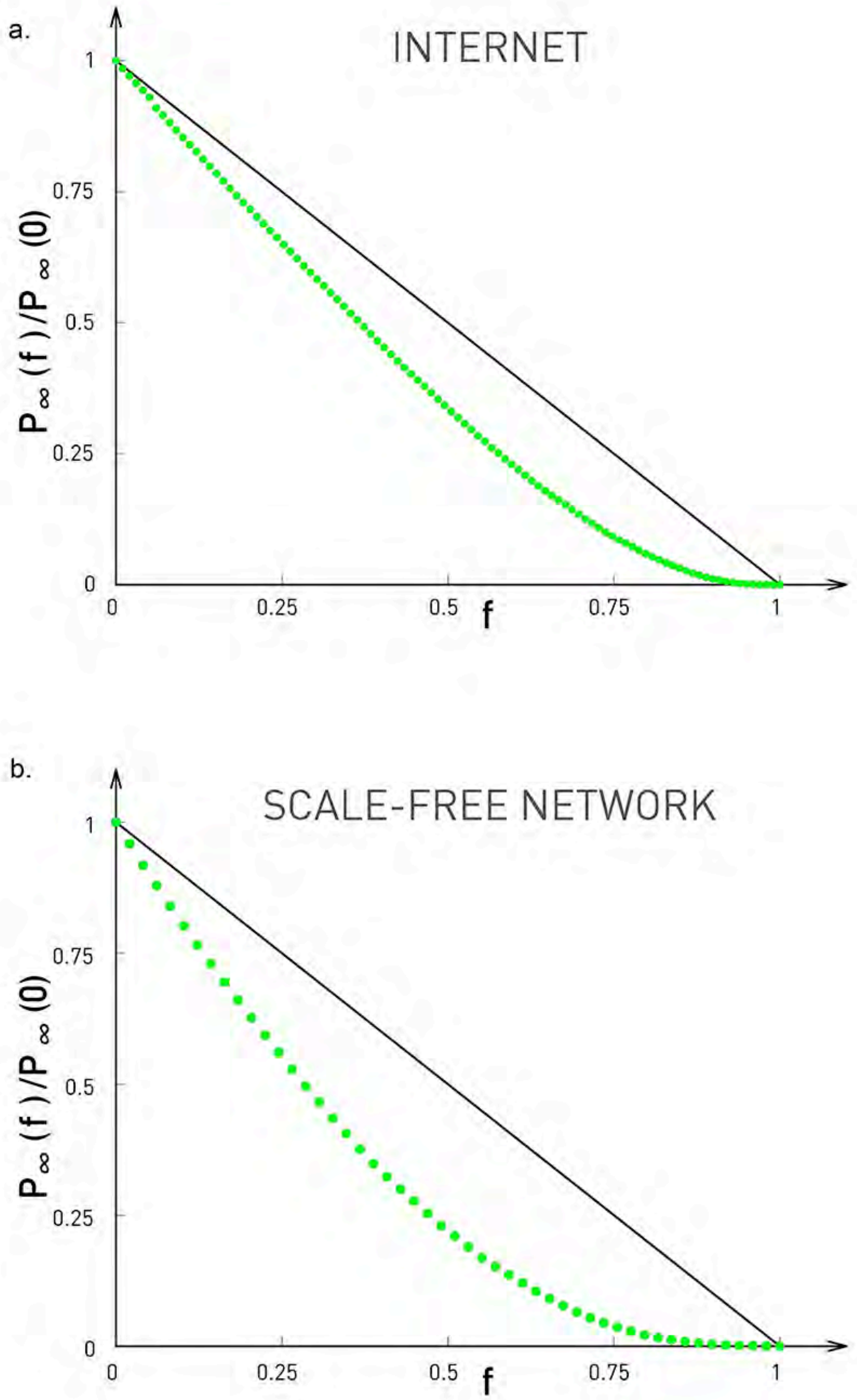
antranias, pixabay.com

Percolation theory

- The breakdown of a network under random node removal is not a gradual process.
- The characteristics of the critical transition depend on the parameters and type of the network (e.g. ER, scale-free, degree distributions).
- Can be calculated analytically or estimated from simulations.



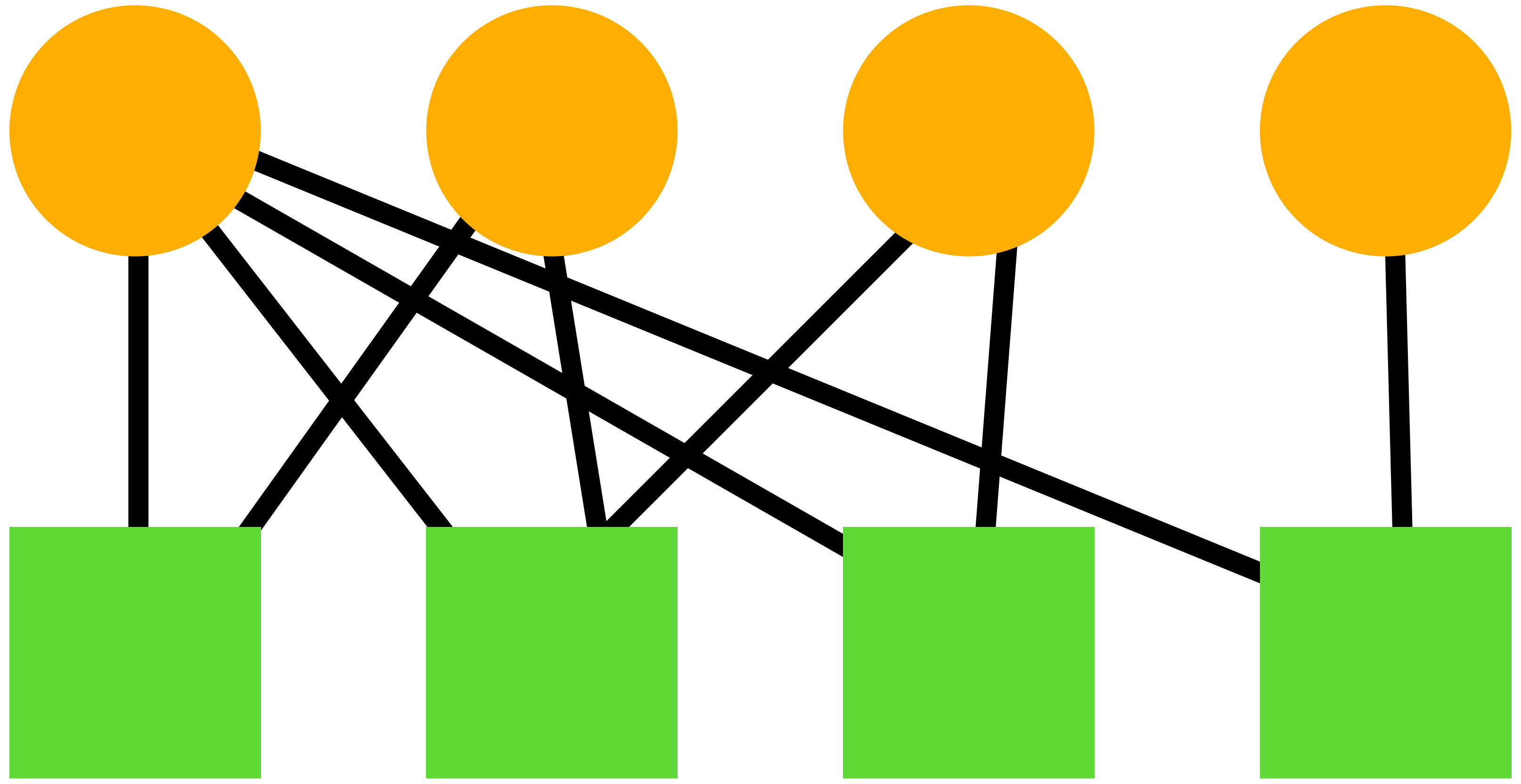


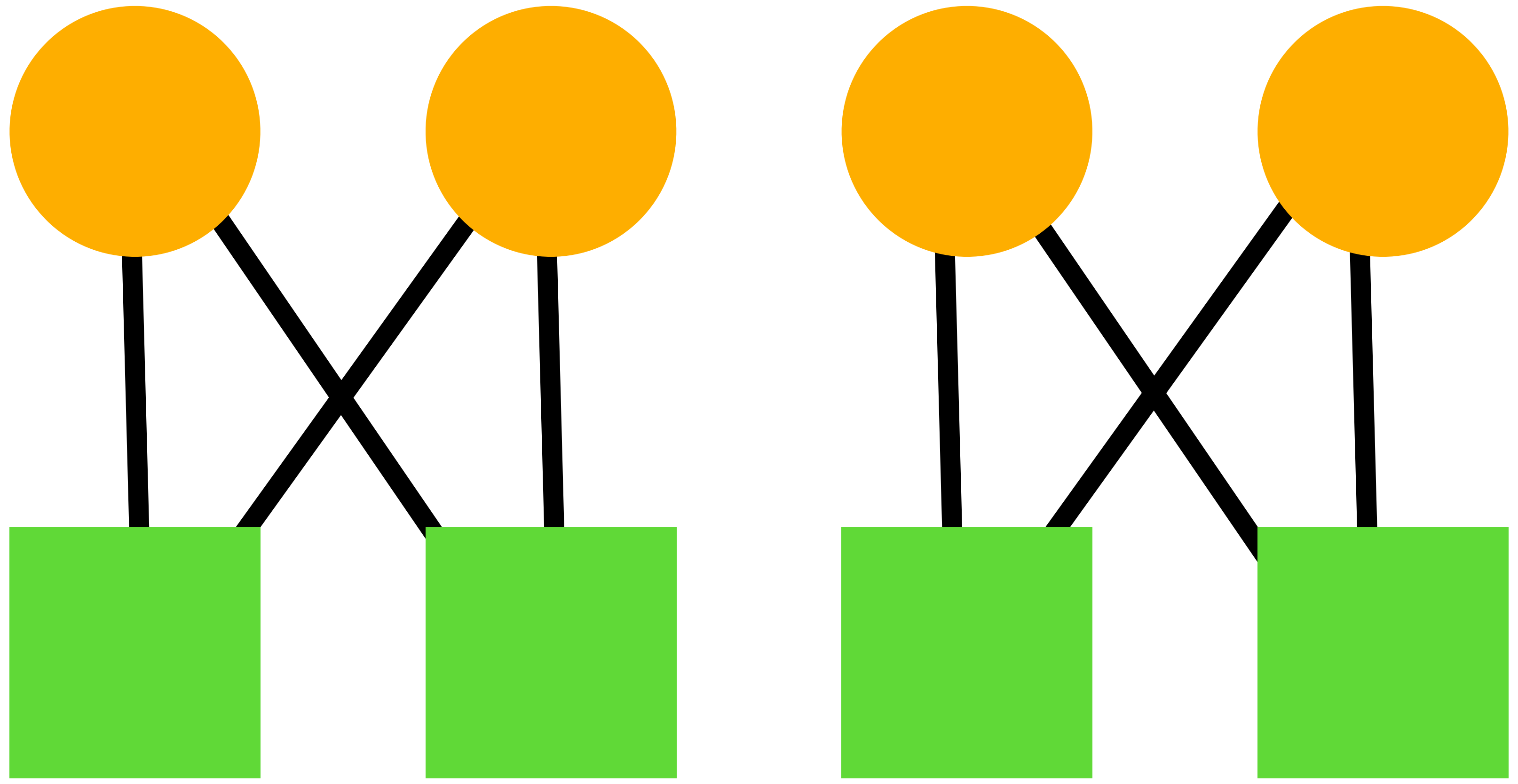


Network Science - Barabasi 2021

Basic algorithm

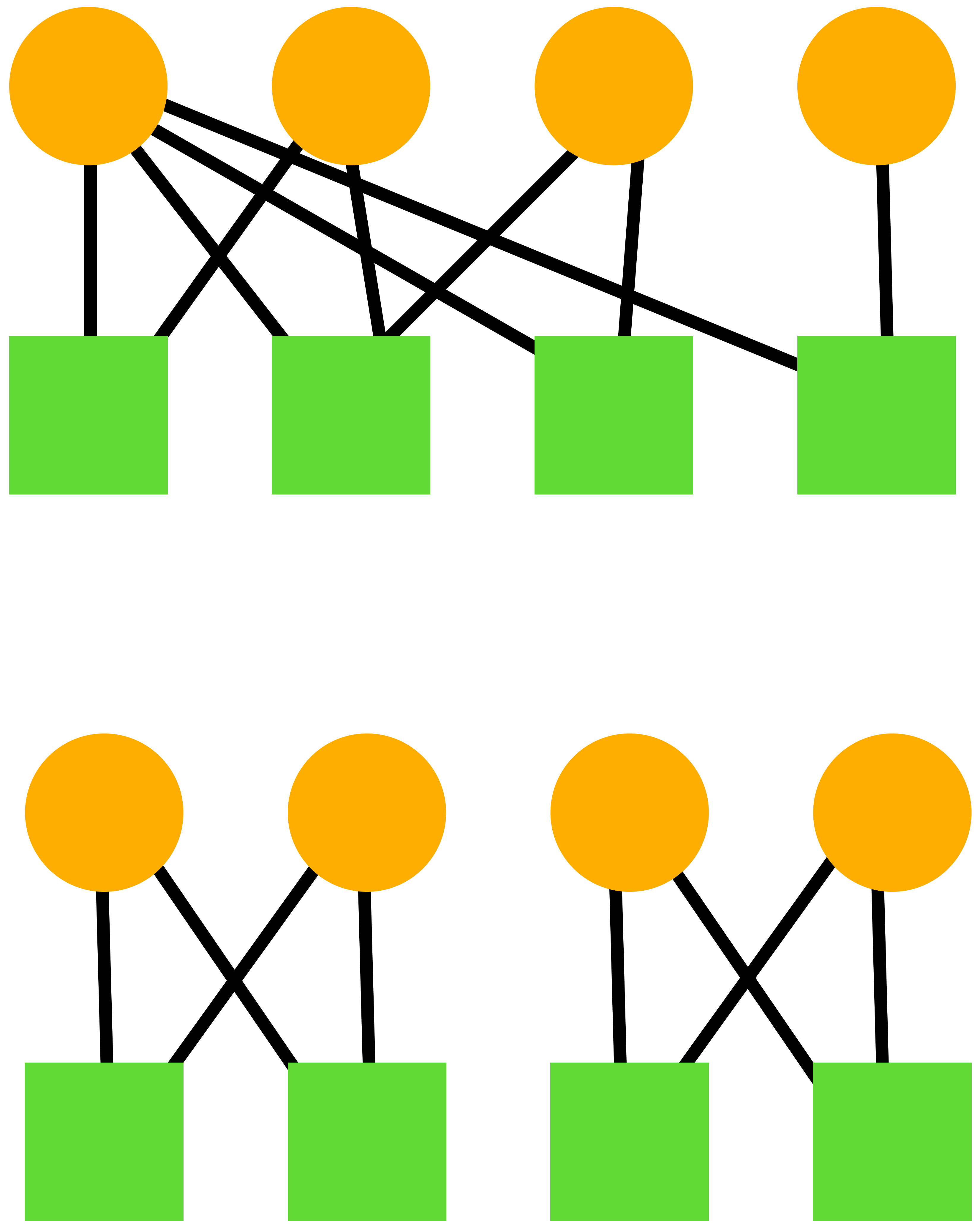
- Let's think about the algorithm





Basic algorithm

- Choose removal order.
- Repeat until no species left:
  - Remove a node and all its edges.
  - Remove nodes left with no interactions (secondary extinctions).
- Plot proportion of nodes left as a function of the proportion removed.



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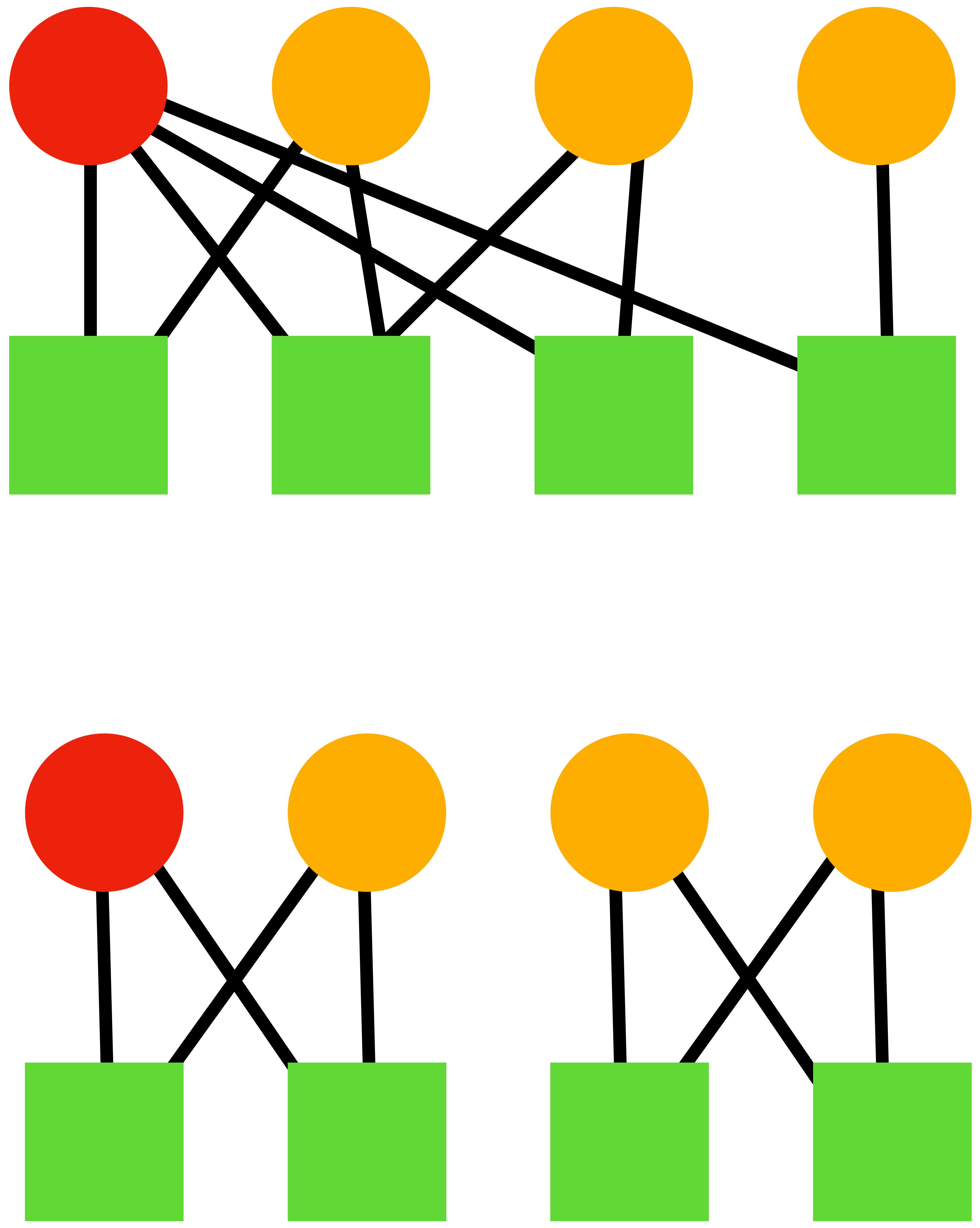

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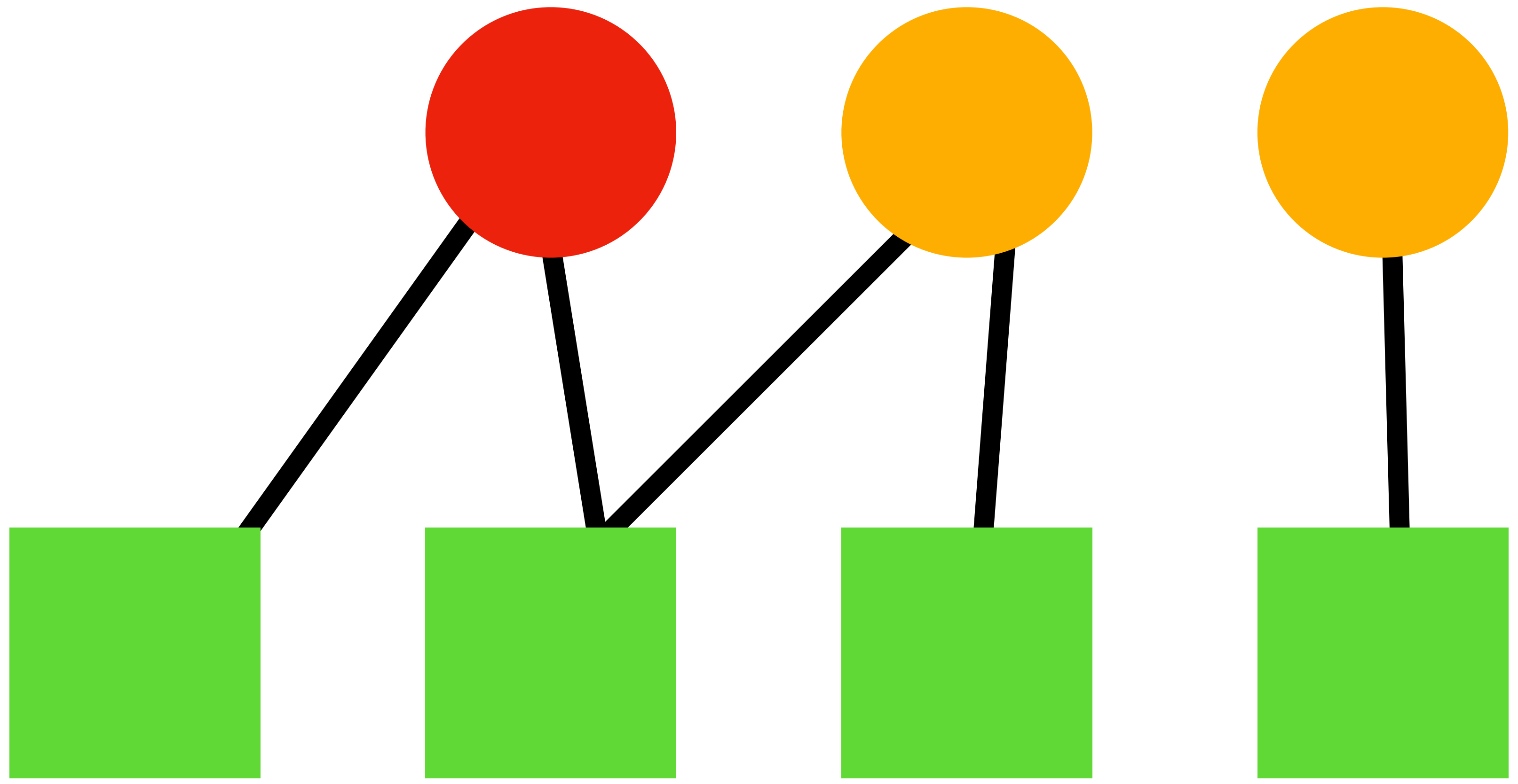

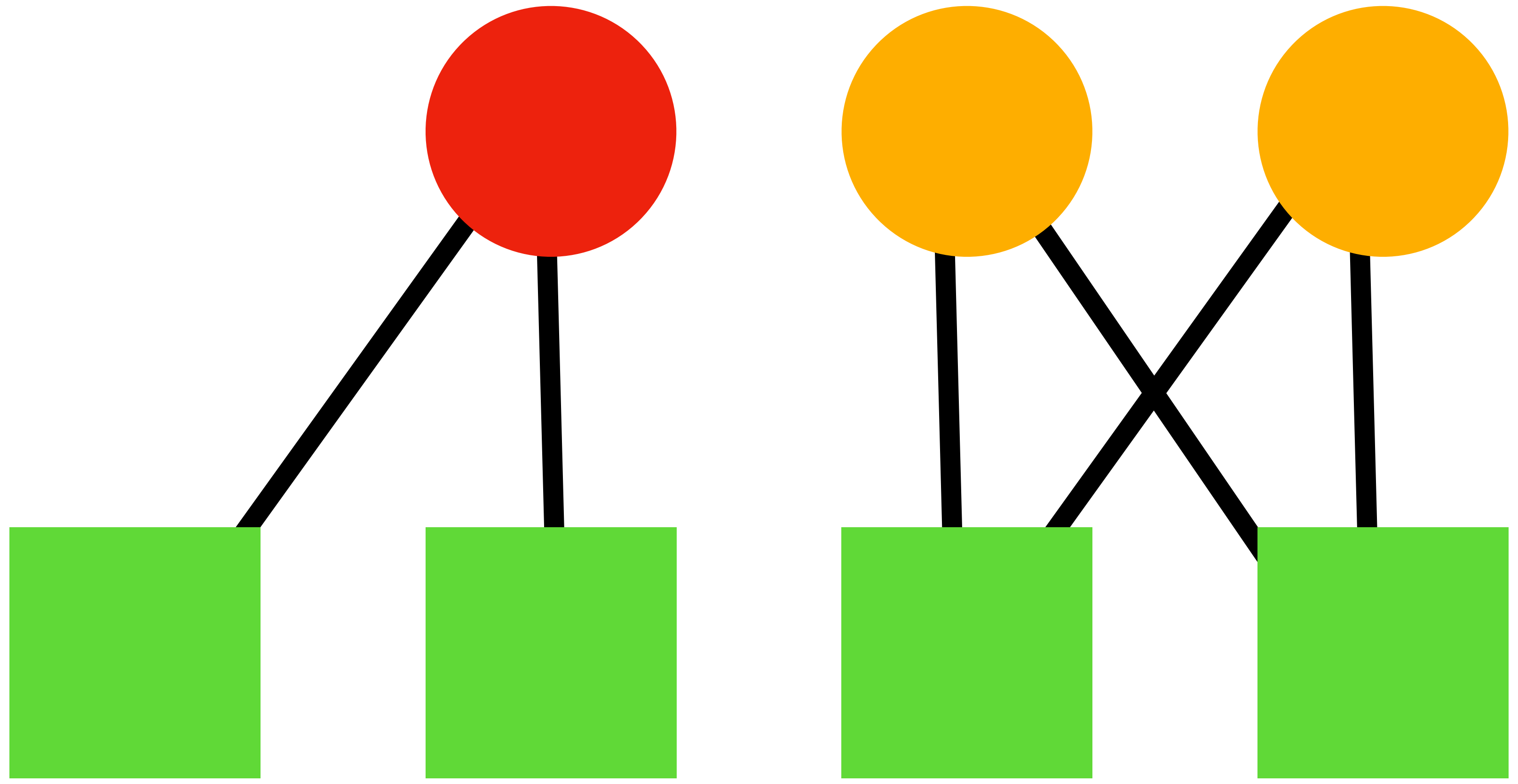

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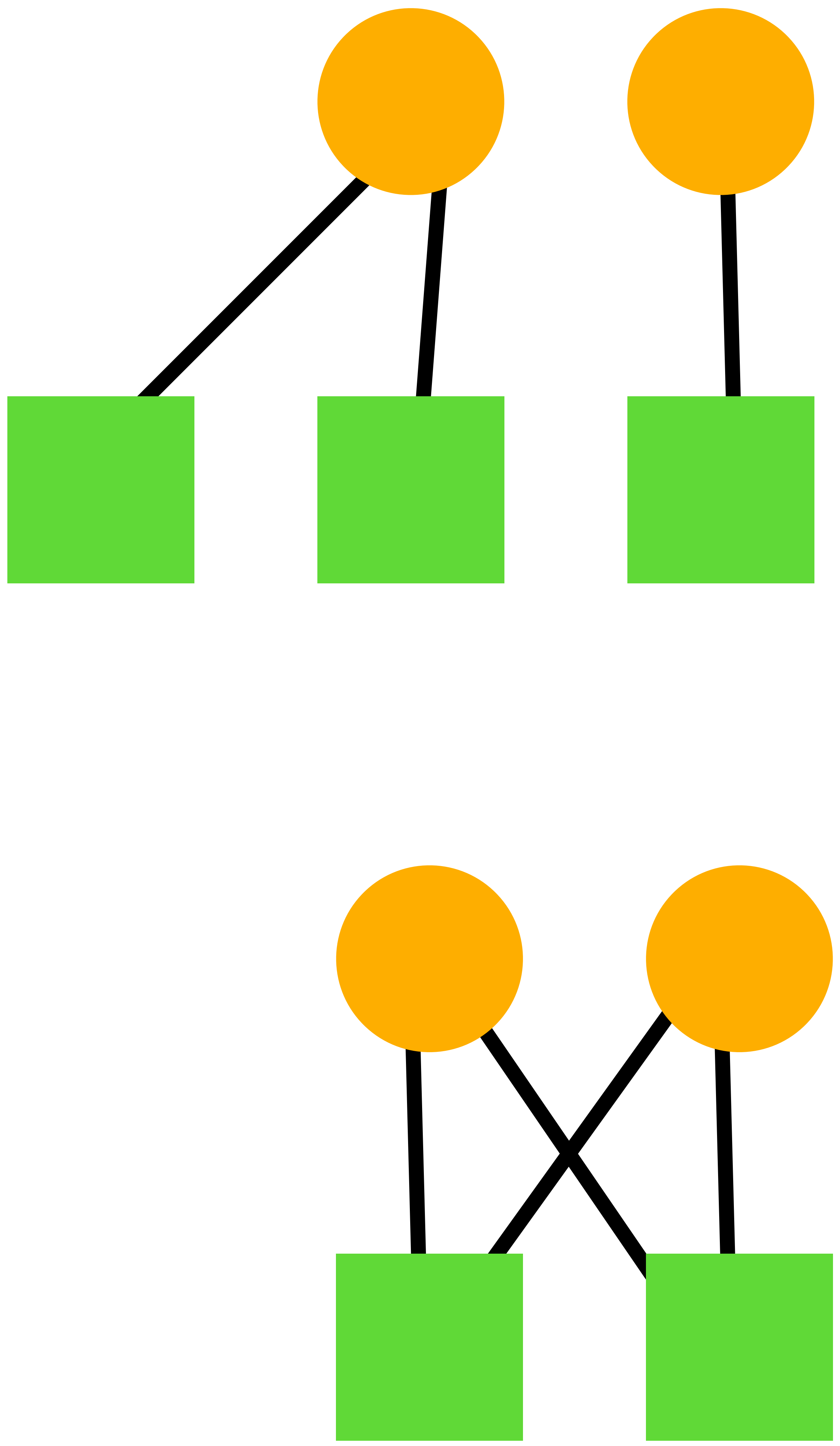
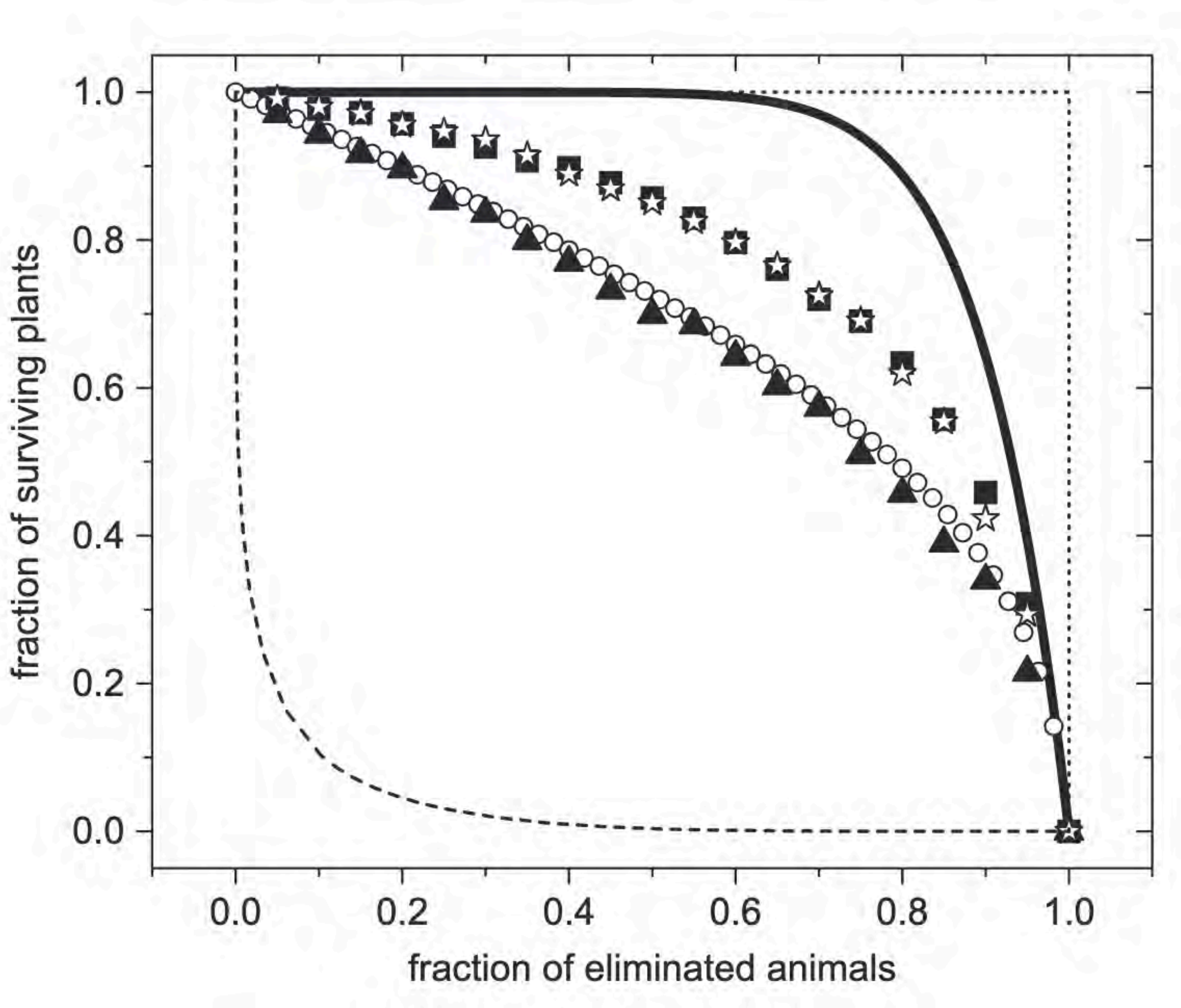
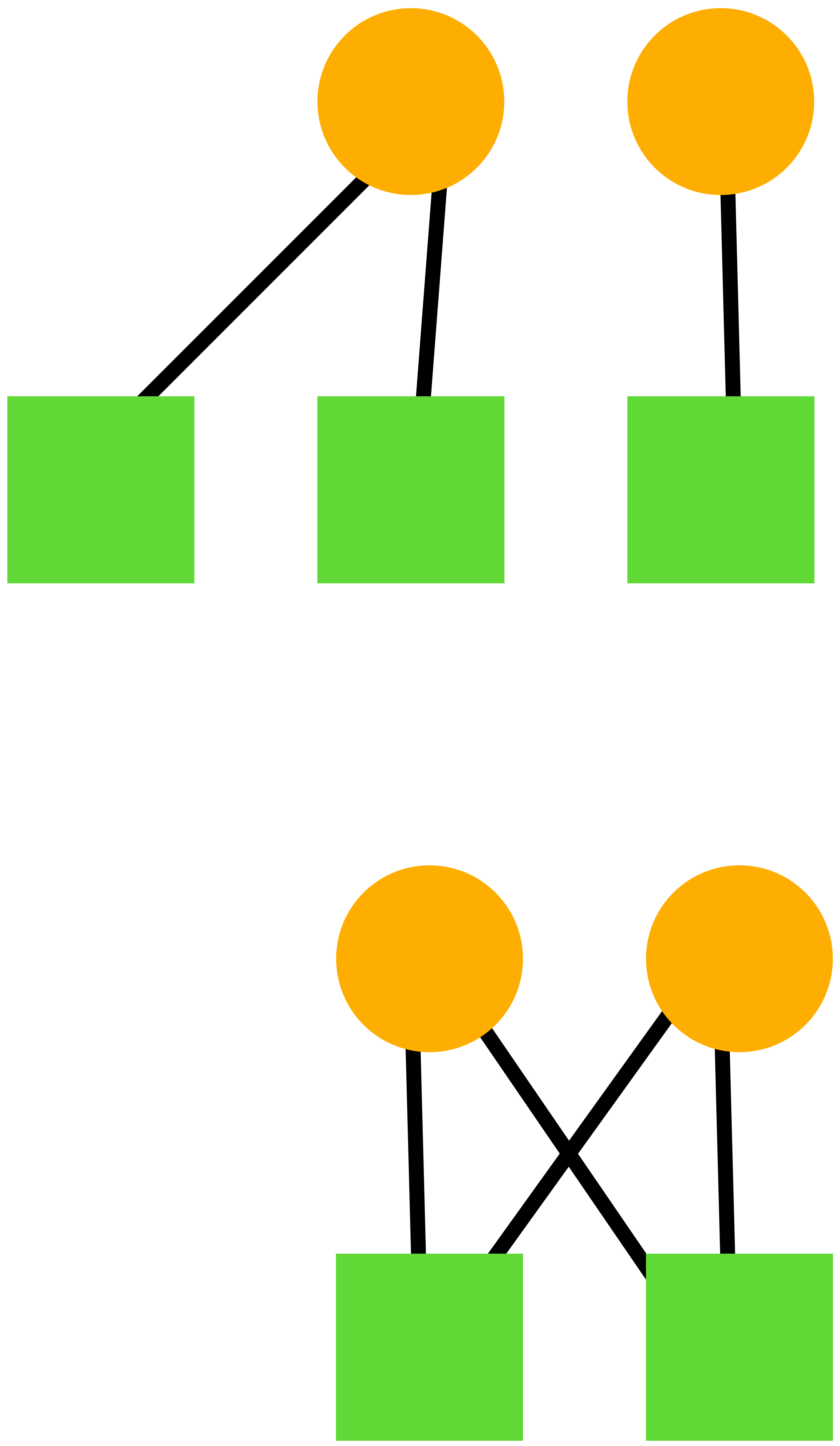


Basic algorithm





Play our stability game

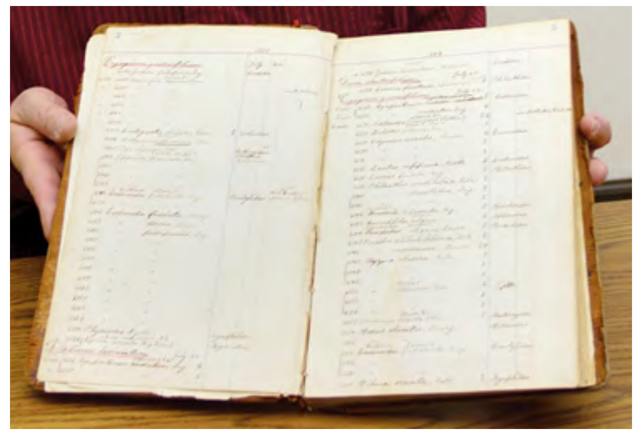
Example with empirical data

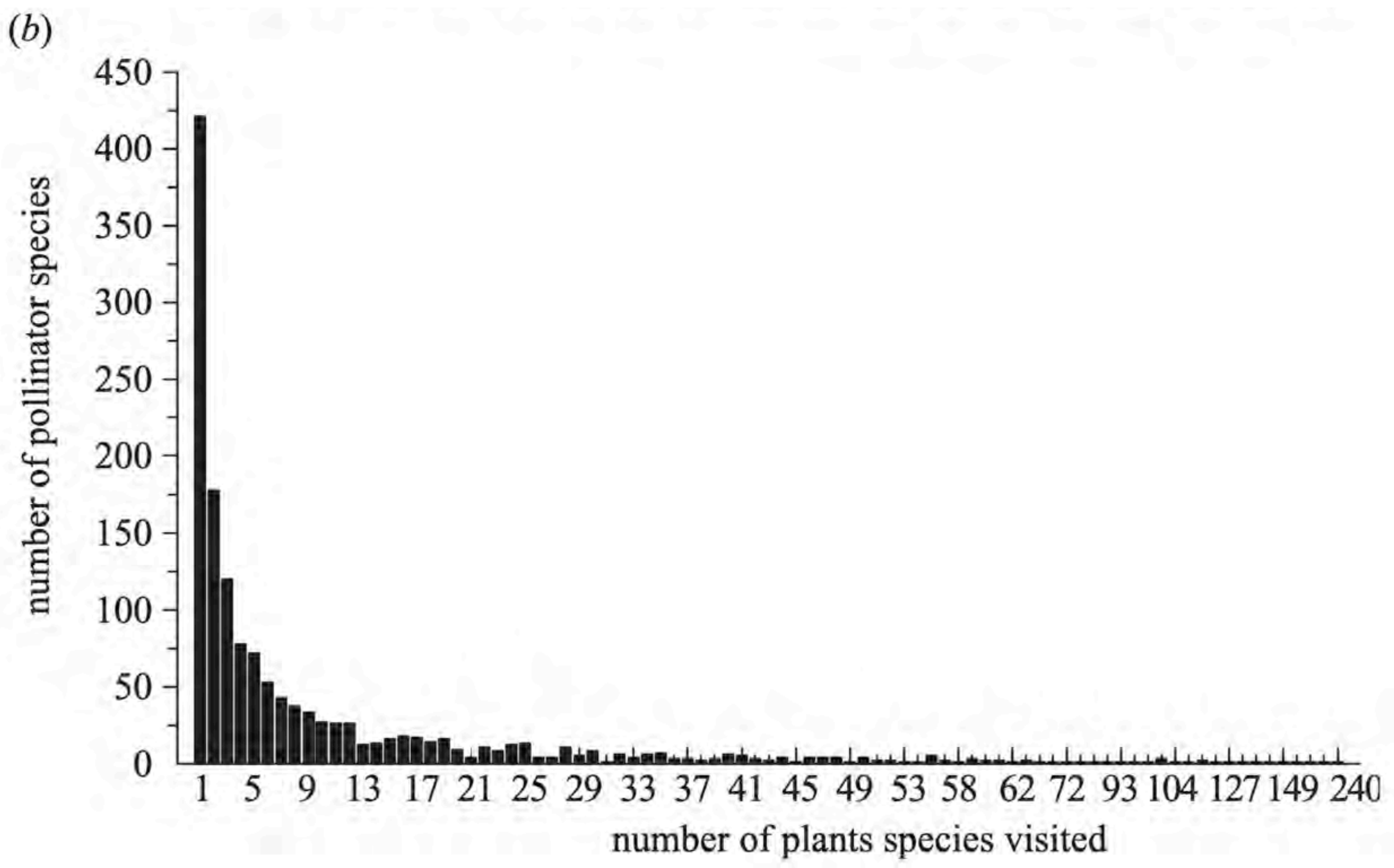
Tolerance of pollination networks to species extinctions

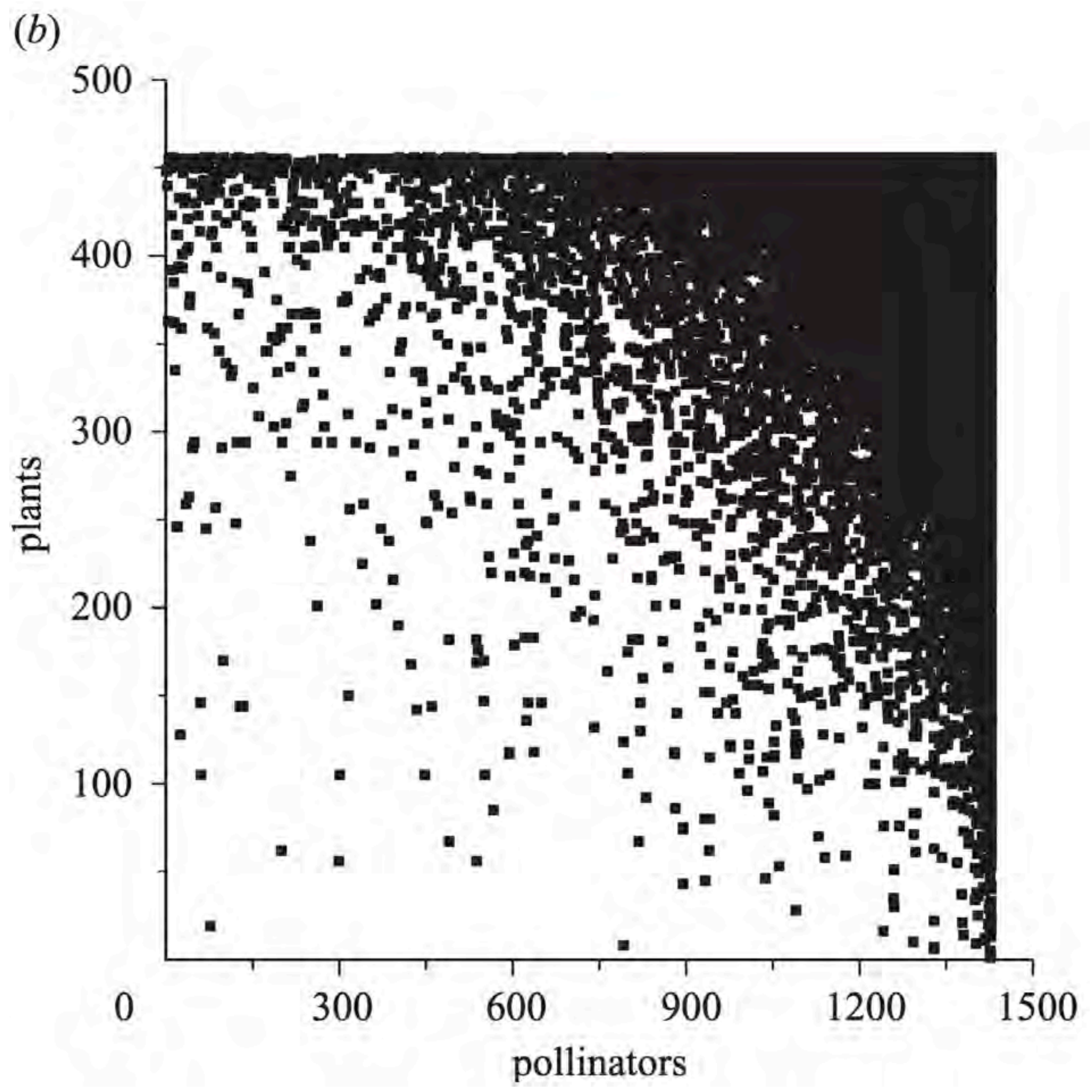
Jane Memmott, Nickolas M. Waser and Mary V. Price

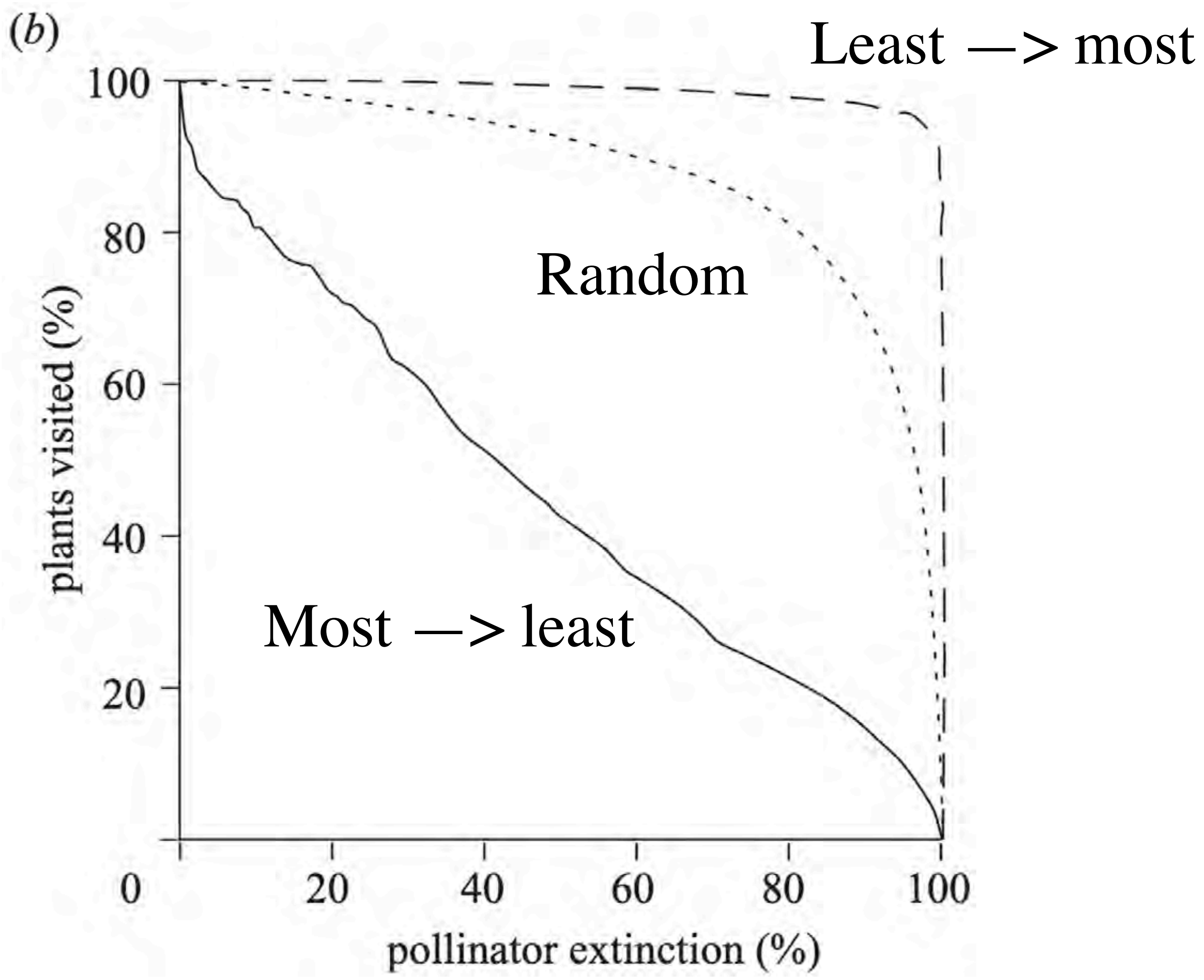
Proc. R. Soc. Lond. B 2004 **271**, 2605-2611
doi: 10.1098/rspb.2004.2909

Charles Robertson (1884-1914)
Professor of Biology and Greek
Blackburn College, Carlinville
Illinois.







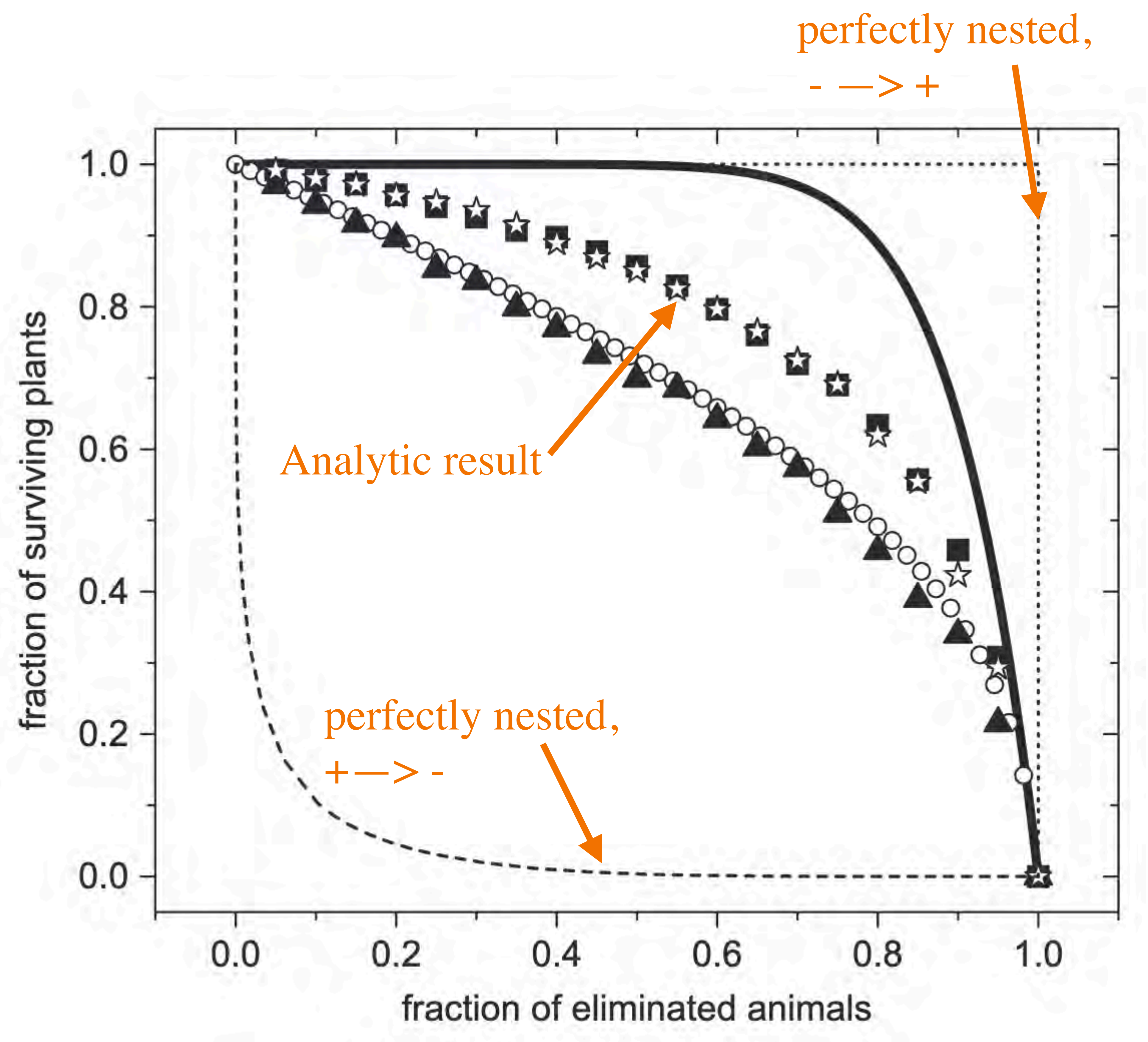


Possible definitions

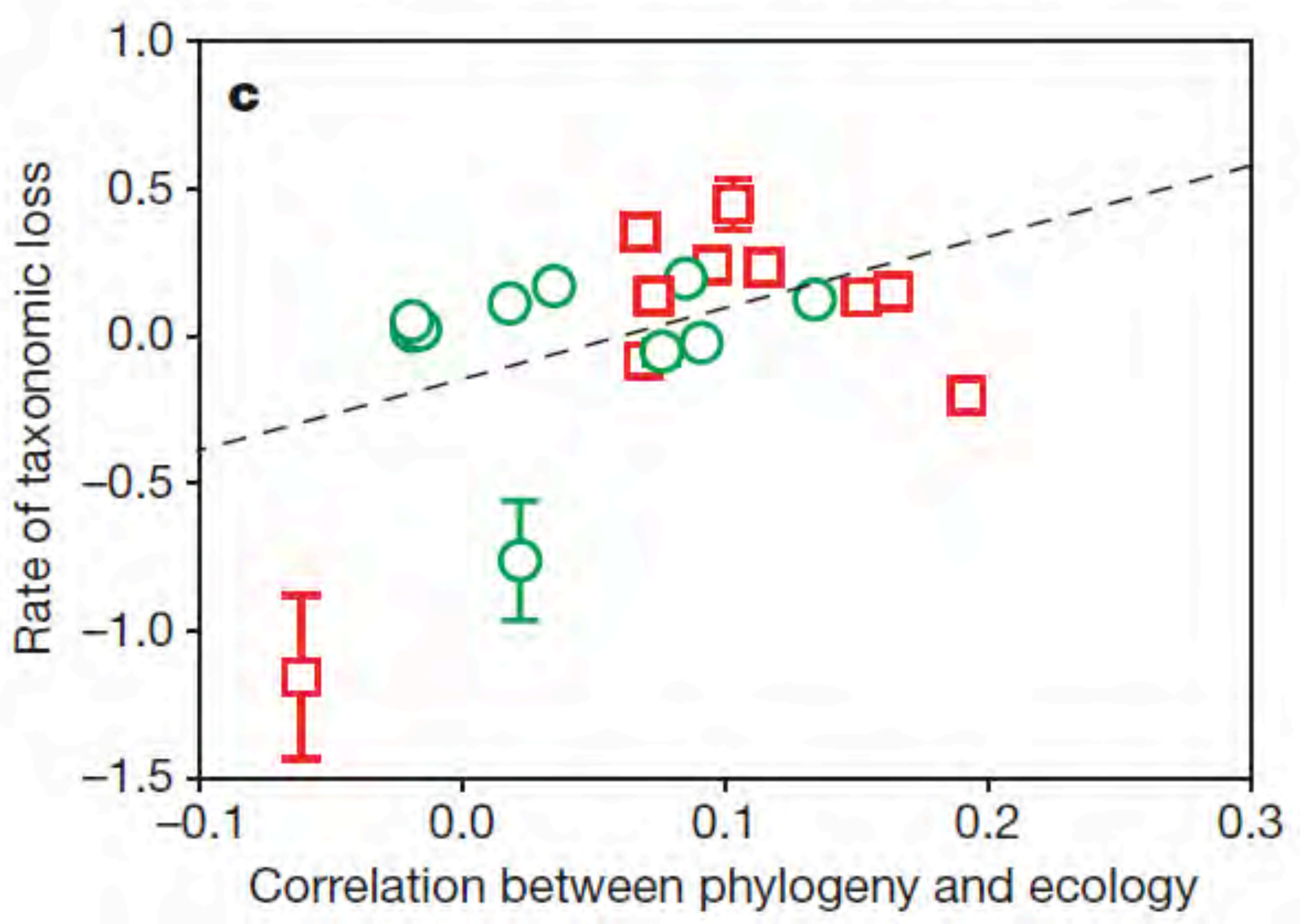
The fraction of species that needs to be removed as primary extinctions to result in a total loss of 50% or more species.

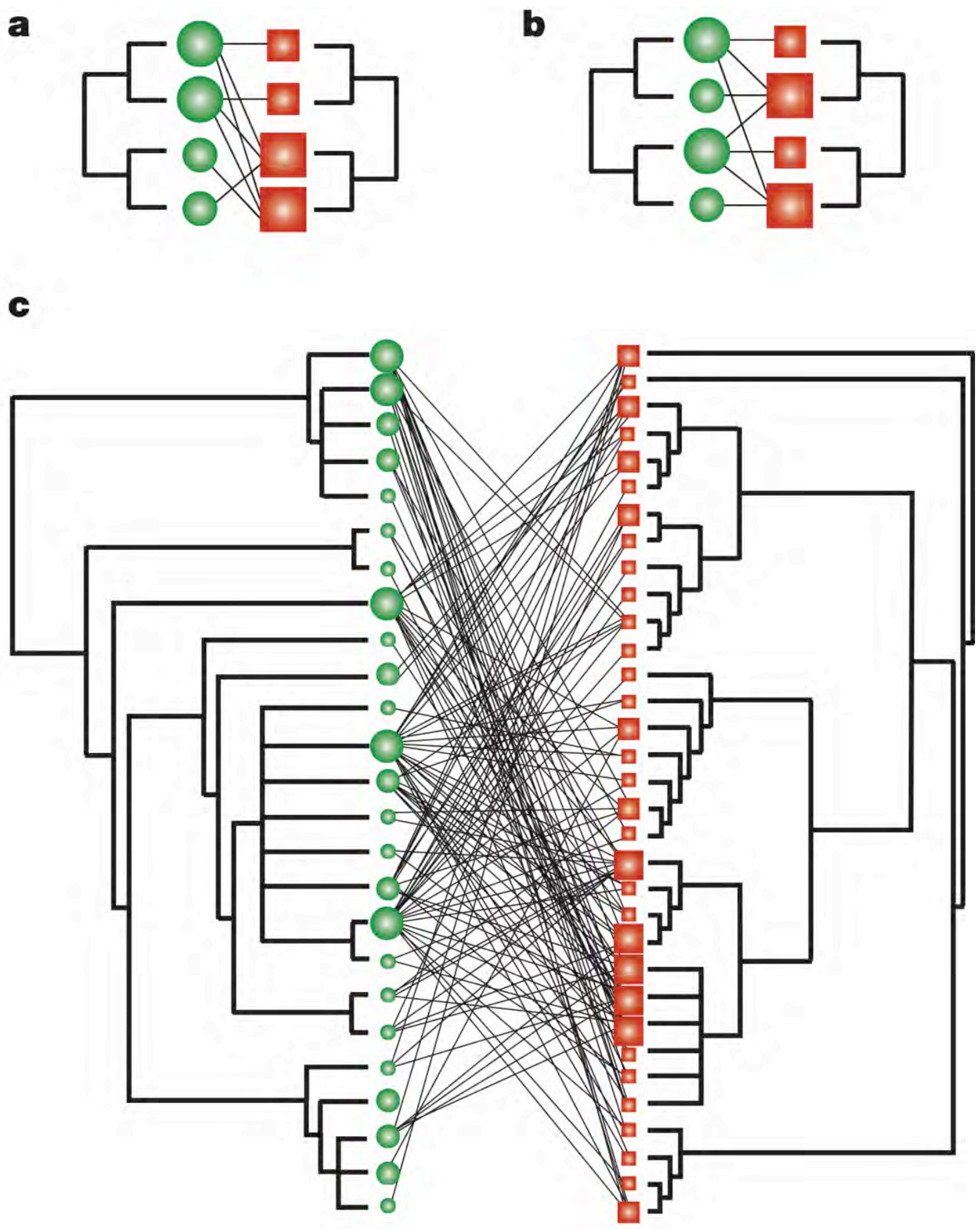
R: The area under the attack tolerance curve [0,1]. (Burgos et al 2007).

Analytical derivation possible.



Communities in which species interactions have a strong phylogenetic component are more prone to have closely related species going coextinct following an extinction event.





Rezende et al 2007, Nature

More computational developments and ideas

Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2013, **4**, 760–770 doi: 10.1111/2041-210X.12062

Secondary extinctions in food webs: a Bayesian network approach

Anna Eklöf[1*†], Si Tang[1] and Stefano Allesina[1,2]

[1]*Department of Ecology & Evolution, University of Chicago, Chicago, IL, USA; and* [2]*Computation Institute, University of Chicago, Chicago, IL, USA*

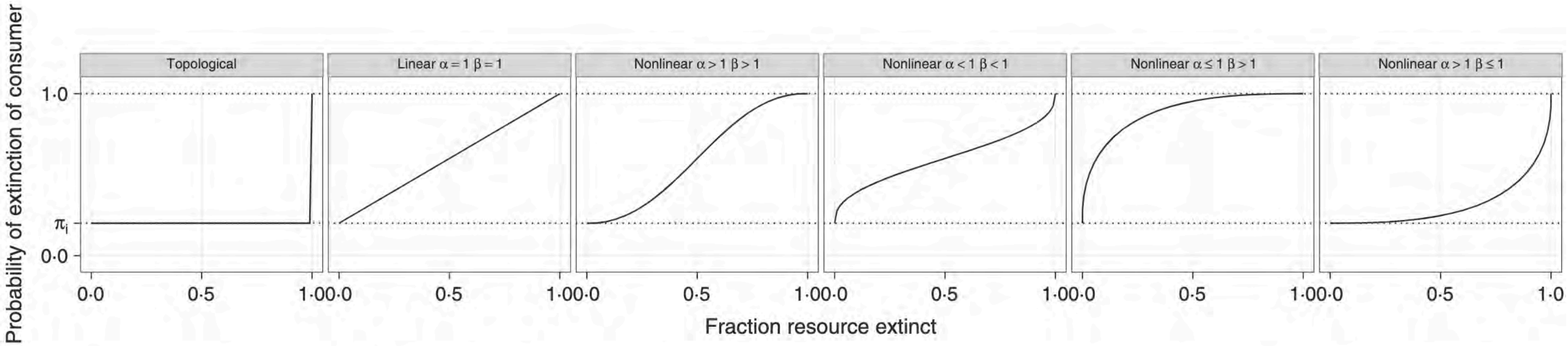


Fig. 2. Schematic description of different functional forms of a consumer's response to loss of resources. From left to right: topological, where a consumer's probability of extinction is unaffected until all resources are lost; linear, where the probability of extinction grows linearly with the fraction of resources lost; nonlinear, taking different shapes according to the parameters α and β.

From the computer to the real world

- Quantitative interactions (e.g., Kaiser-Bunbury et al 2010, Ecology).
- Behavior and rewiring - changes in functional roles (first field test: Brosi & Briggs 2013, PNAS)
- Temporal dynamics.
- Spatial dynamics (e.g., extinction-colonization).

Sergio Timoteo

Courtesy of Jane Memmott

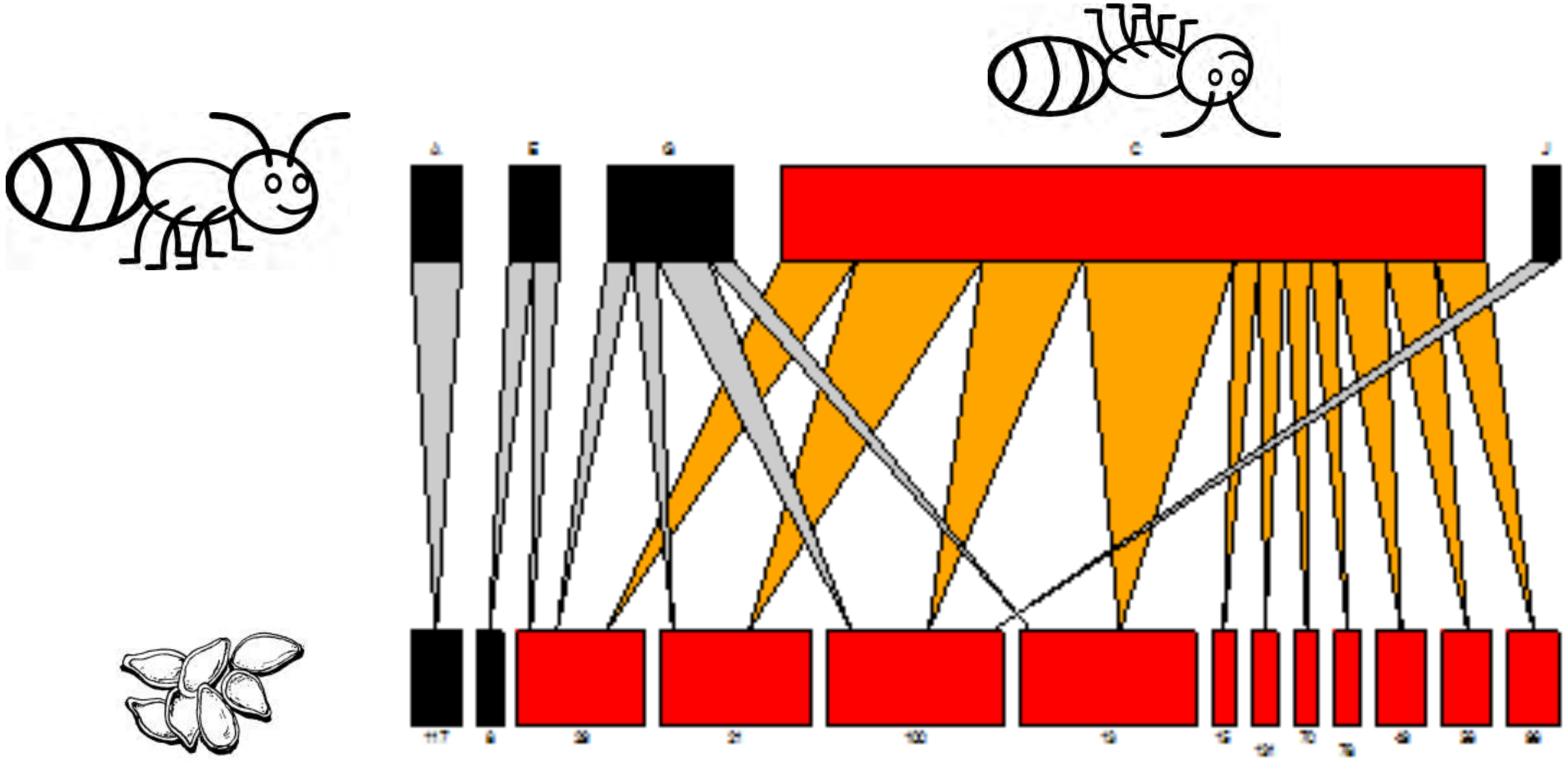
1. How do networks respond to the extinction of their most abundant species?
2. How do simulated extinction models compare with field experiments?

Huge perturbation: removed *B. messor* - 65% of seed dispersal

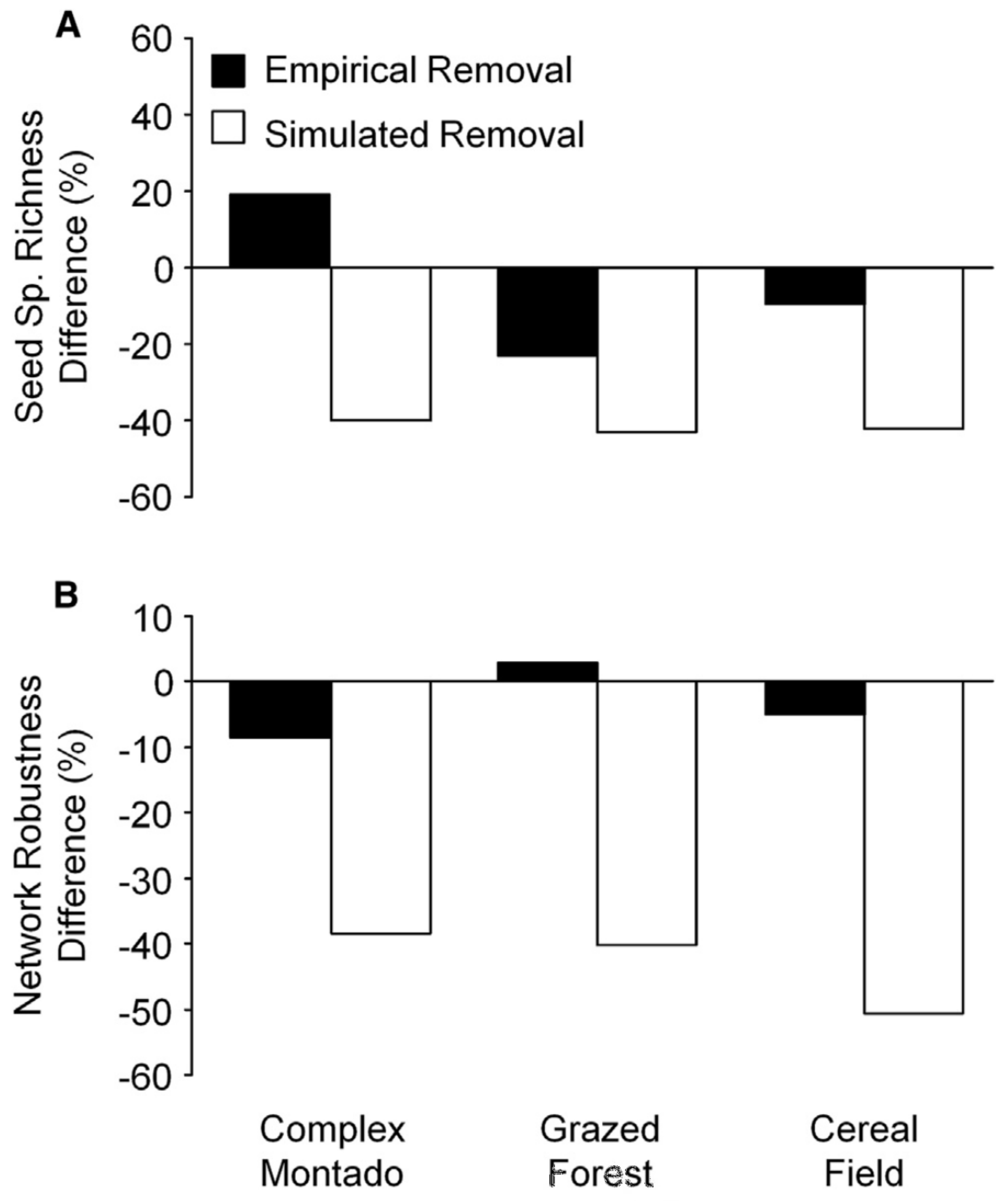
Field experiment: Portugal

Huge perturbation: removed *B. messor* - 65% of seed dispersal

Ant-seed dispersal network



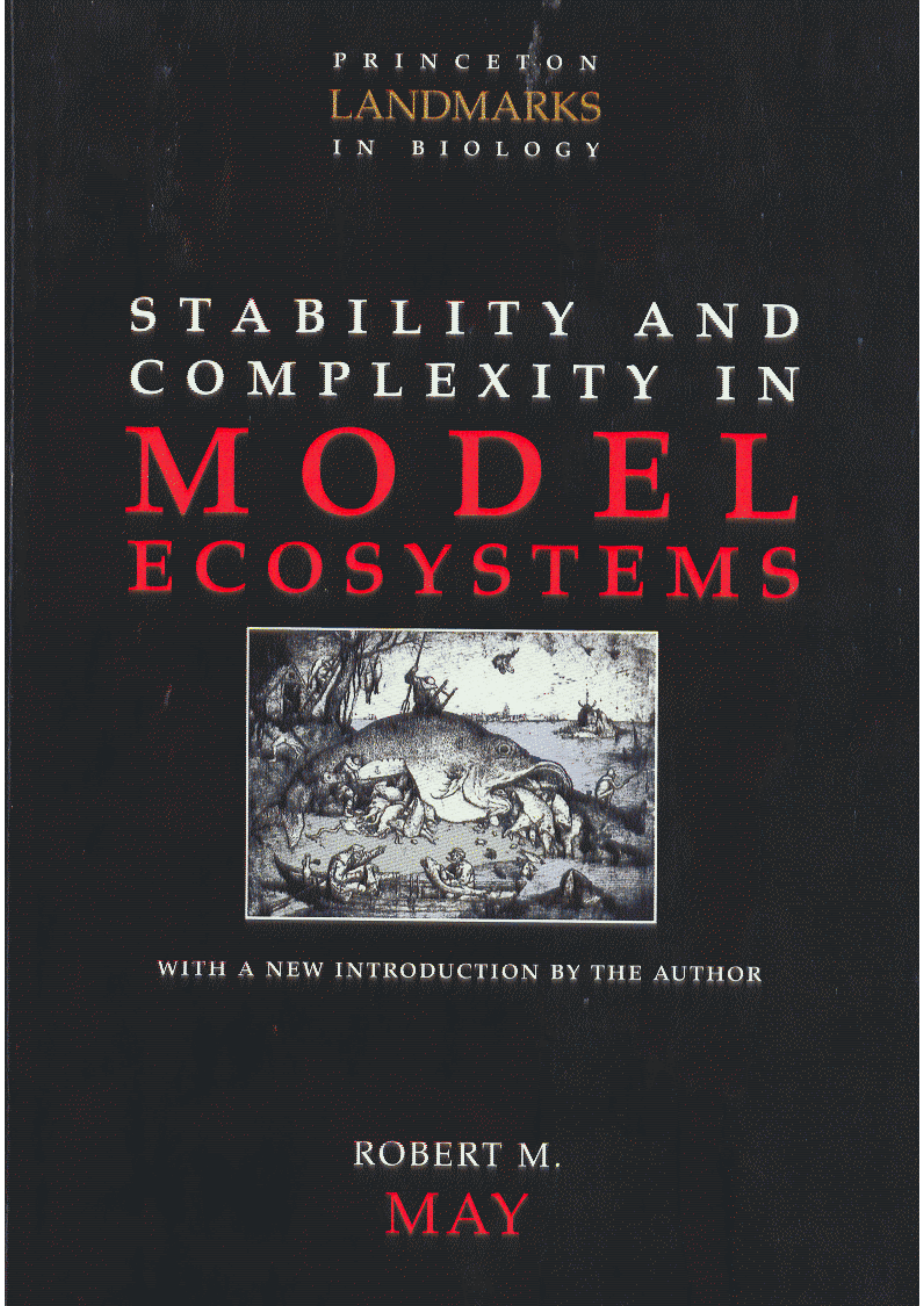
Results: removal did not affect the network



The % difference is to control plots (without removal)

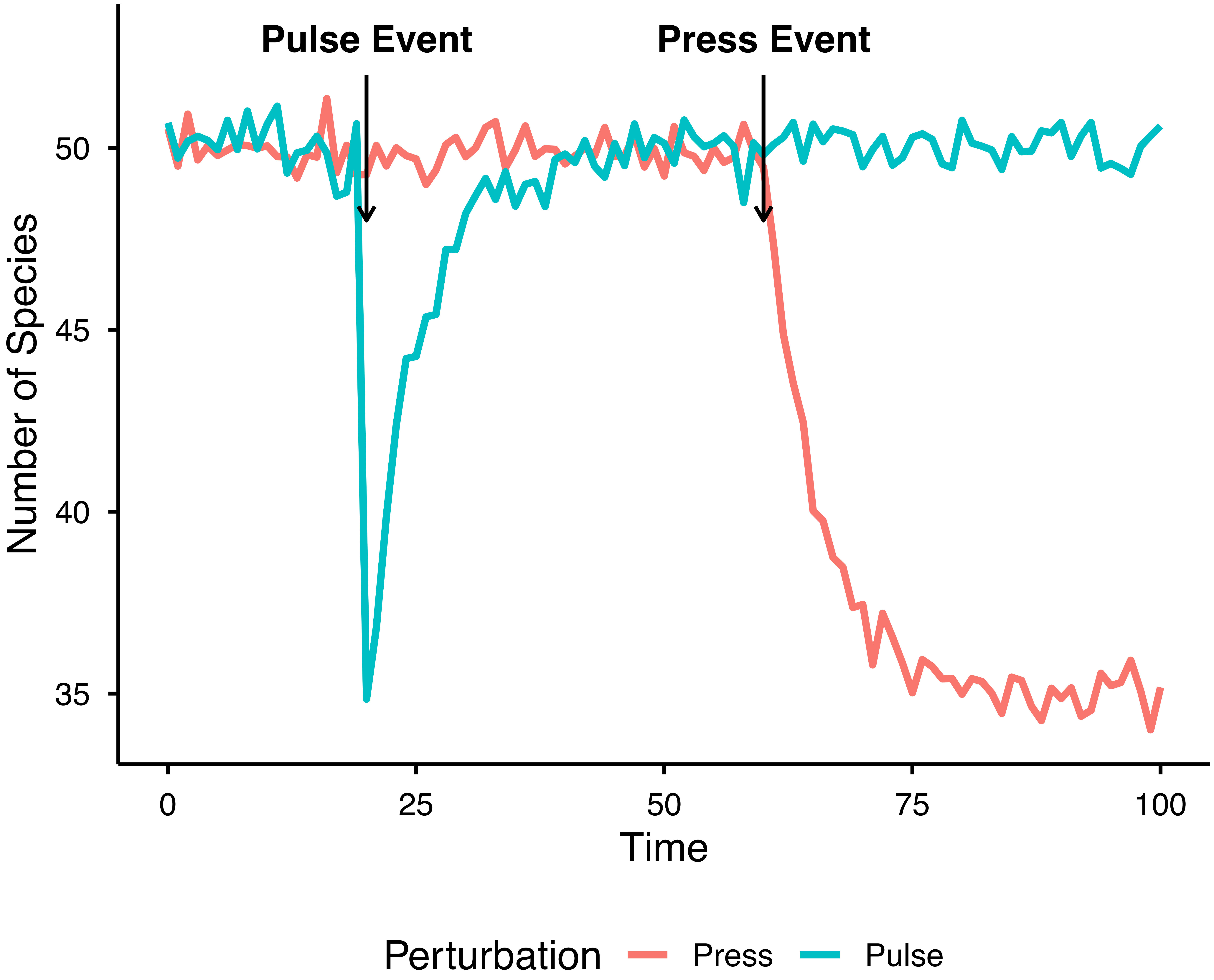
- Extinction models dramatically overestimated the effect of local extinction.
- Need more realistic models which incorporate behavior (here competition) between species
- Need more field tests of species loss models too.

Timoteo, Ramos, Vaughan & Memmott (2016) Current Biology

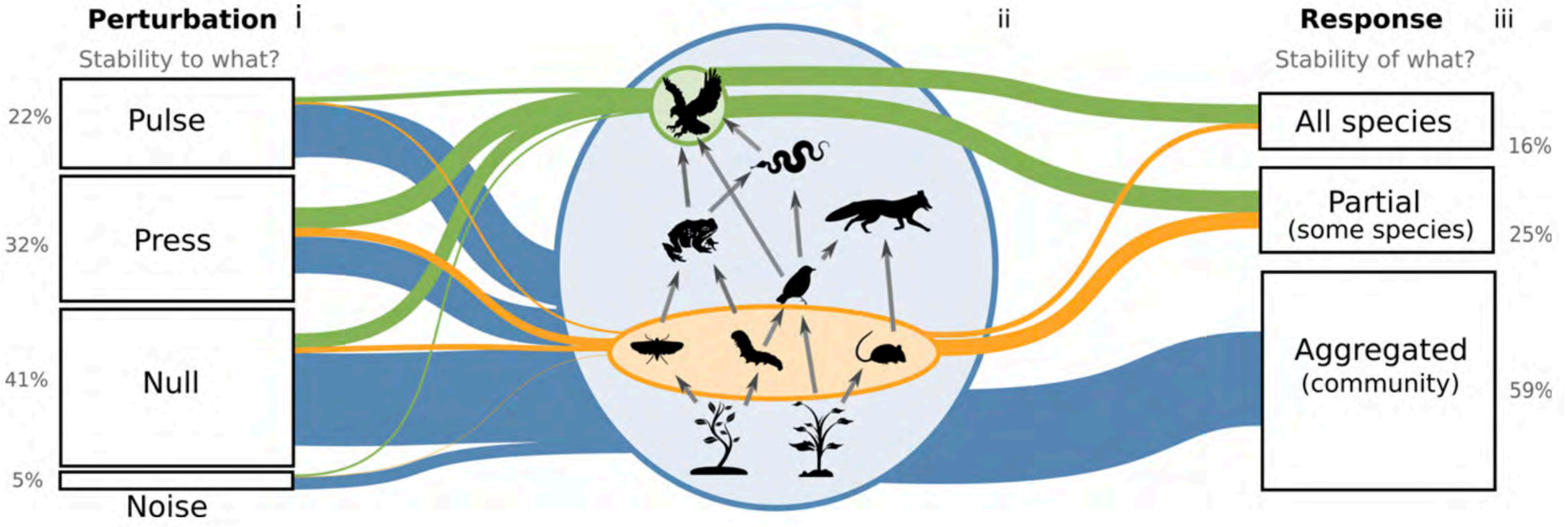


"…the theme of relationship between the network structure of food webs and their ability to handle perturbation is central to ecology…"

"The reorientation of this question to what kinds of connectance patterns are likely to be more resistant to specific kinds of disturbance is of continuing relevance in ecology …" (R. May 2002)



Pulse Event
Press Event
Number of Species
50
45
40
35
0
25
50
75
100
Time
Perturbation
Press
Pulse



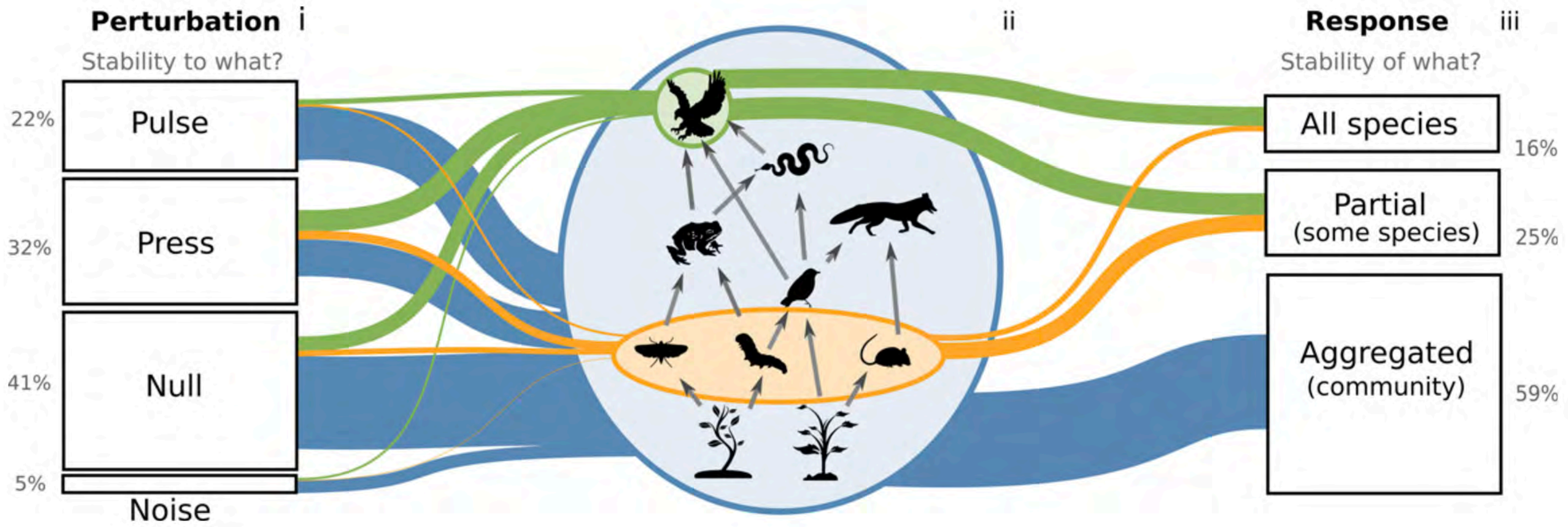
Kefi et al 2019, Ecol Lett

Different concepts/definitions of ‘stability’

- Local asymptotic stability
- Resilience
- Reactivity
- Qualitative global (asymptotic) stability
- Permanence and persistence
- Invasibility
- Variability
- Robustness

How is stability affected by:

- Number of species?
- Network structure?
- Proportion of mutualistic vs competitive interactions?
- underlying model?



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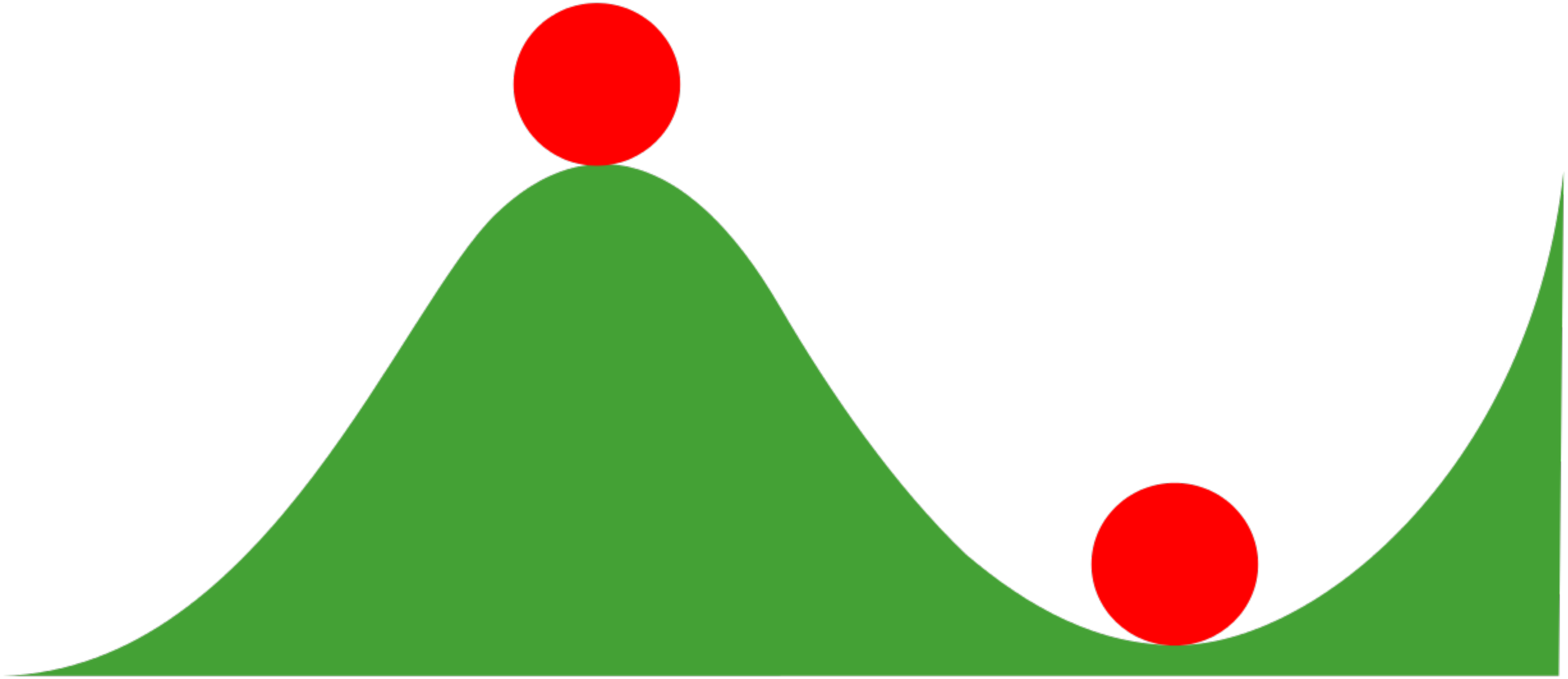
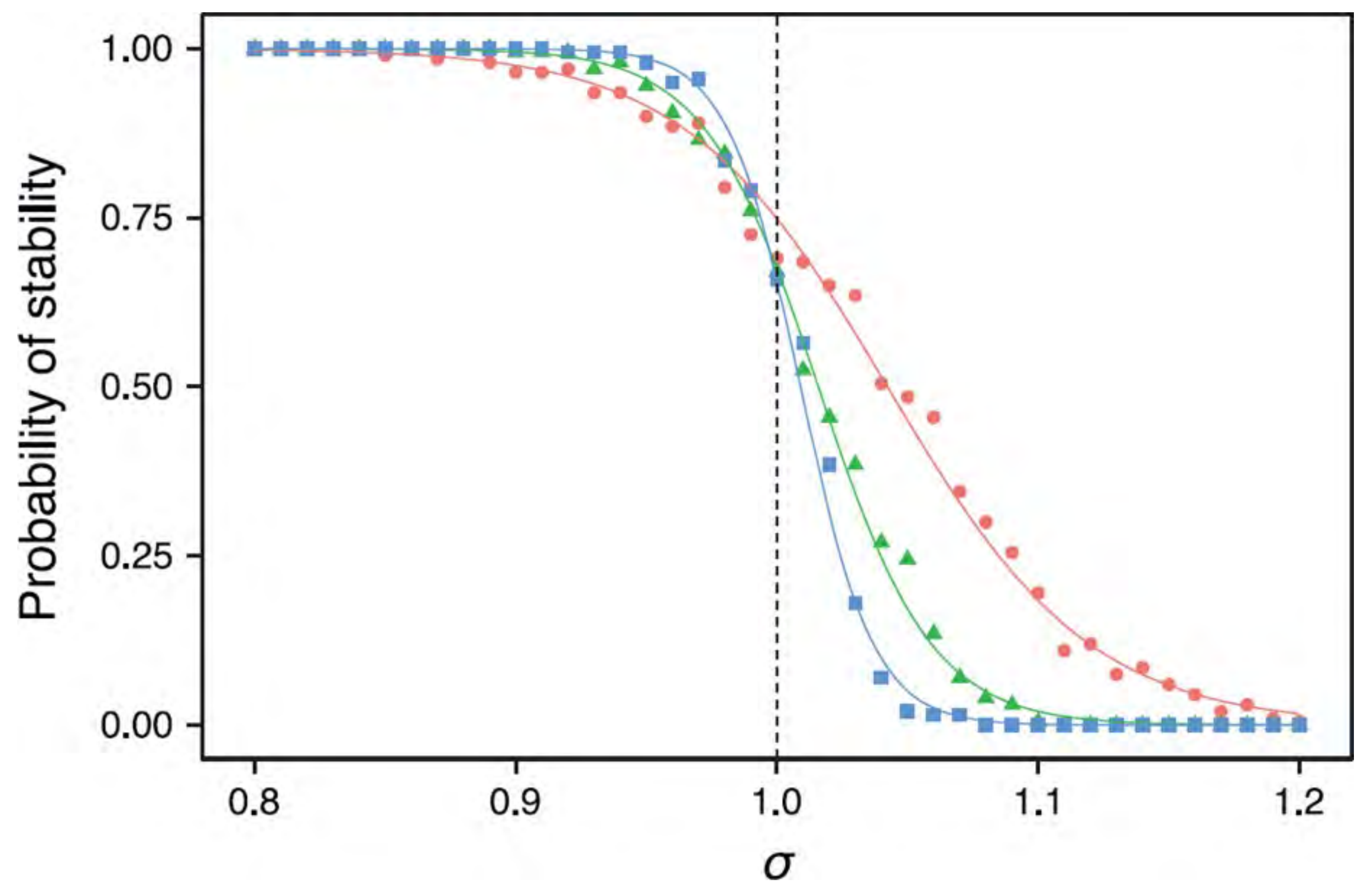


$$\mathbf{A} = \begin{pmatrix} a_{11} & a_{12} & \cdots & \cdots & a_{1N} \\ a_{21} & a_{22} & \cdots & \cdots & a_{2N} \\ \vdots & \cdots & \ddots & \cdots & \vdots \\ \vdots & \cdots & \cdots & \ddots & a_{MN} \\ a_{N1} & a_{N2} & \cdots & a_{NM} & a_{NN} \end{pmatrix}$$



Allesina and Tang, 2015

Hypothesis:
higher diversity
increases stability

Theory:
- Random matrix
- Linear stability analysis

Result:
higher diversity
decreases
stability

A primer on local asymptotic stability

$dX_i/dt = f_i(X(t))$

f_i relates growth rate of i to the density of the S populations — e.g., LV dynamics

Equilibrium $\mathbf{X}^*$ when:

$dX_i/dt\,|\,\mathbf{X}^* = f_i(\mathbf{X}^*(t)) = 0$,

and we also want feasibility: $\mathbf{X}^* > 0$

$$M_{ij} = J_{ij}\big|_{\mathbf{X}^*} = \frac{\partial f_i(\mathbf{X}(t))}{\partial X_j}\bigg|_{\mathbf{X}^*}$$

If linear algebra is not your thing, do not worry about this.

Assumptions:

- Populations are at equilibrium
- Local effects.
- Instability does not preclude persistence.
- infinitesimal perturbations.

Allesina and Tang, 2015

A primer on local asymptotic stability

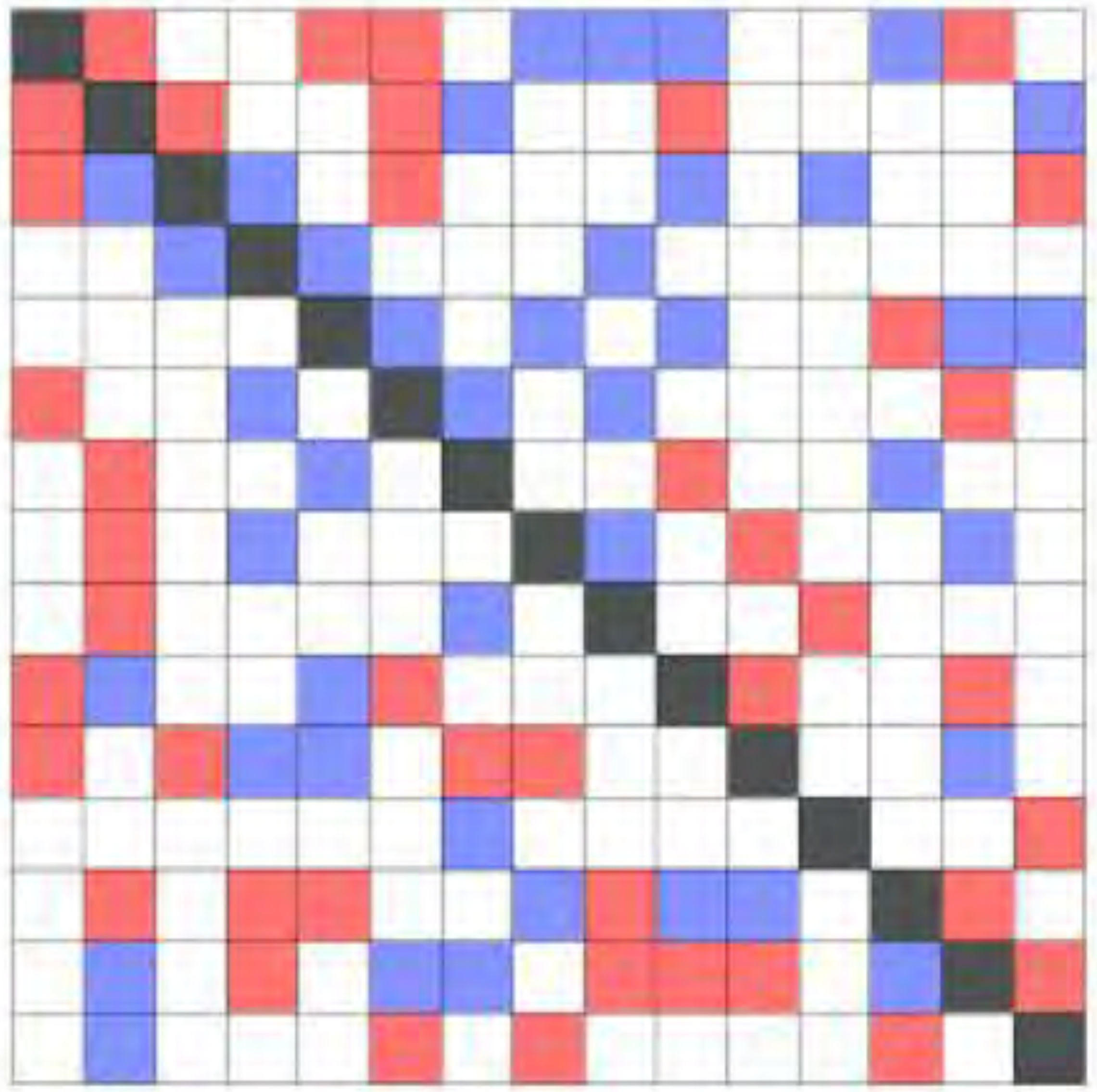
-Random community matrices with S species and connectance C.

-Interactions are drawn from a normal distribution: $\mathcal{N}(0,\sigma^2)$.

-Diagonal of -1

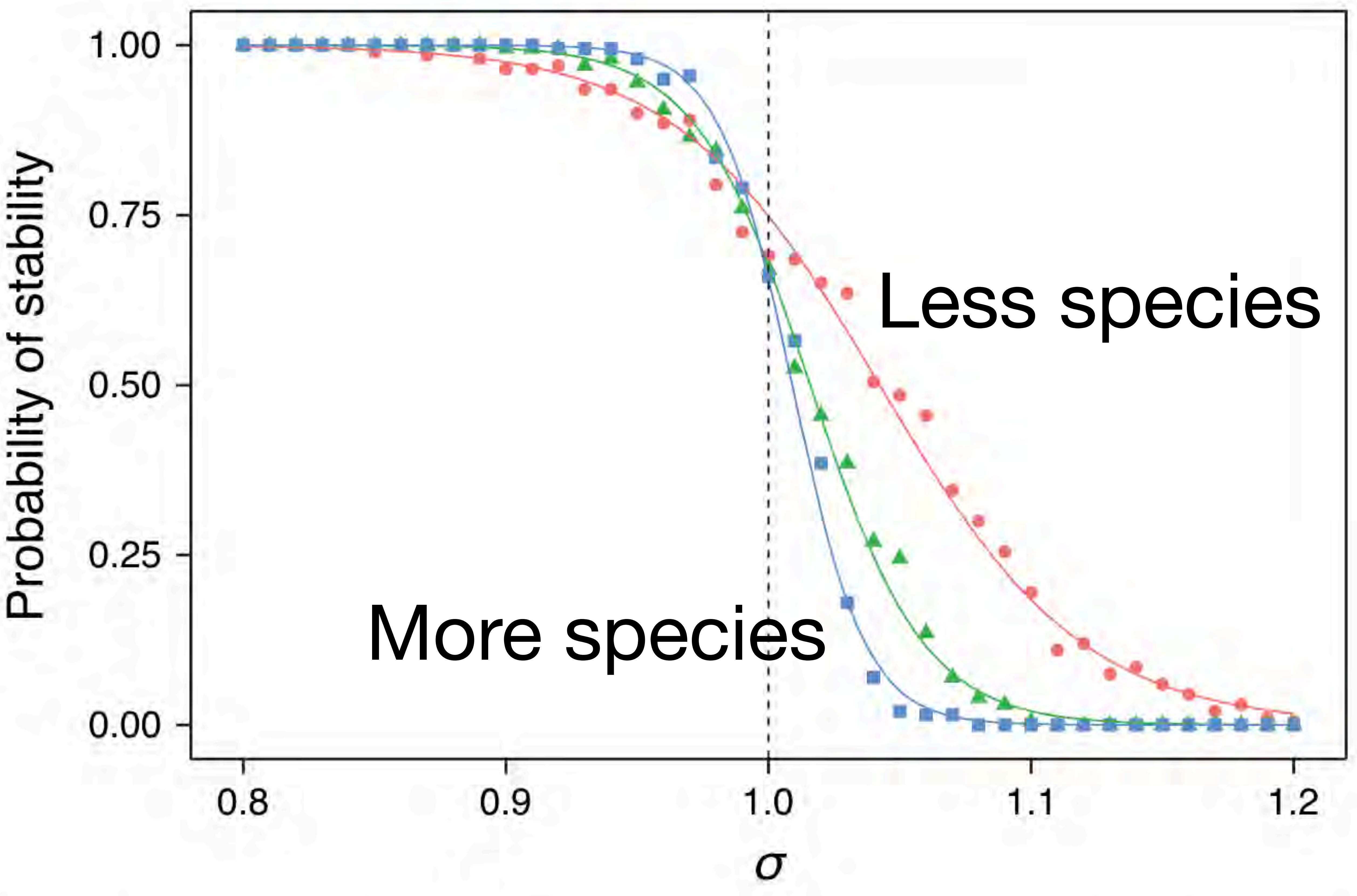
-Stability criterion: $\sigma\sqrt{SC} < 1$

$$A = \begin{pmatrix} a_{11} & a_{12} & \cdots & \cdots & a_{1S} \\ a_{21} & a_{22} & \cdots & \cdots & a_{2S} \\ \vdots & \cdots & \ddots & \cdots & \vdots \\ \vdots & \cdots & \cdots & \ddots & a_{S-1,S} \\ a_{S1} & a_{S2} & \cdots & a_{S,S-1} & a_{SS} \end{pmatrix}$$



May 1972, Nature

A primer on local asymptotic stability



Here: $d = \sqrt{SC}$ so stability

$\sigma\sqrt{SC} < d$ is obtained when $\sigma < 1$

Allesina and Tang, 2015

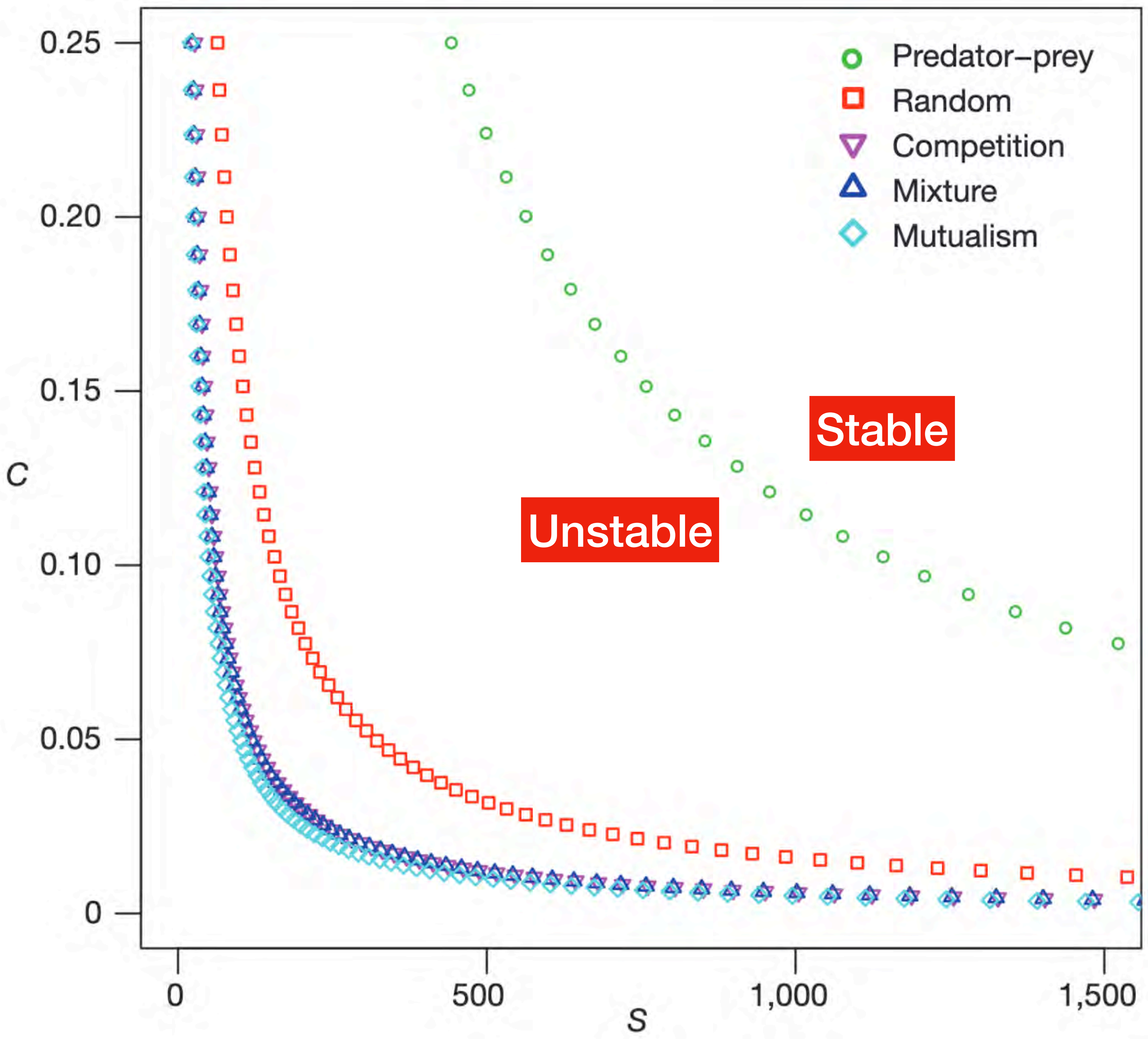


Figure 2 | Stability criteria for different types of interaction. We fixed $\theta = d/\sigma = 4$, and for a given connectance C we solved for the largest integer S that satisfies the stability criterion for each type of interactions. Combinations of S and C below each curve lead to stable matrices with a probability close to 1. The interaction types form a strict hierarchy from mutualism (most unlikely to be stable) to predator–prey (most likely to be stable).

Tang and Allesina, 2012

Does diversity promote stability?

$$A = \begin{pmatrix} a_{11} & a_{12} & \cdots & \cdots & a_{1S} \\ a_{21} & a_{22} & \cdots & \cdots & a_{2S} \\ \vdots & \cdots & \ddots & \cdots & \vdots \\ \vdots & \cdots & \cdots & \ddots & a_{S-1,S} \\ a_{S1} & a_{S2} & \cdots & a_{S,S-1} & a_{SS} \end{pmatrix}$$

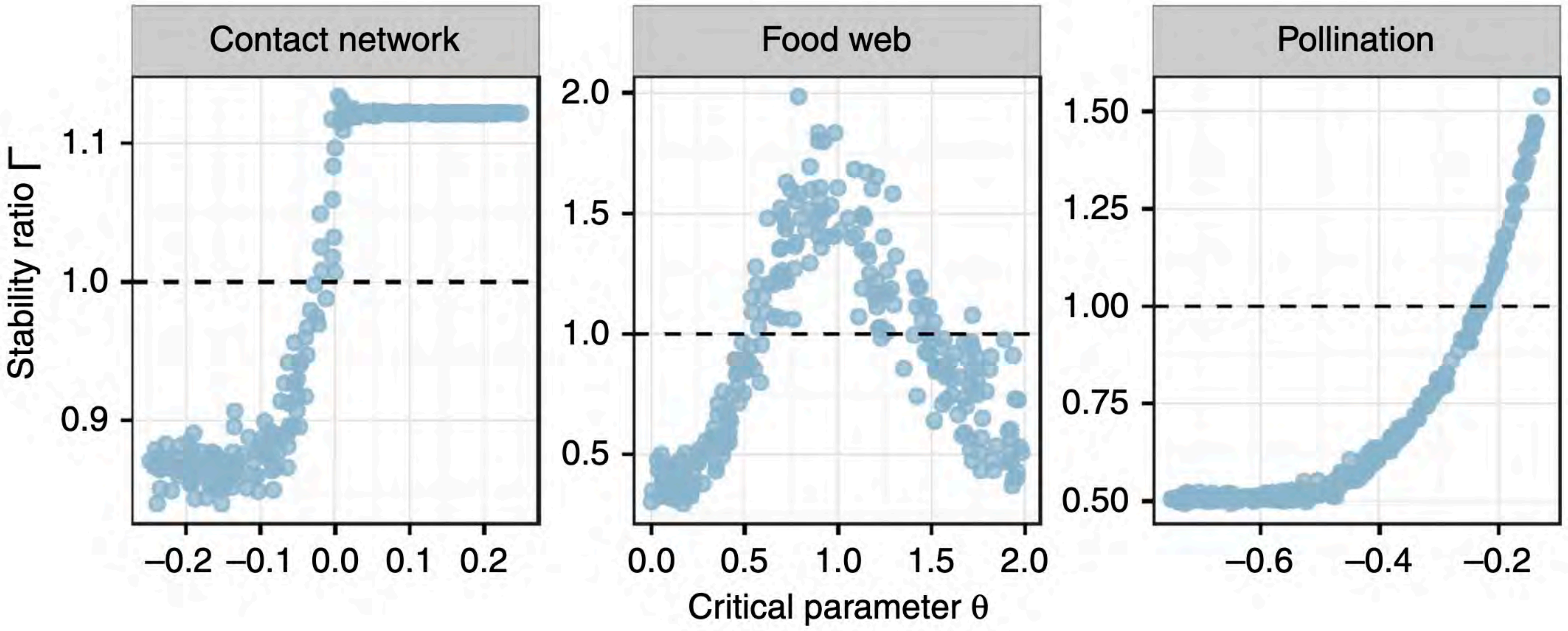
- A is a random matrix.
- Coefficients a_{ij} are an estimate for the strength of species interactions

(Lord) Bob May

"…the task is, therefore, to **elucidate the devious strategies which make for stability** in enduring natural systems."

Allesina and Tang, 2015

Network structure promotes stability



Grilli et al 2016