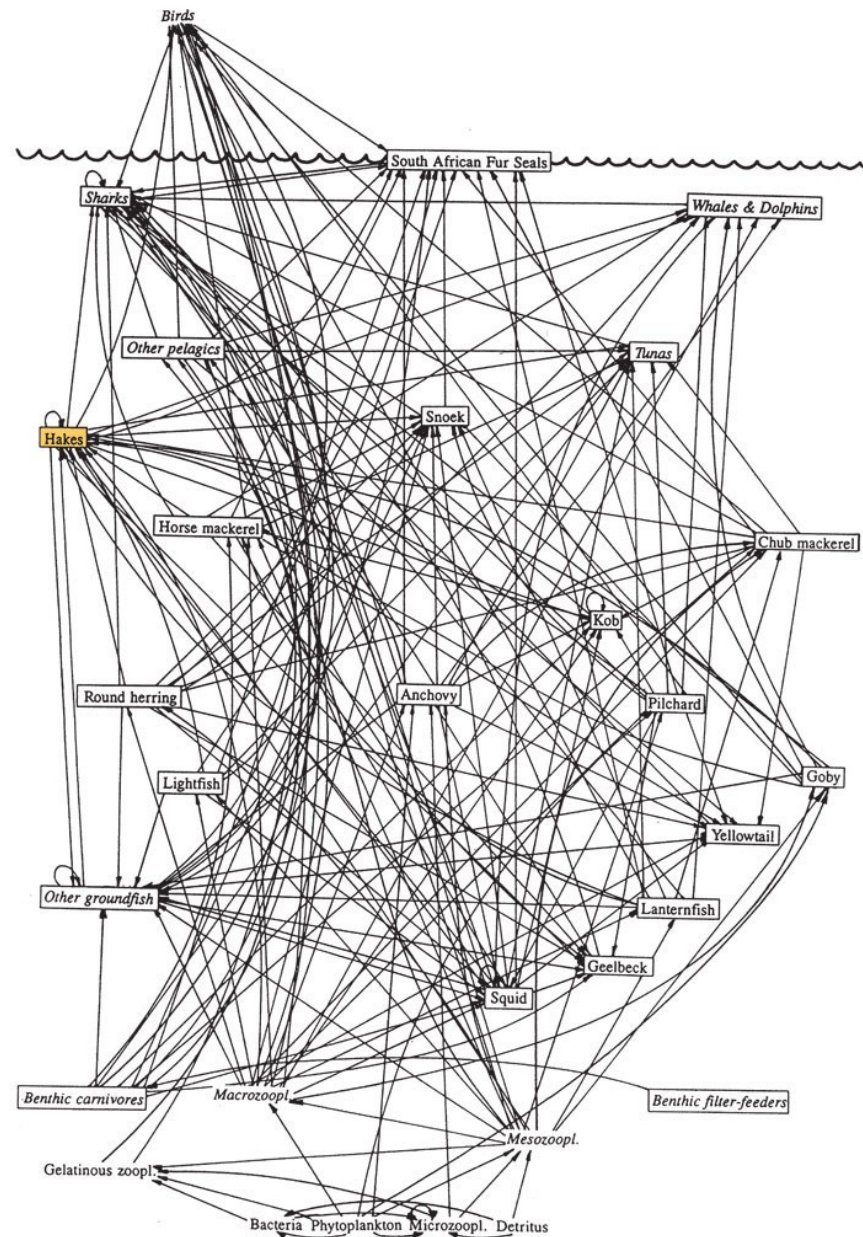


Interações interespecífica inseridas em redes ecológicas

Ao final da aula você deverá saber

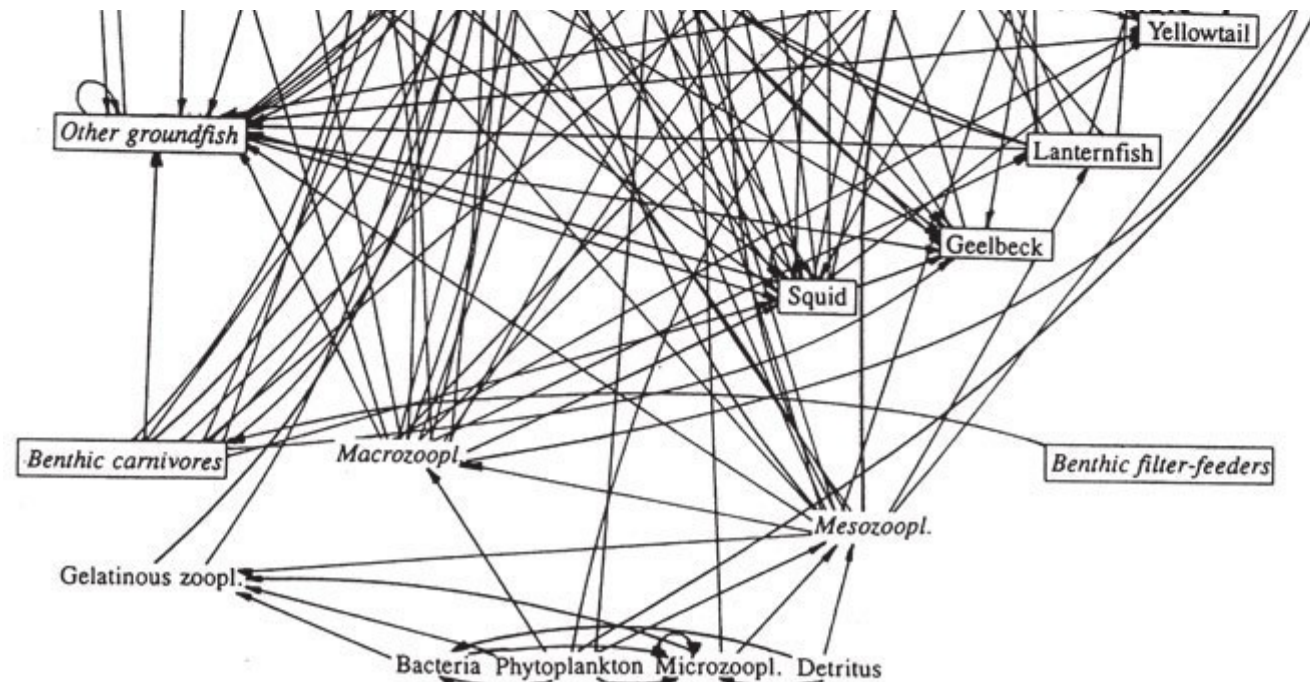
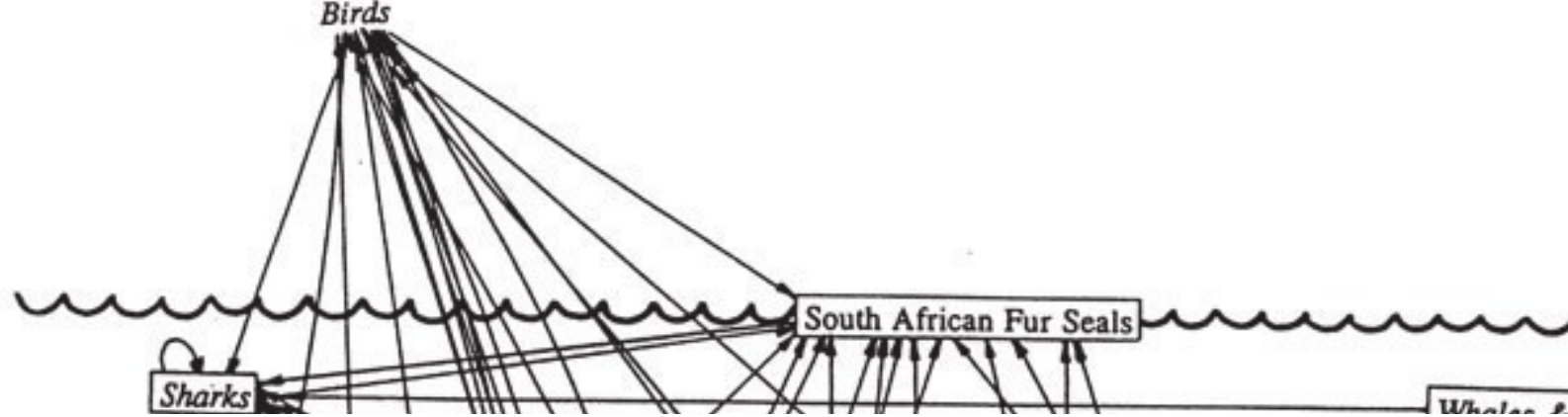
- Principais medidas para descrever estrutura de redes
- Como redes podem descrever tanto interações antagonísticas quanto mutualísticas
- Como a biodiversidade pode influenciar a estabilidade de um ecossistema
- O que são estados estáveis alternativos em comunidades e as suas consequências



COMMUNITY ECOLOGY, Figure 10.2

© 2012 Sinauer Associates, Inc.

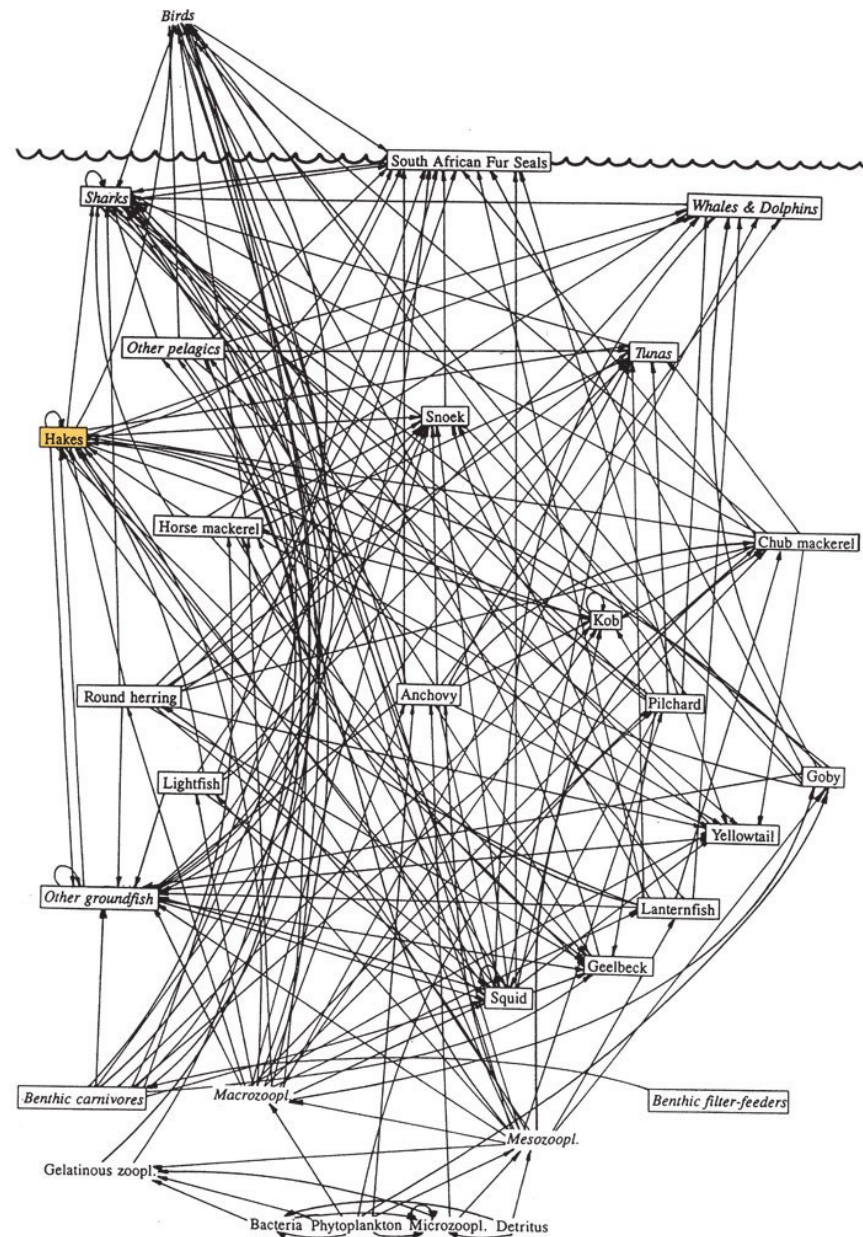
Figure 10.2 Rede trófica para o ecossistema marinho de Benguela na costa da África do Sul



COMMUNITY ECOLOGY, Figure 10.2

© 2012 Sinauer Associates, Inc.

Figure 10.2 Rede trófica para o ecossistema marinho de Benguela na costa da África do Sul



Tamanho de corpo

COMMUNITY ECOLOGY, Figure 10.2

© 2012 Sinauer Associates, Inc.

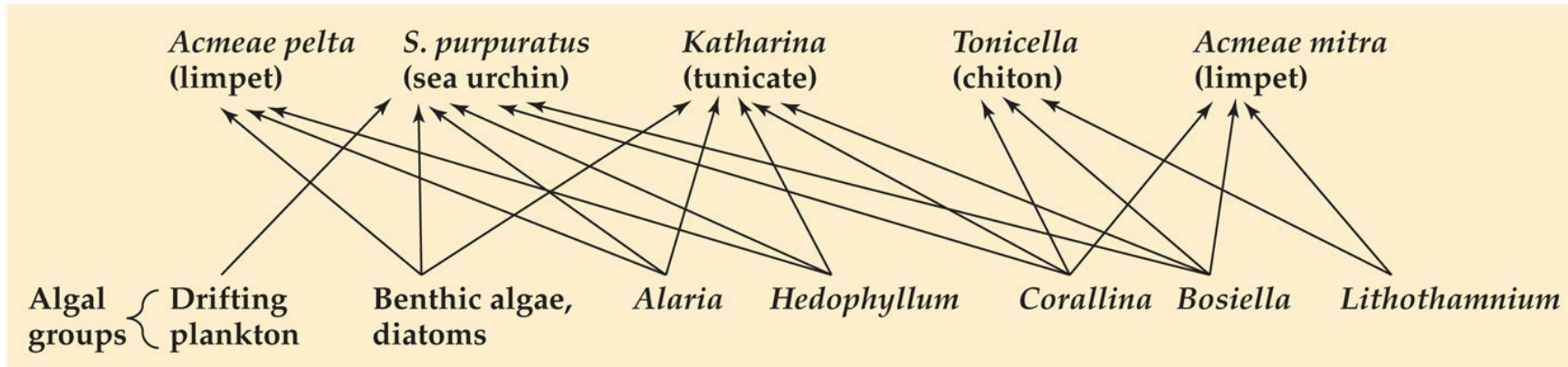
Figure 10.2 Rede trófica para o ecossistema marinho de Benguela na costa da África do Sul

Redes de interação

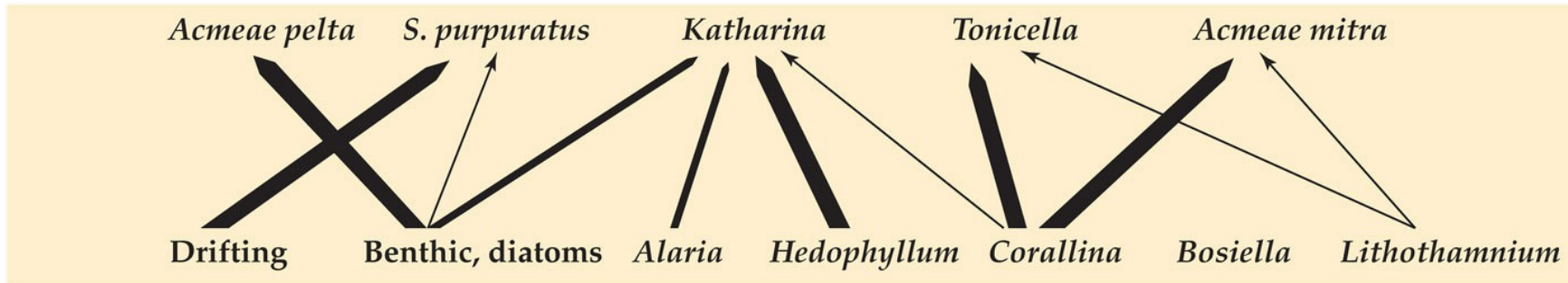
- Interações tróficas => teias alimentares
- Outros tipos de interações (mutualismo, hospedeiro-parasitóide)
 - Redes bipartidas
 - Parasitas são ainda pouco incluídos
- Redes de **conectividade**
- Redes de **fluxo de energia**
- Redes **funcionais**

Figure 10.3 Three distinct approaches for constructing food webs

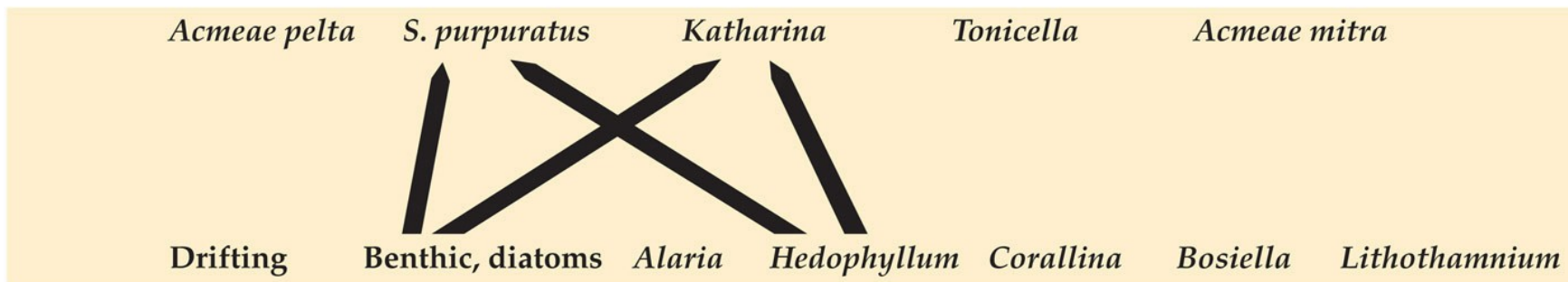
(A)



(B)



(C)



[home](#)[resources](#)[contribute data](#)[pics](#)[blog](#)[who we are](#)

Welcome to the Interaction Web Database. This is a nonprofit, cooperative database containing published data on species interaction networks. It is hosted by the [National Center for Ecological Analysis and Synthesis](#), at the University of California, Santa Barbara, U.S.A.

You must read our [Privacy Policy](#) before using the Interaction WebDatabase website



iwdb
blog



iwdb
dataset



iwdb
pics

updates

February 03, 2017

Atlantic Forest bromeliad-pollinator network from [Kaehler et al. \(2005\)](#) added to IWDB.

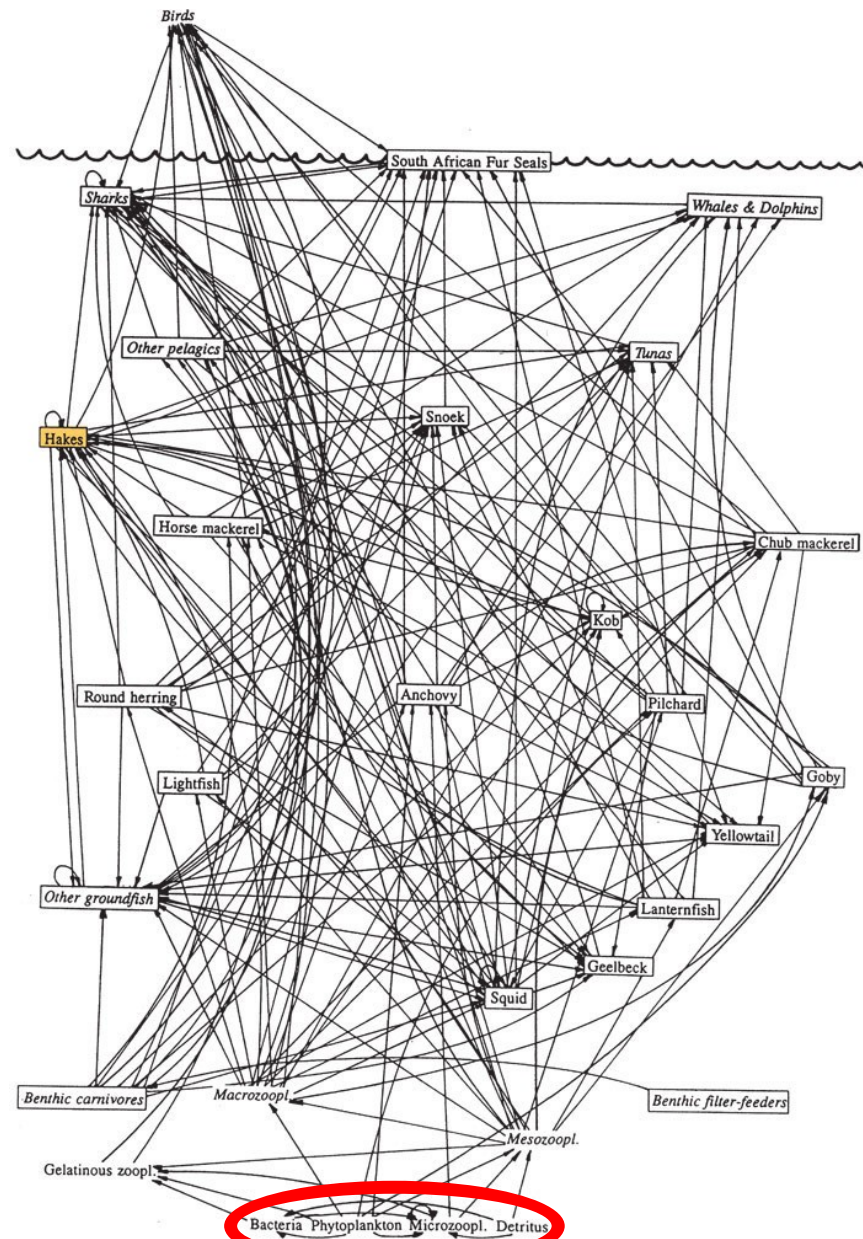
Atlantic Forest plant-hummingbird networks from [Kohler \(2011\)](#) added to IWDB.

Atlantic Forest bromeliad-pollinator network from [Varassin & Sazima \(2012\)](#) added to IWDB.

Cayaballao restoration networks from [Keizer-Burbury et al. \(2017\)](#) added to IWDB.

Redes de conectividade

- Somente mostram a presença de uma interação, mas não sua intensidade

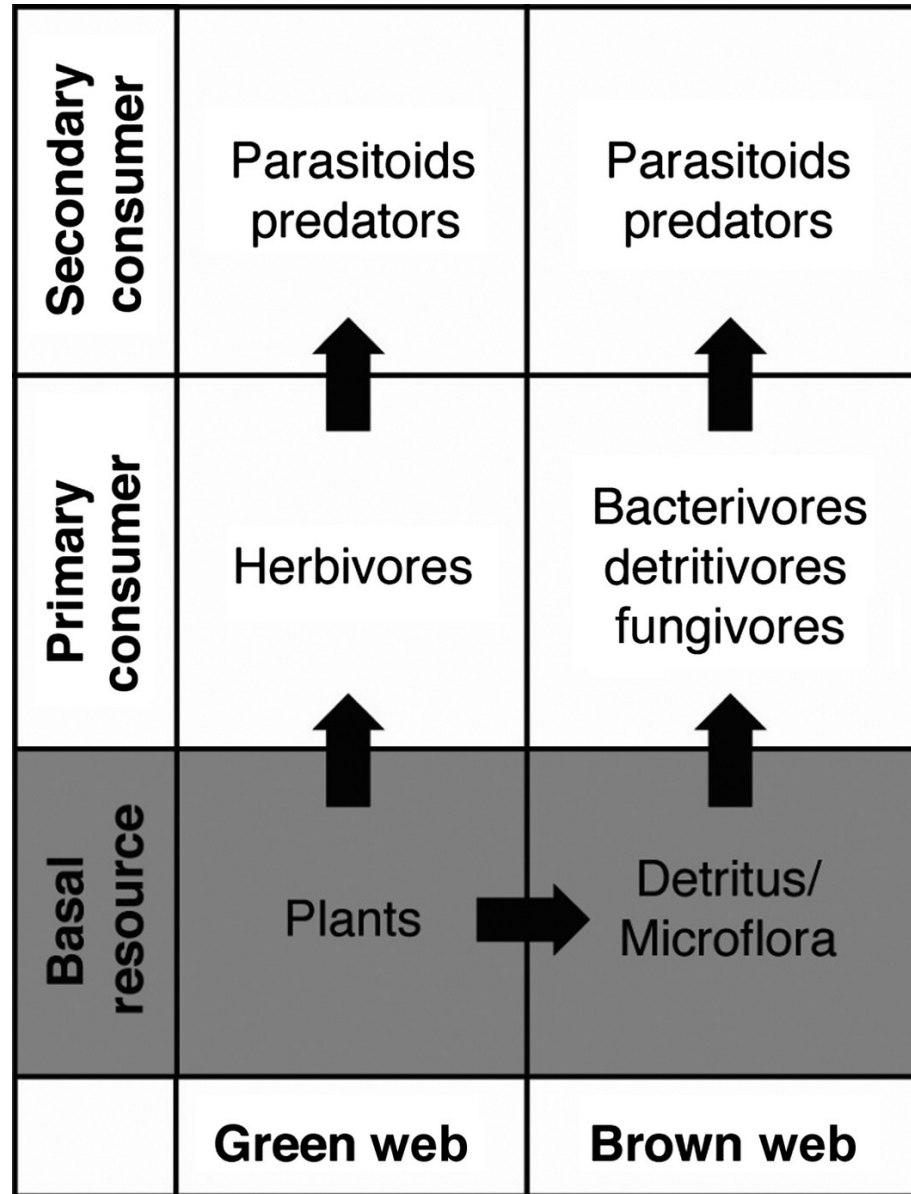


Tamanho de corpo

Figure 10.2 Rede trófica para o ecossistema marinho de Benguela na costa da África do Sul

COMMUNITY ECOLOGY, Figure 10.2
© 2012 Sinauer Associates, Inc.

Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: a meta-analysis



Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: a meta-analysis

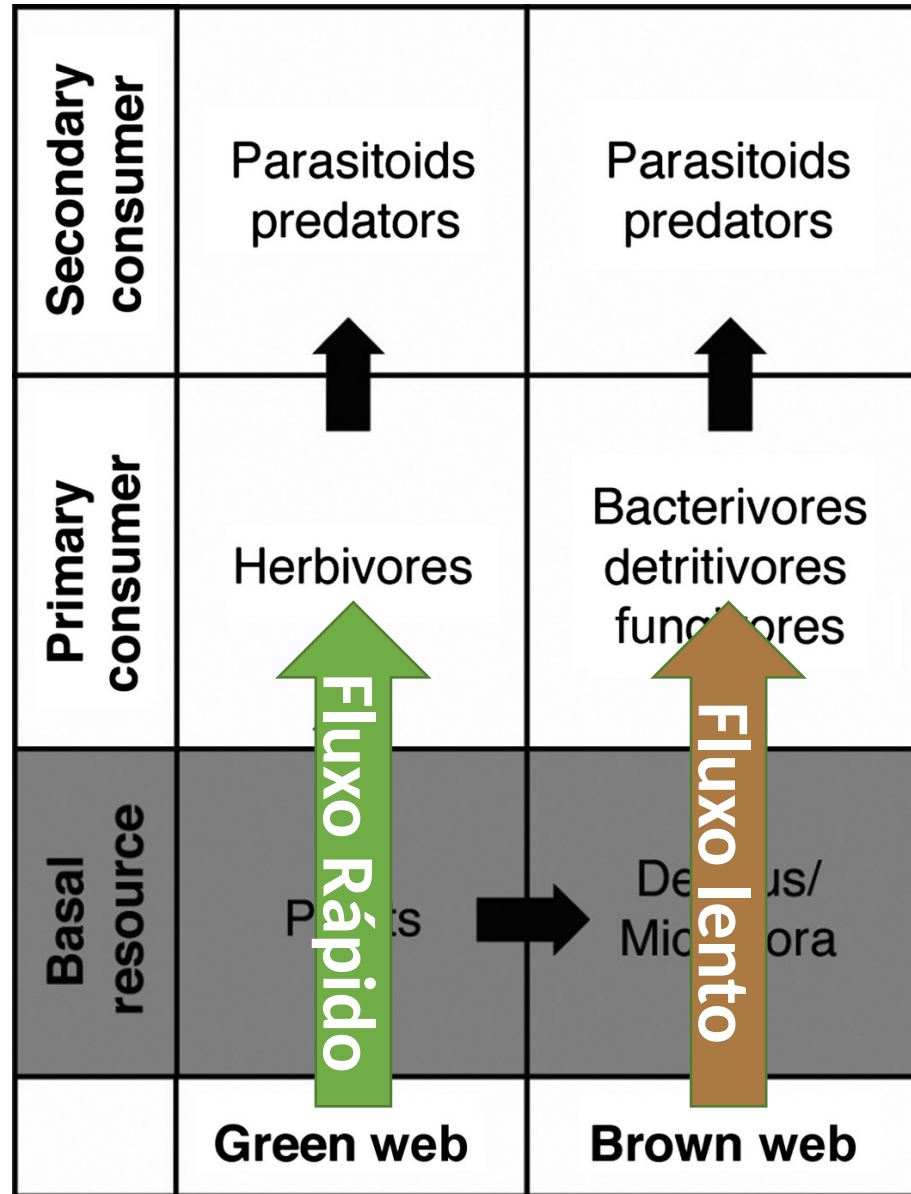
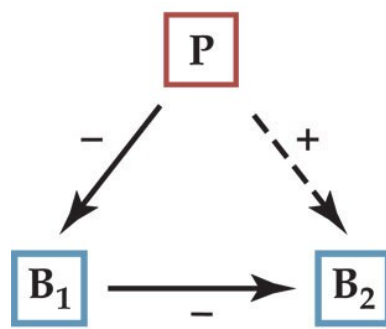


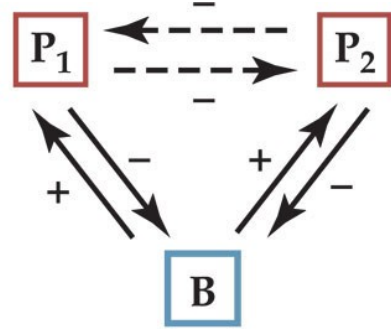


Figure 10.2 Rede trófica para o ecossistema marinho de Benguela na costa da África do Sul

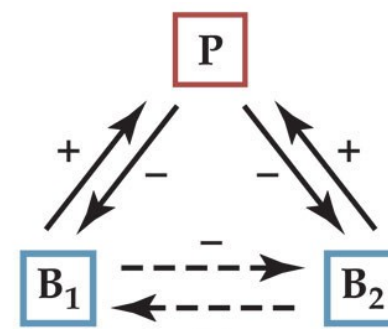
Figure 10.13 Modelos de 7 tipos de efeitos indiretos



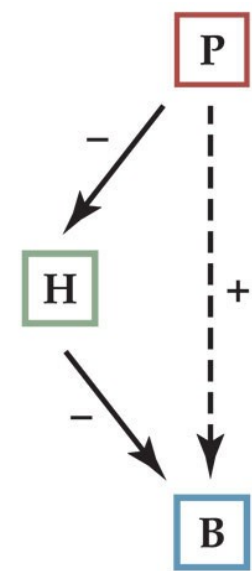
Keystone predation



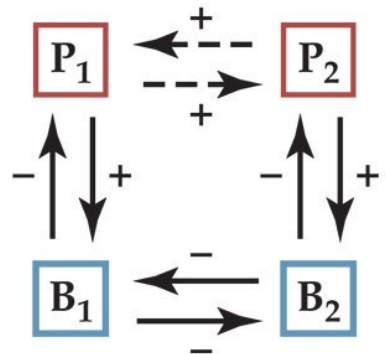
Exploitation competition



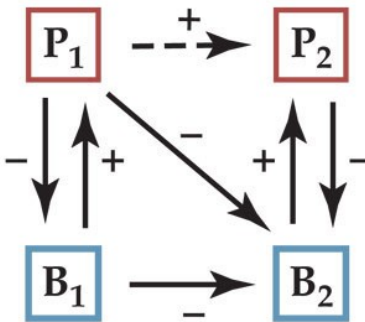
Apparent competition



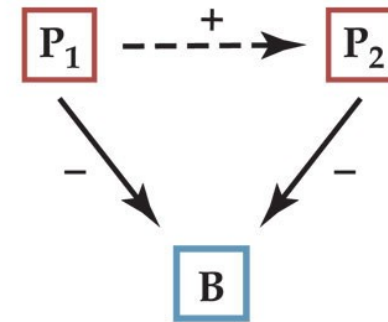
Trophic cascade



Indirect mutualism



Indirect commensalism



Habitat facilitation

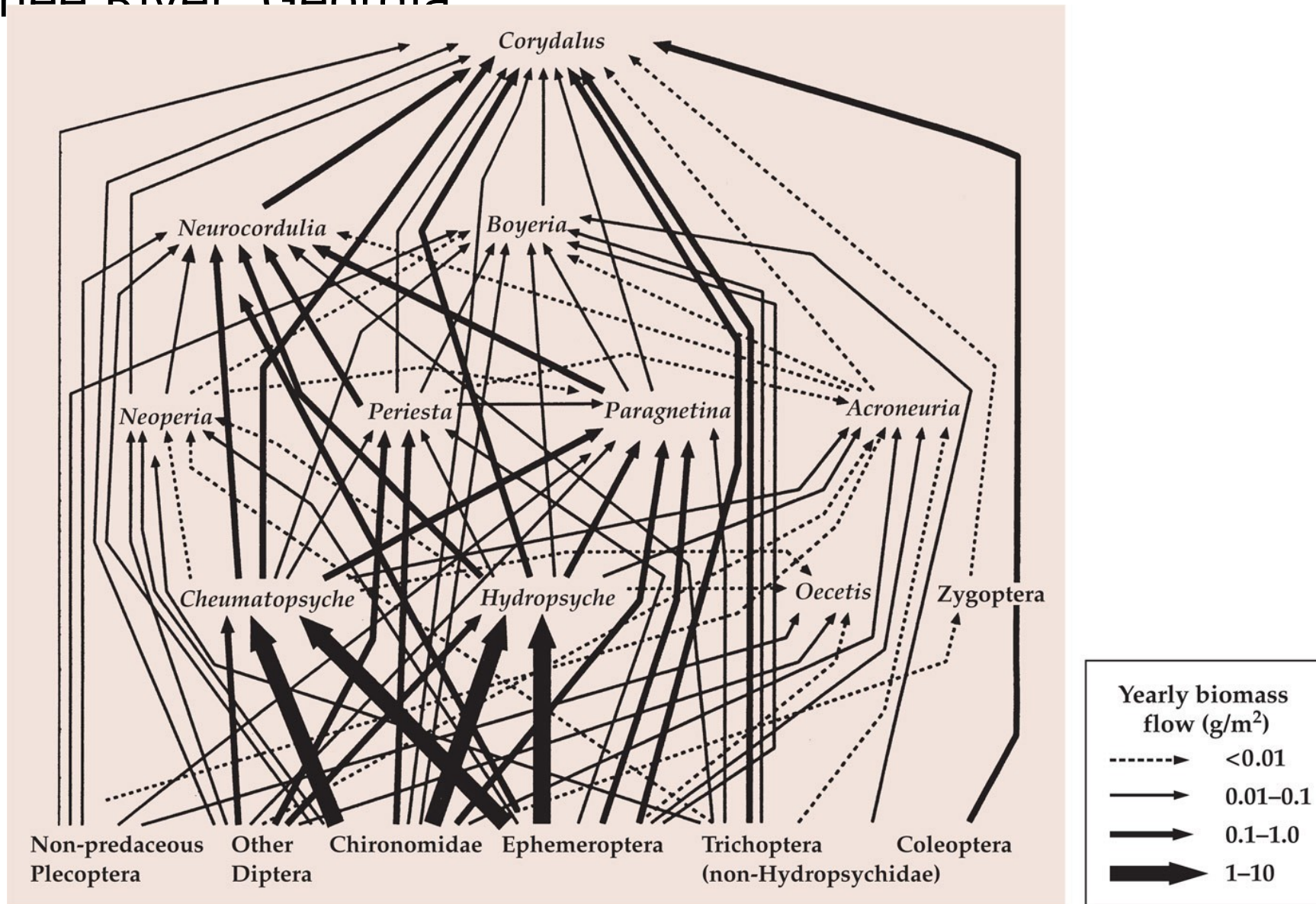
Efeitos indiretos em redes ecológicas

- Definição: uma espécie afeta uma outra espécie por meio de uma mudança numa terceira espécie
- Podem ser mediados por atributos/fenótipos (trait-mediated) ou por densidade (density-mediated)
 - Fenótipo = alteração no comportamento
- Relativamente comum em redes
- Efeitos diretos e indiretos têm magnitudes similares, ao menos em comunidades de entremarés
- Podem gerar resultados contraintuitivos

Redes de fluxo de energia

- Mede a quantidade de energia (em termos de biomassa) se movendo entre espécies numa rede trófica
- Podem ser preditor ruim do *impacto* que uma espécie em particular ou grupo de espécies podem ter numa rede trófica

Figure 10.4 Rede de fluxo de energia para os os maiores invertebrados predadores vivendo em restos de madeira no Ogeechee River, Georgia

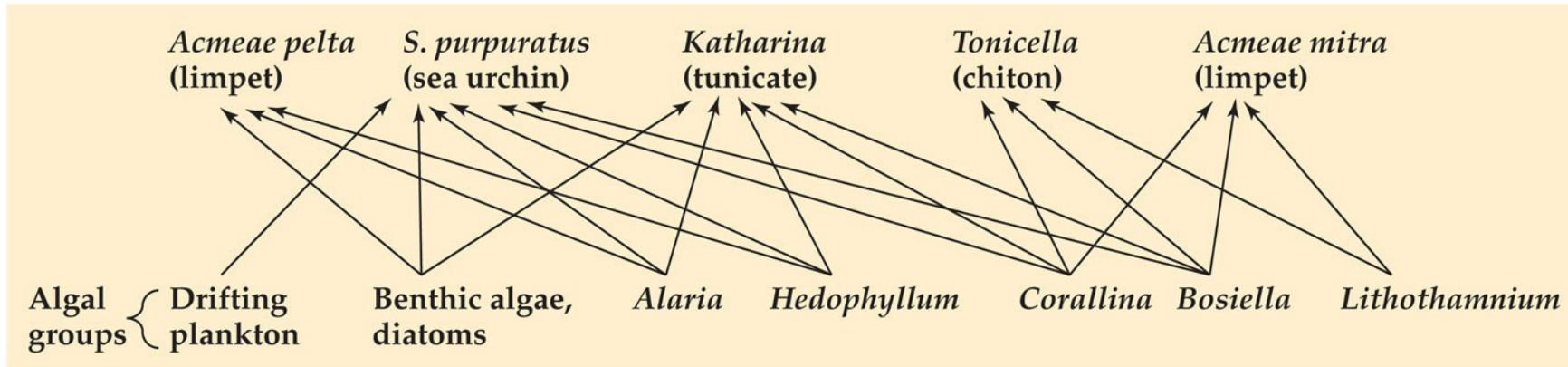


Redes funcionais (ou de interação)

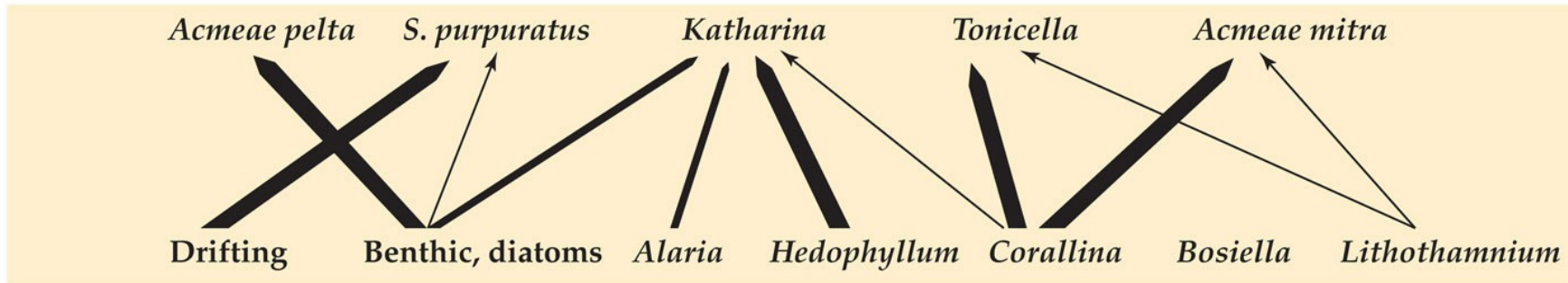
- Demonstra a **Força de interação** entre espécies numa comunidade, reconhecendo que nem todas as interações e espécies são igualmente importantes
- Experimentos de remoção de espécies e analisando as respostas das espécies restantes
- Paine (1992): poucas interações fortes inseridas numa maioria com efeitos negligenciáveis
- No entanto, interações fracas podem ser uma poderosa força estabilizadora em redes tróficas

Figure 10.3 Três abordagens diferentes para construir teias tróficas

(A)



(B)



(C)

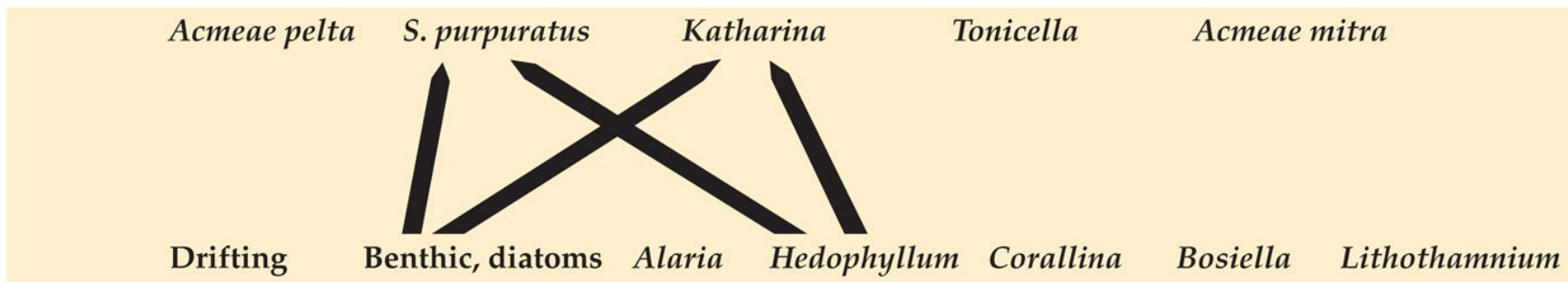
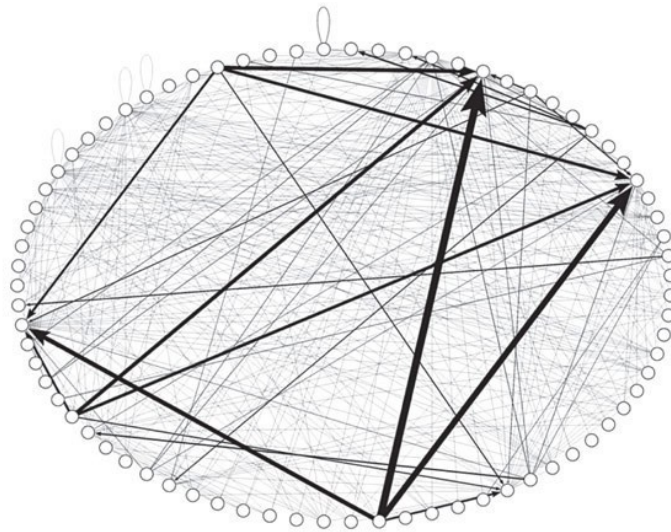
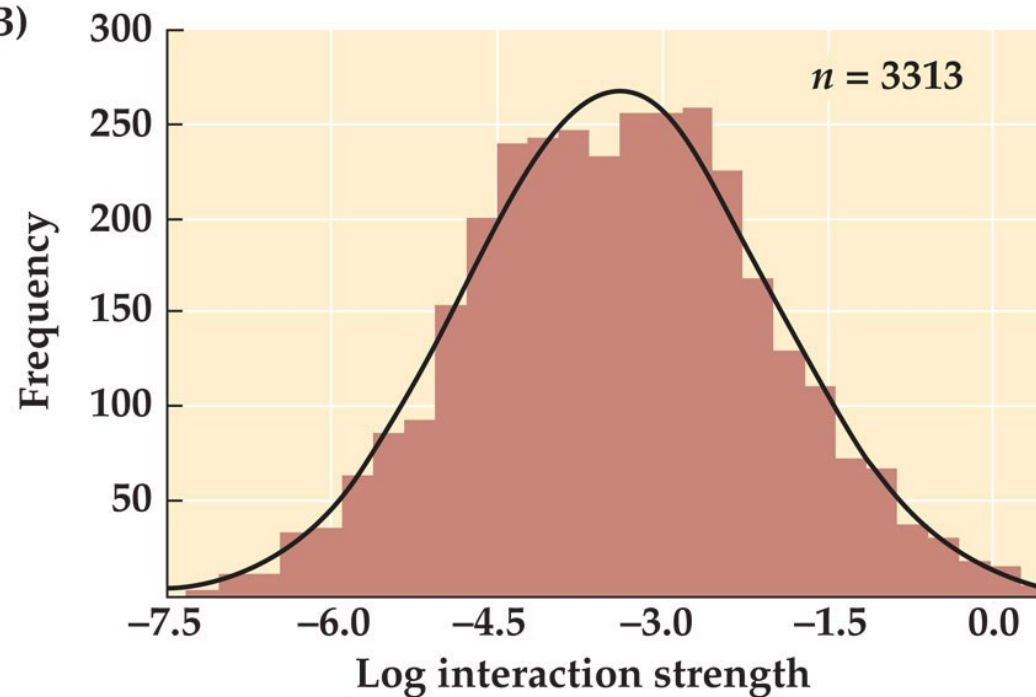


Figure 10.6 Variação na força de interação numa rede trófica real

(A)

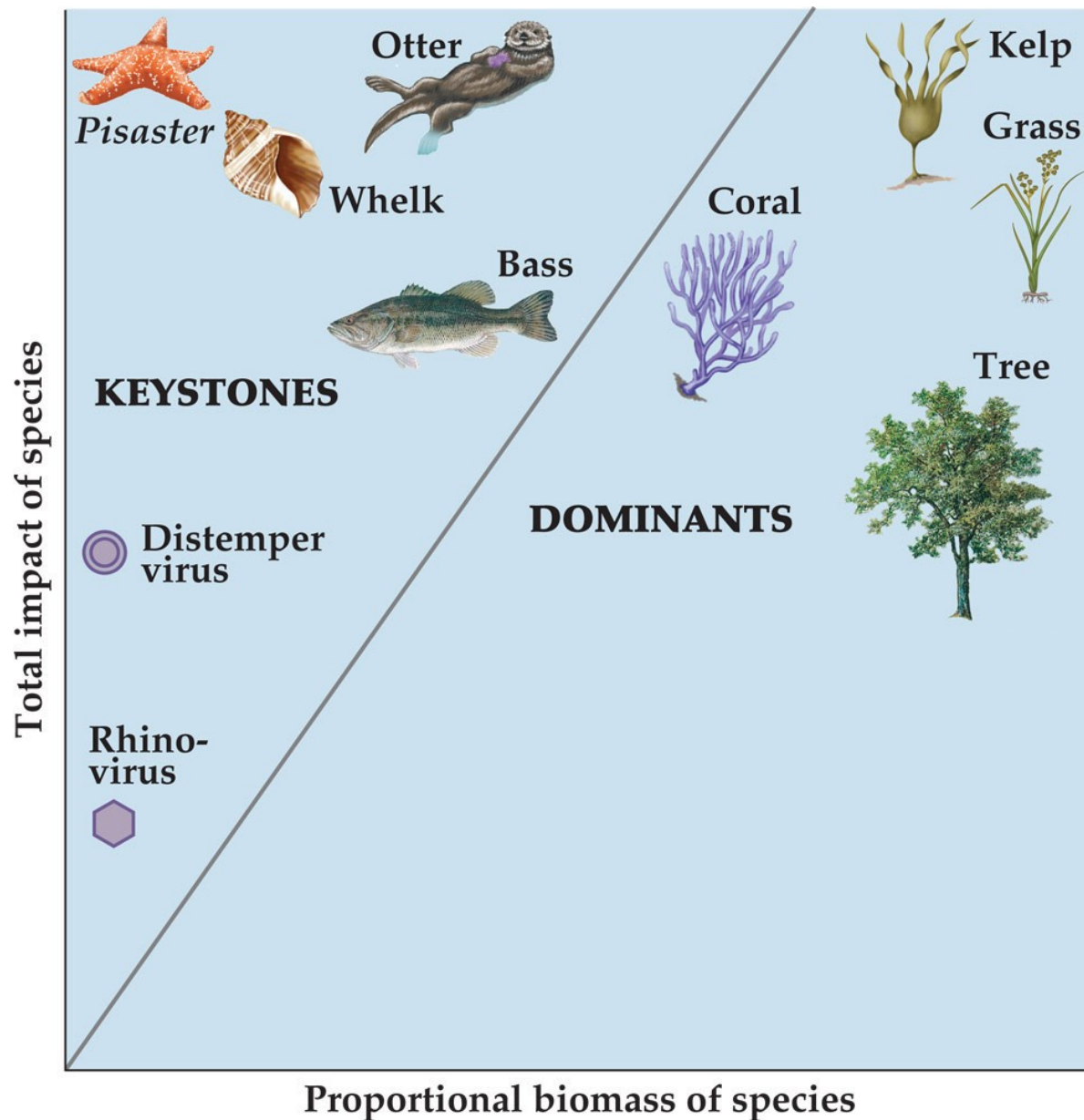


(B)



Food Webs

Kevin S. McCann



Poucas interações fortes são consistentes com a existência de *espécies chave*

Challenges in the Quest for Keystones

Identifying keystone species is difficult — but essential to understanding how loss of species will affect ecosystems

Mary E. Power, David Tilman, James A. Estes, Bruce A. Menge, William J. Bond, L. Scott Mills, Gretchen Daily, Juan Carlos Castilla, Jane Lubchenco, and Robert T. Paine



Starfish may seem
like unlikely predators,



5:10 / 19:28



Some Animals Are More Equal than Others: Keystone Species and Trophic Cascades

Watch Later Playlist

Diogo Borges Provete - 9 / 25

<https://youtu.be/hRGg5it5FMI>

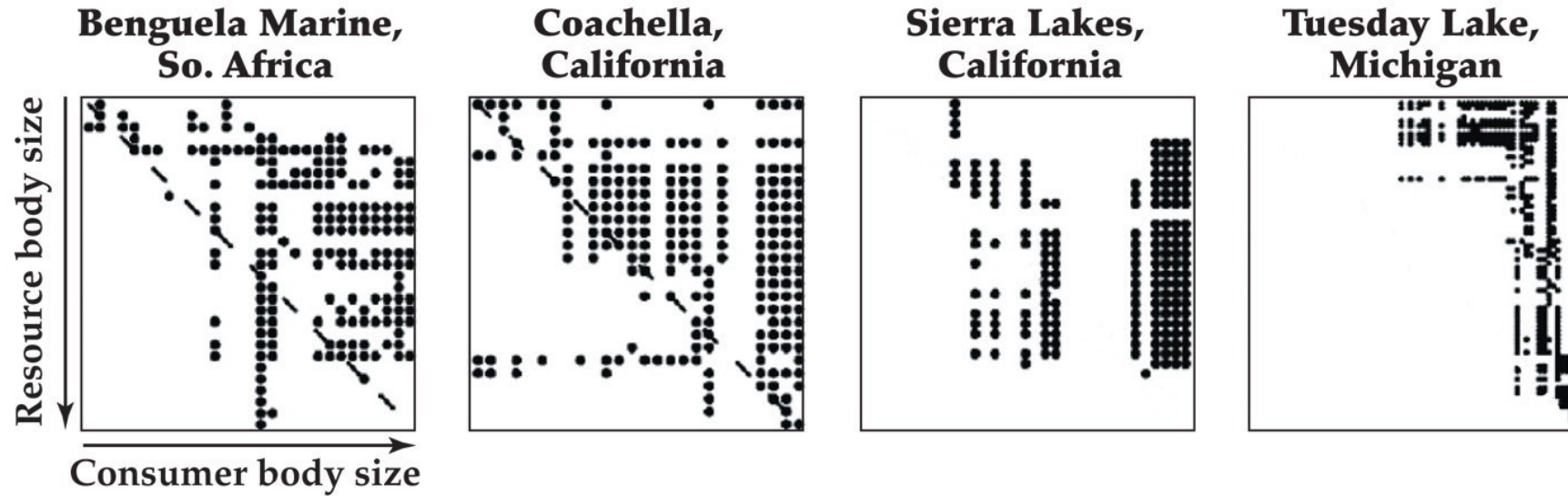
...mas quais os padrões gerais que
emergem de teias tróficas

Atributos são a chave!

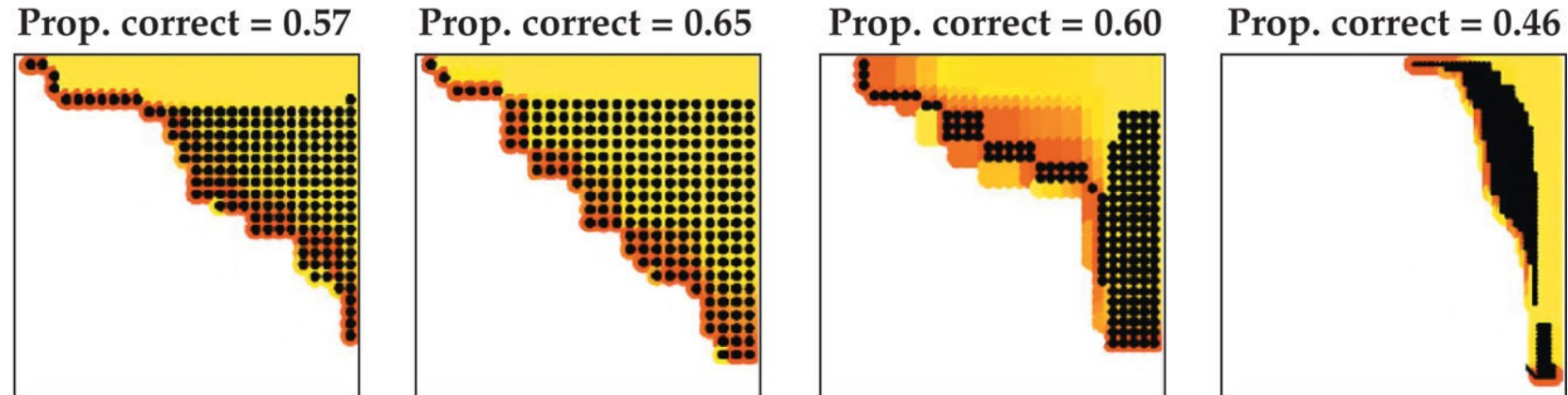
- Tamanho do corpo é um ótimo atributo para caracterizar força de interação
- Atributos de influenciam interação entre espécies escalonam com o tamanho do corpo (e.g., taxa metabólica, velocidade de movimento, taxa de encontro, tempo de manuseio)
- Modelos que incorporam tamanho da presa, conteúdo energético da presa, e tempo de manuseio predizem o número de ligações tróficas em redes

Figure 10.9 Relações de forrageamento baseadas no tamanho predizem a estrutura da teia trófica

(A) Actual



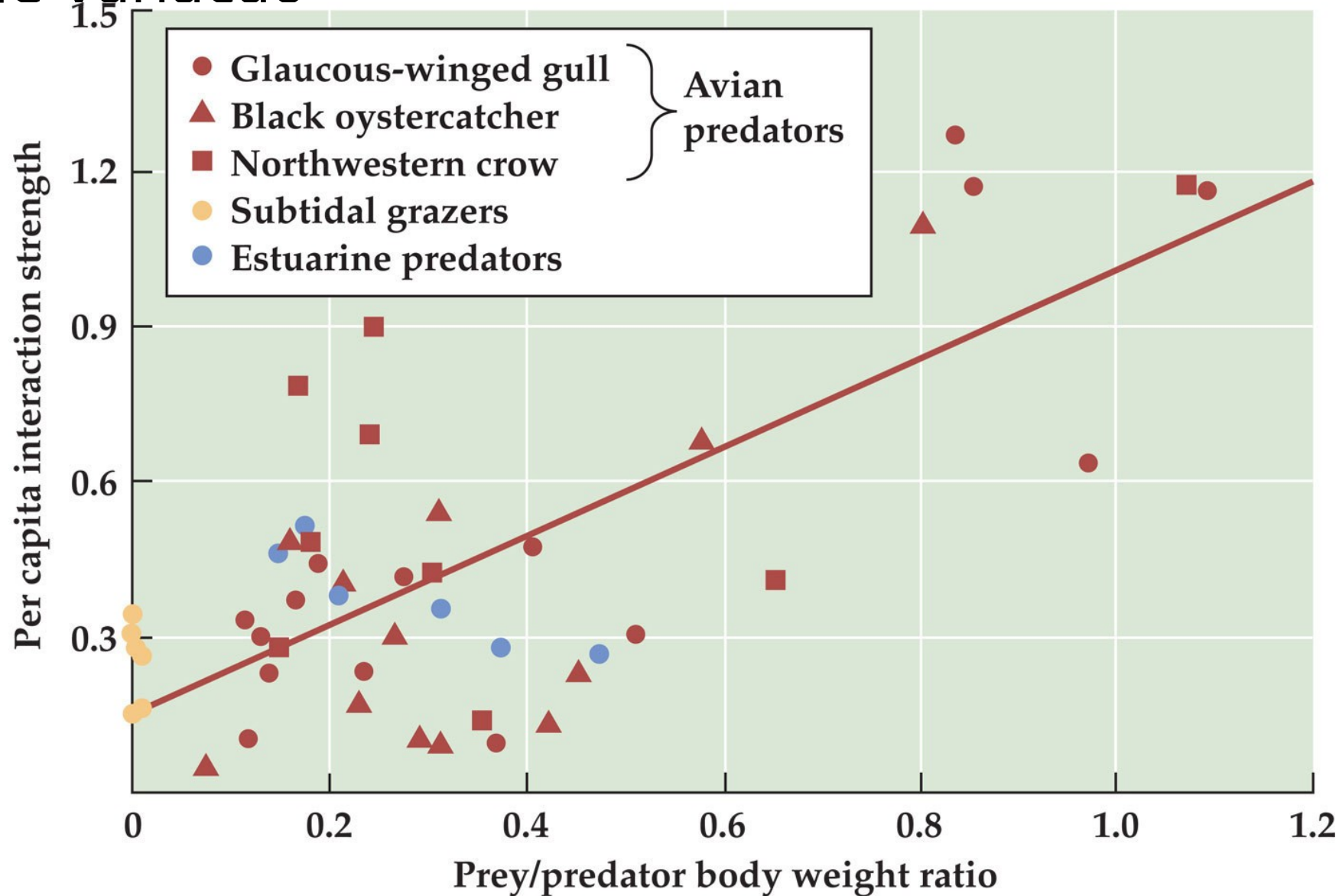
(B) Predicted



Atributos são a chave!

- Tamanho do corpo é um ótimo atributo para caracterizar força de interação
- Atributos de influenciam interação entre espécies escalonam com o tamanho do corpo (e.g., taxa metabólica, velocidade de movimento, taxa de encontro, tempo de manuseio)
- Modelos que incorporam tamanho da presa, conteúdo energético da presa, e tempo de manuseio predizem o número de ligações tróficas em redes
- Tamanho de corpo de presas e predadores = força de interação?

Figure 10.10 Força de interação per capita aumenta com a razão de massa corpórea predador-presa...mas há grande variação

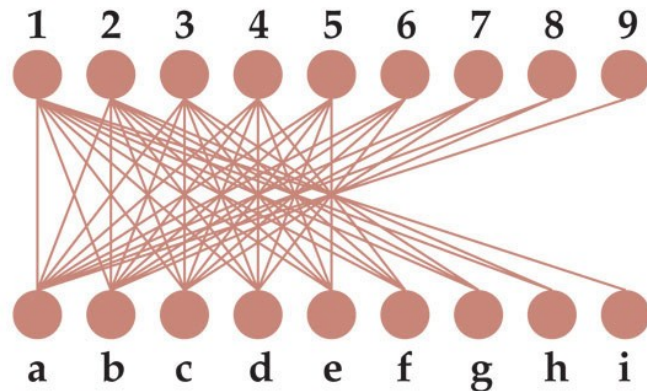
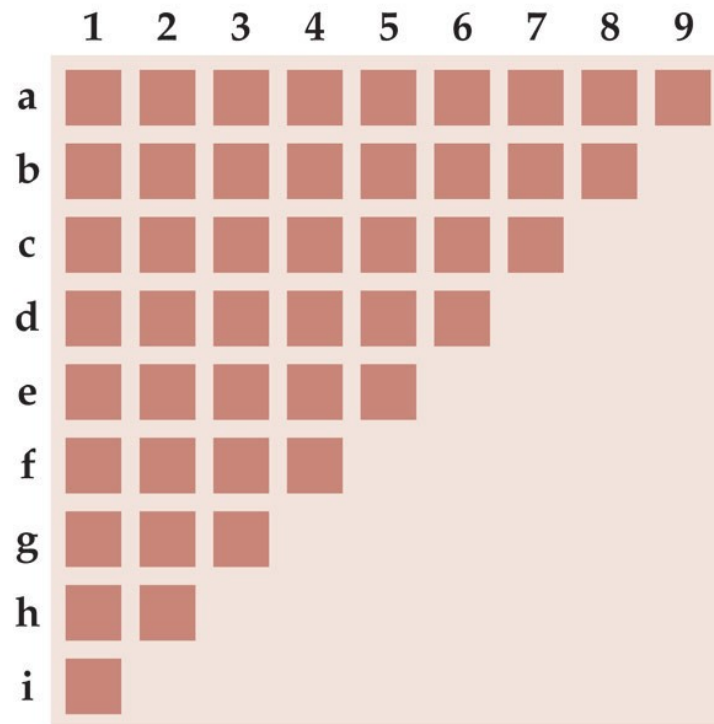


Redes bipartidas

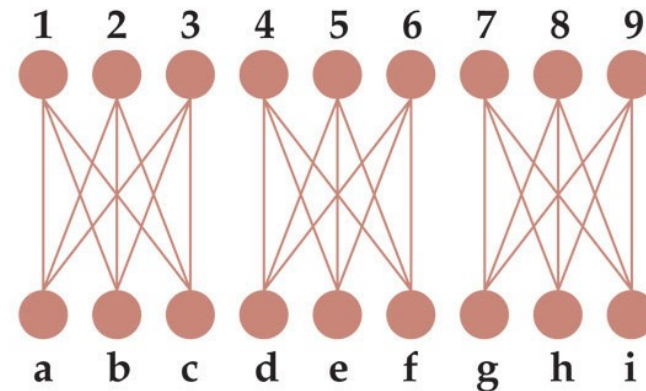
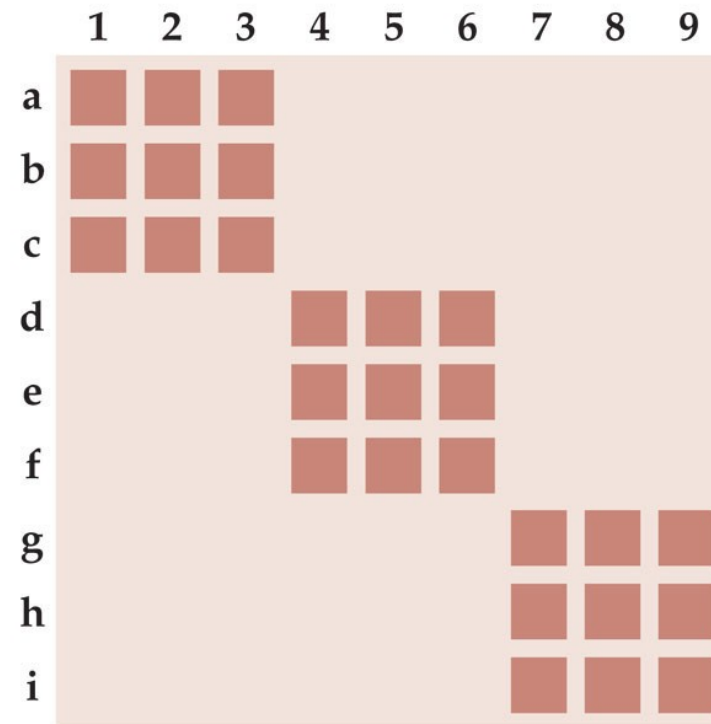
- Usada para descrever relações mutualísticas, parasitas-hospedeiro, parasitóide-hospedeiro
 - Polinização, dispersão de sementes
- Principais características
 - Alta conectância (Nº observado de ligações/possíveis)
 - Alto aninhamento (especialistas interagem com generalistas, subconjunto)
 - Baixa modularidade (grupos de espécies que interagem entre si, mas não com outras)

Figure 10.16 Representação esquemática de uma rede bipartida aninhada (A) e modular (B)

(A) Nested network



(B) Modular network



Padrões em redes bipartidas

- Aninhamento é comum em redes de polinização, dispersão de sementes, e organismos limpadores
- **Estabilidade aumenta** à medida que aumenta o **aninhamento** e conectância em redes **mutualísticas**, enquanto **modularidade** aumentou estabilidade em **redes tróficas**
- Cada tipo de rede desenvolve estrutura de maneira a promover estabilidade

ARTICLE

Received 16 Sep 2015 | Accepted 23 May 2016 | Published 23 Jun 2016

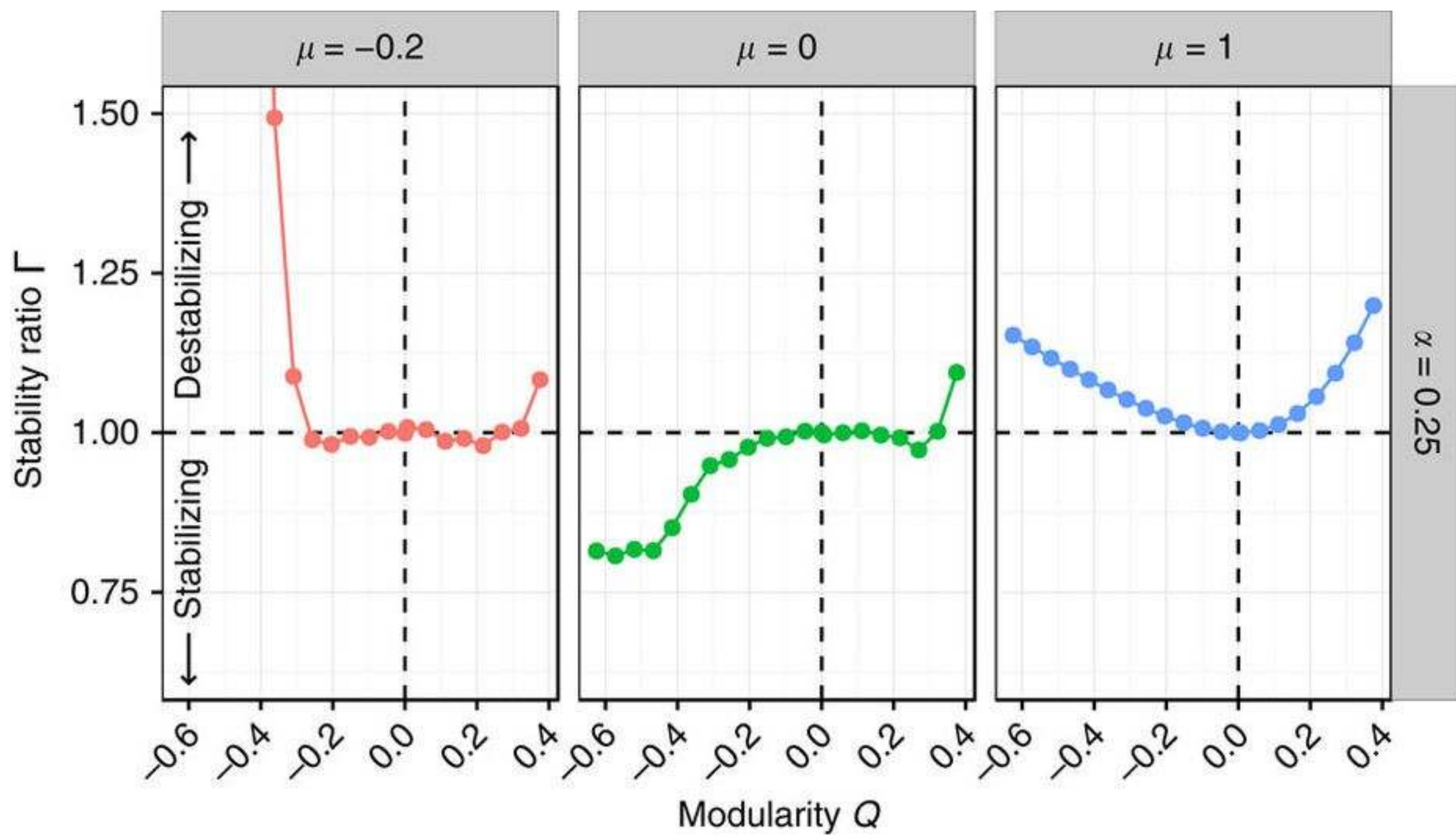
DOI: 10.1038/ncomms12031

OPEN

Modularity and stability in ecological communities

Jacopo Grilli¹, Tim Rogers² & Stefano Allesina^{1,3,4}

Modularidade pode estabilizar moderadamente redes ecológicas em relação a alguns parâmetros, enquanto anti-modularidade pode grandemente desestabilizá-las



Complexidade vs. Estabilidade

O que é estabilidade?

Complexidade vs. Estabilidade

O que é estabilidade?

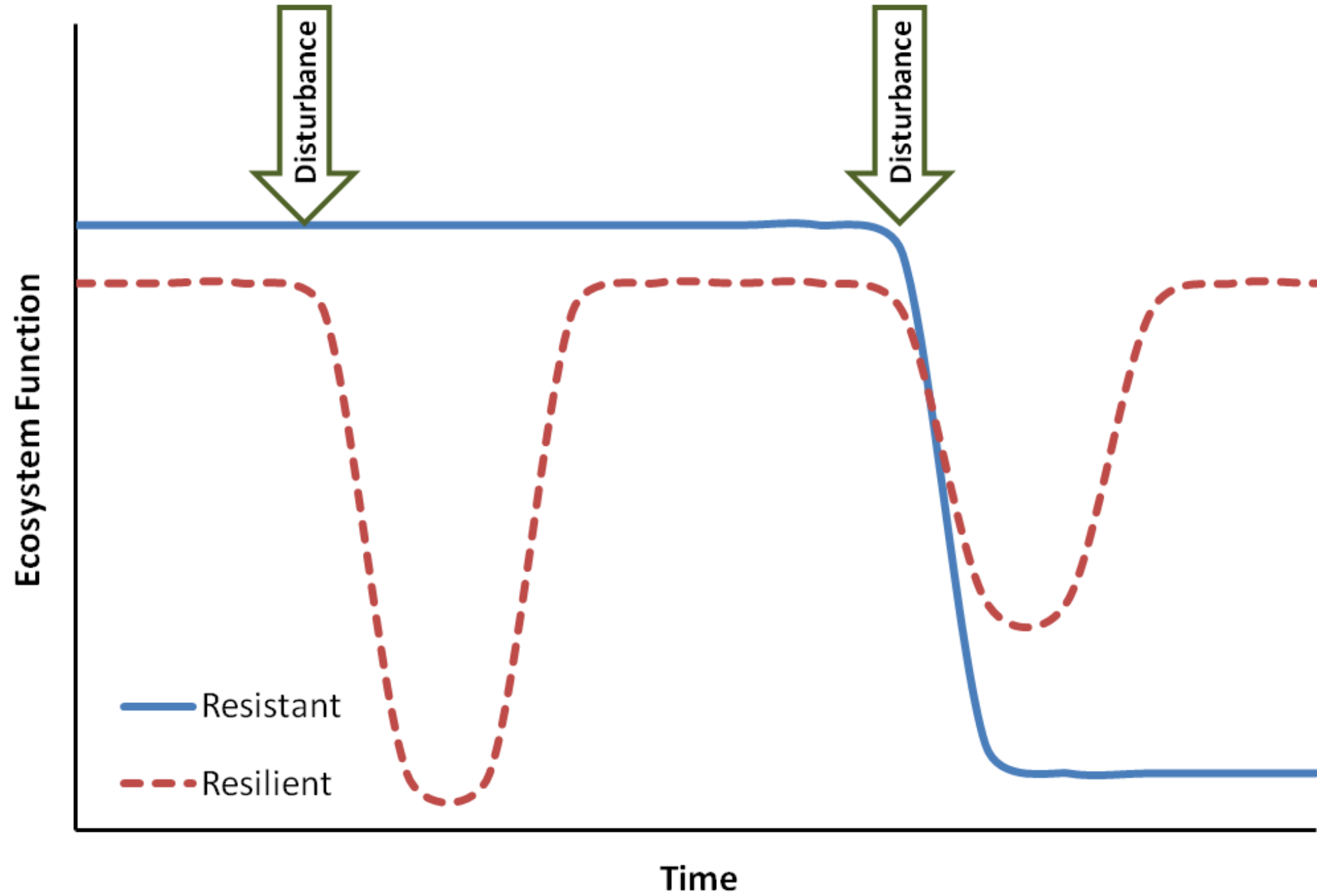
Resiliência

Resistência

MUSE



**THE
RESISTANCE**



Conceitos

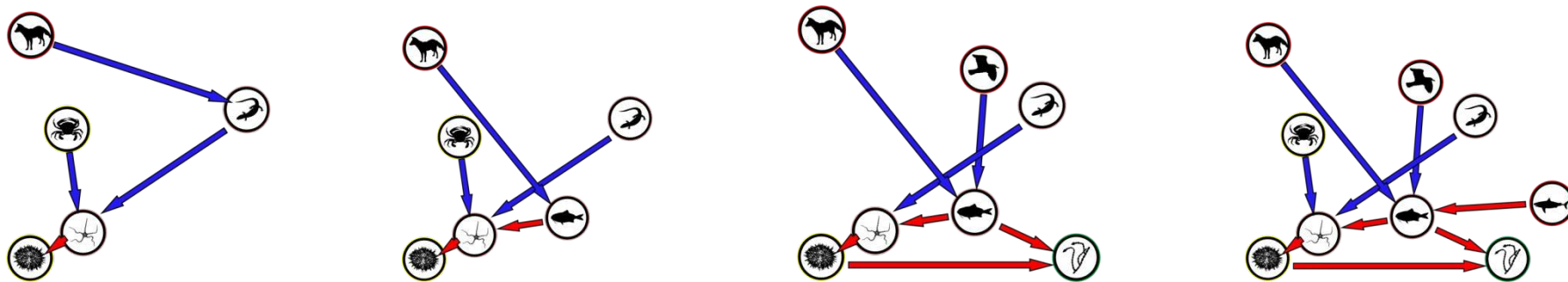
- **Estabilidade:** capacidade de uma comunidade em *manter* uma estrutura específica após um distúrbio/perturbação
 - **Resistência:** o *quanto* uma comunidade muda quando é afetada por algum distúrbio
 - **Resiliência:** o *tempo* que uma comunidade leva para retornar ao estado original depois de perturbada

Mas que diabos isso tem a ver com
redes ecológicas?

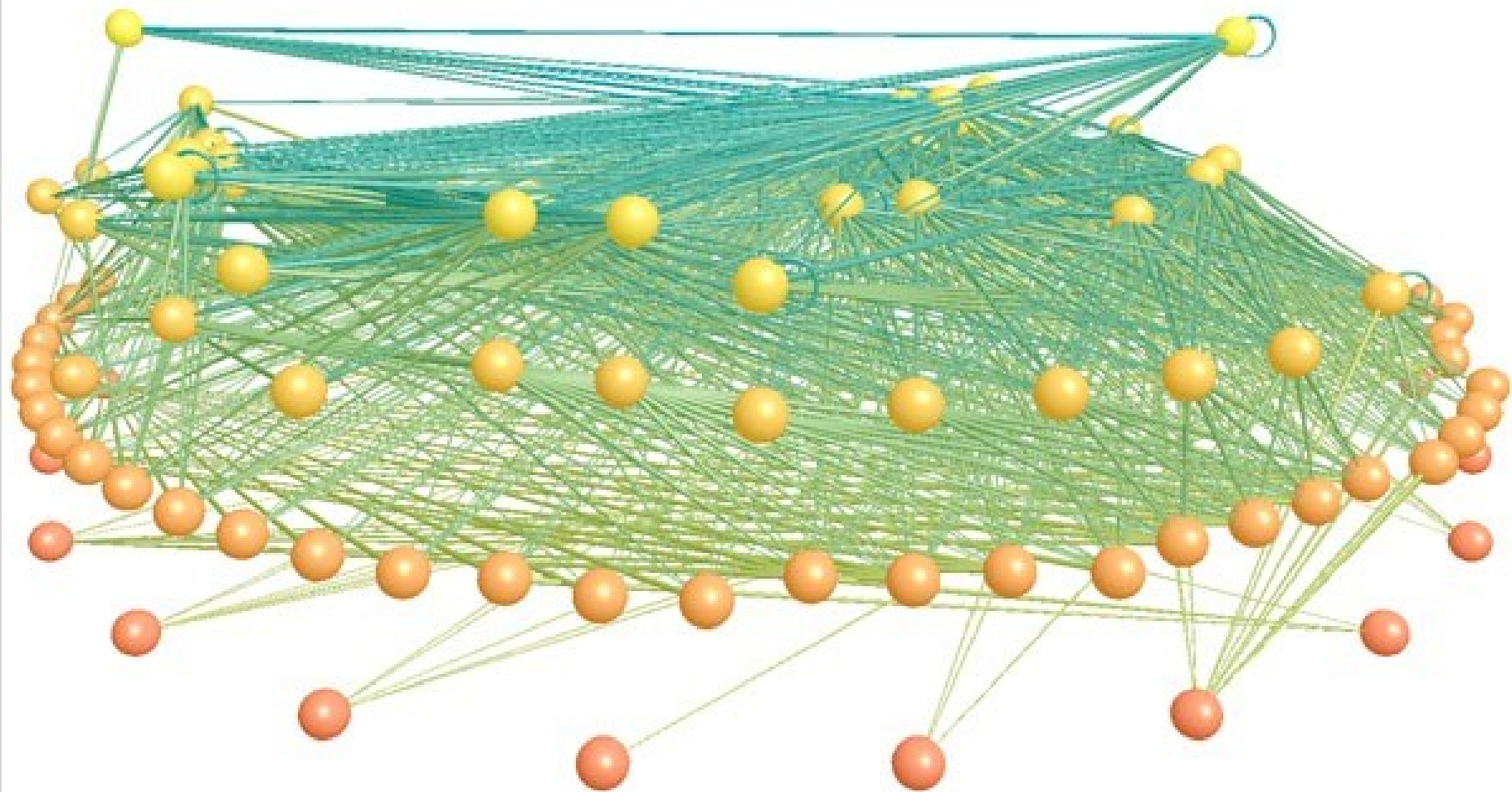
Relação complexidade-estabilidade

Quanto maior número de rotas de energia passando através da comunidade, menos provavelmente as densidades das espécies constituintes **mudariam em resposta** a um aumento ou diminuição **anormais** na densidade de uma dessas espécies (MacArthur 1955).

Complexidade (aumento da conectância)



REDES ECOLÓGICAS COMPLEXAS



SUA LINDA!

Table 1. Ecological network metric summary and classification.

Sub.discipline	Level	Metric	Concept	References
General	W	Density	The proportion of possible edges that are actually associated with nodes; called Connectance in Food-web ecology	
General	N	Centrality	Multiple ways to characterize the relative importance of nodes	Wasserman and Faust (1994)
General	N	Degree	Number of edges connected to a given node, which is a type of local centrality	
General	N	Eigenvector centrality	Global centrality metric based on number of walks that travel through a node	
General	W	Centrality distribution	Shape of the frequency distribution of edges among nodes	Barabási and Albert (1999); Dunne et al. (2002)
General	W	Centralization	The concentration (vs. evenness) of centrality among the nodes	Freeman (1979)
General	W	Graph diameter	The longest path between any two nodes in a graph	Barabási et al. (2000); Urban and Keitt (2001)
General	W	Modularity	Degree to which edges are distributed within rather than between distinct sets of nodes	Newman (2010)
General	G	Motifs	Small sets of nodes with similar distributions of edges	Milo et al. (2002)
General	W	Link density	Average number of edges per node	Martinez (1992)
Community	N	Temperature	Measures the nestedness of a bipartite network	Ulrich and Gotelli (2007)
Community	W	Co-occurrence	Degree of overlapping spatial or temporal distributions of species relative to a null model	Gotelli (2000)
Community	N	Indicator species	The degree to which the abundance of a taxonomic group responds to an environmental gradient	
Community	W	Nestedness	The degree to which interactions can be arranged into subsets of the larger community	
Community	W	Evenness	Deviation of the distribution of observed abundances relative to an even distribution among taxonomic groups in a community	
Community	W	Diversity	Distribution of abundances among taxonomic groups in an observed community	
Community	W	Richness	The number of taxonomic groups in a community	
Community	W	Stability	The change in the abundances of taxonomic groups across a set of observations	

Table 1. Ecological network metric summary and classification.

Sub.discipline	Level	Metric	Concept	References
General	W	Density	The proportion of possible edges that are actually associated with nodes; called Connectance in Food-web ecology	
General	N	Centrality	Multiple ways to characterize the relative importance of nodes	Wasserman and Faust (1994)
General	N	Degree	Number of edges connected to a given node, which is a type of local centrality	
General	N	Eigenvector centrality	Global centrality metric based on number of walks that travel through a node	Bonacich (1987)
General	W	Centrality distribution	Shape of the frequency distribution of edges among nodes	Barabási and Albert (1999); Dunne et al. (2002)
General	W	Centralization	The concentration (vs. evenness) of centrality among the nodes	Freeman (1979)
General	W	Graph diameter	The longest path between any two nodes in a graph	Barabási et al. (2000); Urban and Keitt (2001)
General	W	Modularity	Degree to which edges are distributed within rather than between distinct sets of nodes	Newman (2010)
General	G	Motifs	Small sets of nodes with similar distributions of edges	Milo et al. (2002)
General	W	Link density	Average number of edges per node	Martinez (1992)
Community	N	Temperature	Measures the nestedness of a bipartite network	Ulrich and Gotelli (2007)
Community	W	Co-occurrence	Degree of overlapping spatial or temporal distributions of species relative to a null model	Gotelli (2000)
Community	N	Indicator species	The degree to which the abundance of a taxonomic group responds to an environmental gradient	
Community	W	Nestedness	The degree to which interactions can be arranged into subsets of the larger community	
Community	W	Evenness	Deviation of the distribution of observed abundances relative to an even distribution among taxonomic groups in a community	
Community	W	Diversity	Distribution of abundances among taxonomic groups in an observed community	
Community	W	Richness	The number of taxonomic groups in a community	
Community	W	Stability	The change in the abundances of taxonomic groups across a set of observations	

Food-web	N	Removal importance	observations The degree to which removal of a compartment or species produces subsequent removals in the ecosystem	Borrvall et al. (2000); Dunne et al. (2002); Eklöf and Ebenman (2006); Solé and Montoya (2001)
General	N	Connectance	Proportion of realized out of possible edges	Pimm (1982); Vermaat et al. (2009)
Food-web	G	Food-chain length	The number of feeding relationships among a set of compartments in a food-web	Post et al. (2000); Ulanowicz et al. (2014)
Ecosystem	W	Finn cycling index	Degree to which matter or energy passes through the same set of compartments	Finn (1980)

(Table 1. *Continued*)

Sub.discipline	Level	Metric	Concept	References
Ecosystem	G	Environ	The sub-network of the probability of movement of energy or matter among compartments generated by a single unit of input (output) into a selected node	Patten (1978); Patten and Auble (1981)
Ecosystem	N	Throughflow	Amount of energy or matter passing into or out of a node	Finn (1976)
Ecosystem	N	Throughflow centrality	The proportion of energy or matter that passes through a given compartment in an ecosystem	Borrett (2013)
General	G	Chain length	Number of edges between two nodes in a group	
Food-web	G	Average path length	The average number of times a unit of matter or energy travels from one compartment to another before exiting the ecosystem	Finn (1976)
Ecosystem	W	Pathway proliferation	Rate of increase in the number of edges between nodes with increasing path length	Borrett et al. (2007)
Ecosystem	W	Ascendency	Measures the average similarity in matter or energy flows among compartments in an ecosystem	Ulanowicz (1986)
Food-web	N	Trophic level	Ordinal classification of a compartment or taxonomic group based on the relative position in the ecosystem	Allesina and Pascual (2009); Fath (2004); Williams et al. (2002)

Notes: Level indicates the hierarchy of the metric (W, Whole network; G, Group or sub-network; N, Node). The Sub-disciplines include “General” network theory, “Community” ecology, “Food-web” and “Ecosystem” ecology. Also available at <https://figshare.com/s/1bf1a7e0a6ee3ac97a4b>.



APPLICATION

enaR: An R package for Ecosystem Network Analysis

Stuart R. Borrett^{1,2*} and Matthew K. Lau^{3†}

Histórico de idéias

- Elton (1927) => abundância de espécies flutuava mais em comunidades simples e estas eram mais suscetíveis à invasões.
- MacArthur (1955) => comunidades mais complexas (com mais interações) eram mais estáveis em relação à flutuações ambientais e perda de espécies
- Sir R. May (1973) => comunidades mais diversas são menos estáveis
 - Força de interação era aleatória no modelo!
- McCann (2000) => diferença na força de interação na comunidade estabiliza redes (tampona oscilações populacionais)

Complexidade vs. estabilidade

insight review articles NATURE | VOL 405 | 11 MAY 2000 | www.nature.com

The diversity–stability debate

Kevin Shear McCann

1) Diversidade geralmente aumenta a estabilidade;

Complexidade vs. estabilidade

insight review articles NATURE | VOL 405 | 11 MAY 2000 | www.nature.com

The diversity–stability debate

Kevin Shear McCann

- 1) Diversidade geralmente aumenta a estabilidade;
- 2) Esta relação depende de espécies-chave com maior contribuição para os valores de conectância;

Table 1 Definitions of stability

Term	Definition
<i>Definitions of dynamic stability</i>	
Equilibrium stability	A discrete measure that considers a system stable if it returns to its equilibrium after a small perturbation away from the equilibrium. A stable system, therefore, has no variability in the absence of perturbations.
General stability	A measure which assumes that stability increases as the lower limit of population density moves further away from zero. Under non-equilibrium dynamics, such limits to population dynamics generally imply a decrease in population variance (see variability definition below).
Variability	The variance in population densities over time, usually measured as the coefficient in variation. Common in experimental tests of stability.
<i>Definitions of resilience and resistance stability</i>	
Equilibrium resilience	A measure of stability that assumes system stability increases as time required to return to equilibrium decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium state.
General resilience	A measure of stability that assumes system stability increases as return time to the equilibrium/non-equilibrium solution decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium/non-equilibrium state.
Resistance	A measure of the degree to which a variable changes after a perturbation. Frequently used as a discrete measure that assesses a community's ability to resist invasion (that is, if an invader fails, the community resists invasion).

Histórico de idéias

- Diversidade pode promover estabilidade se o número de interações tróficas fracas aumenta com a diversidade
- Modularidade aumenta persistência de teias tróficas por tamponar perturbações de extinções locais de espécies

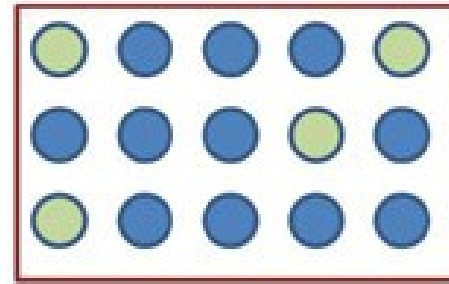
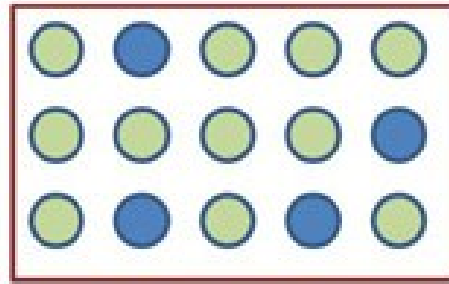
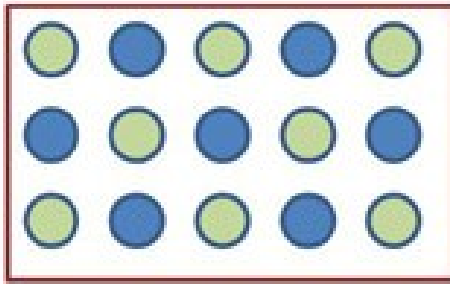
**IDEA AND
PERSPECTIVE**

Biodiversity and ecosystem stability: a synthesis of underlying mechanisms

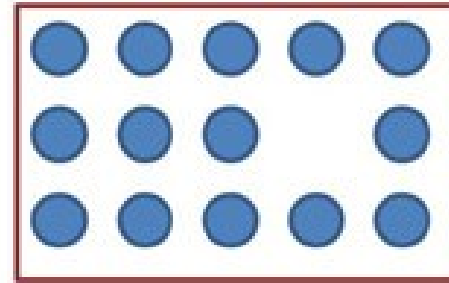
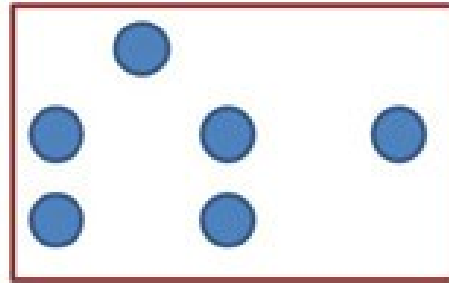
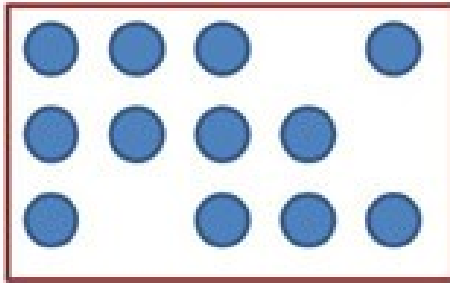
Michel Loreau^{1*} and Claire de
Mazancourt

- 1) Assincronia na resposta de espécies à flutuações ambientais;
- (2) diferenças na velocidade com a qual espécies respondem à perturbações;
- (3) redução da intensidade de competição.

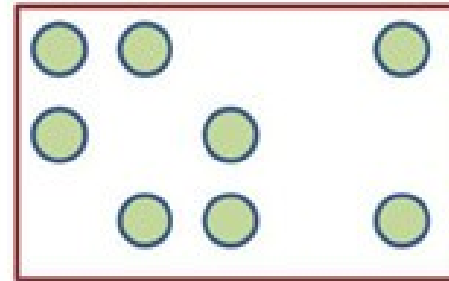
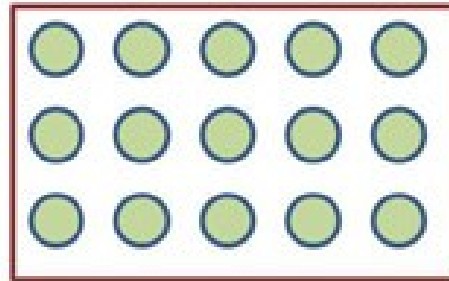
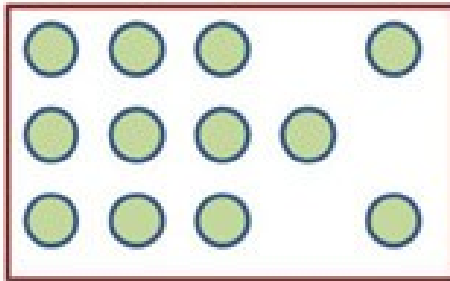
Diverse
community



Community
dominated
by “blue”
species



Community
dominated
by “green”
species

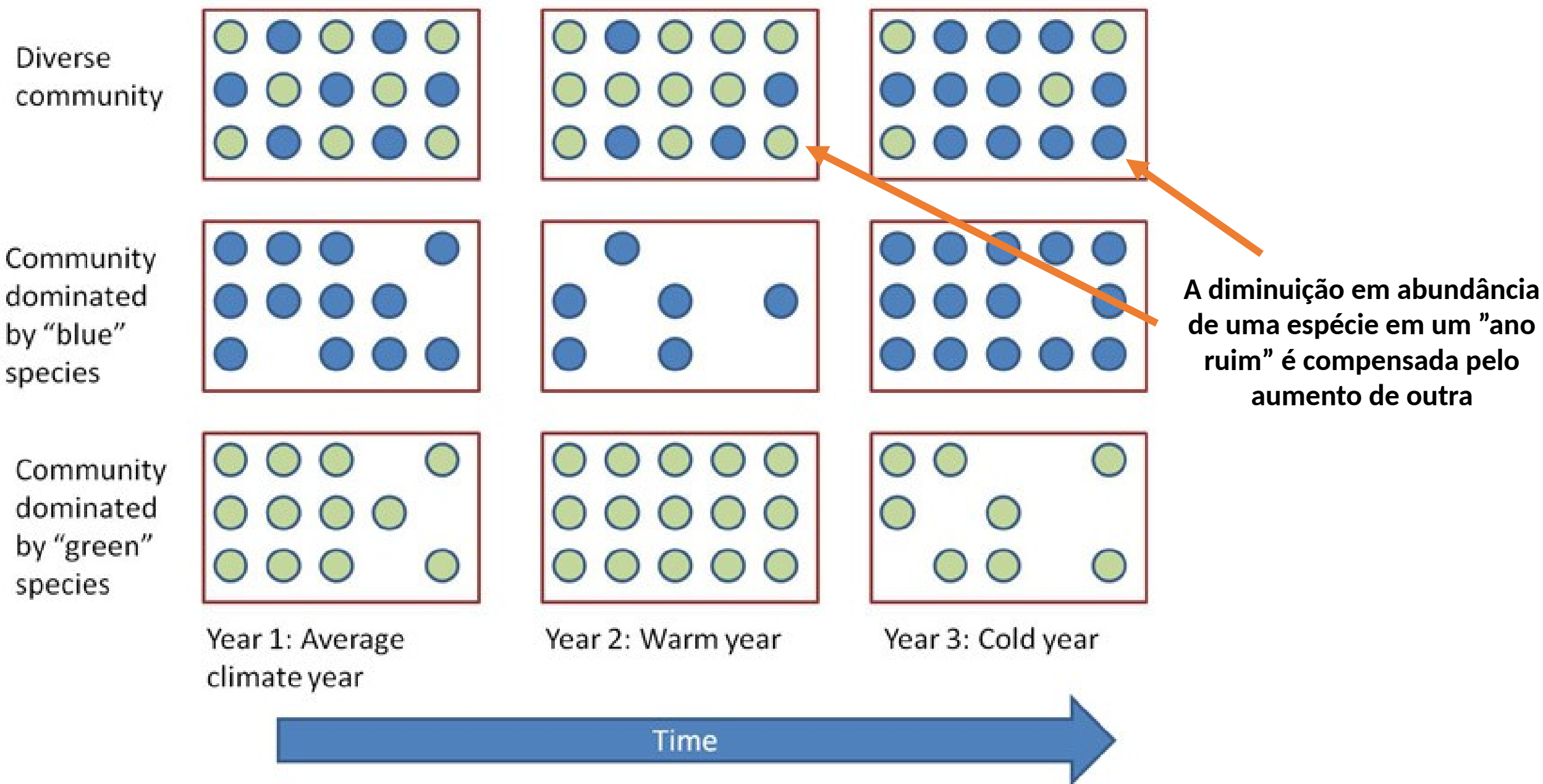


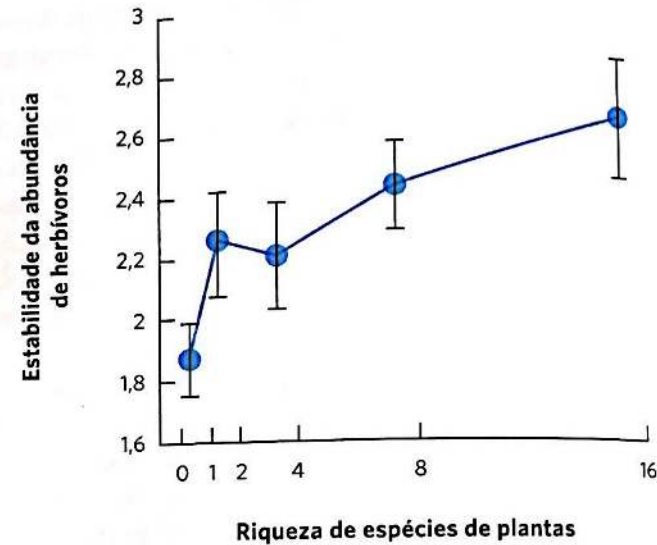
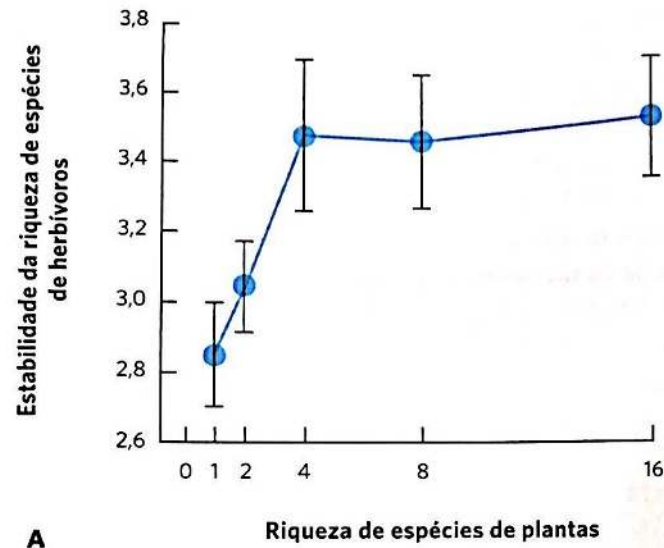
Year 1: Average
climate year

Year 2: Warm year

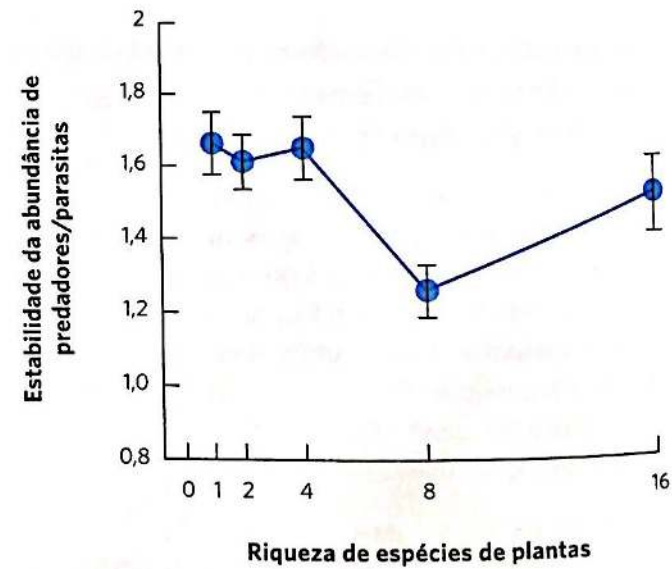
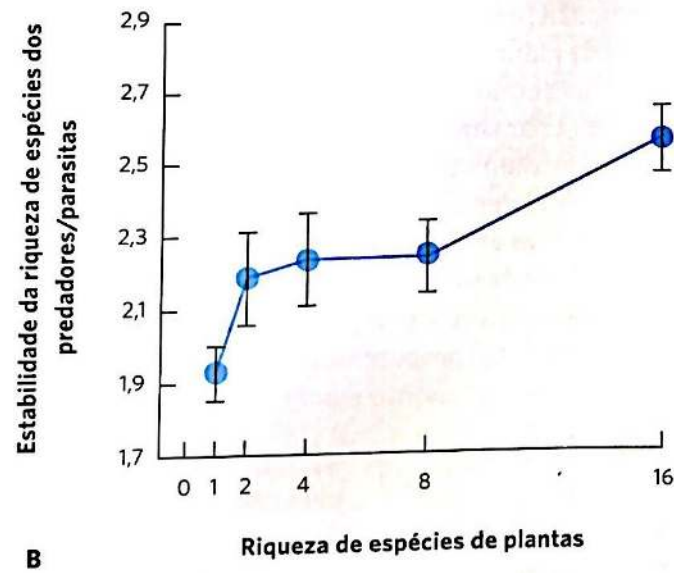
Year 3: Cold year







Comunidades de plantas mais ricas em espécie eram mais estáveis (media como a variação anual na riqueza) e tornavam as comunidades de herbívoros mais estáveis...



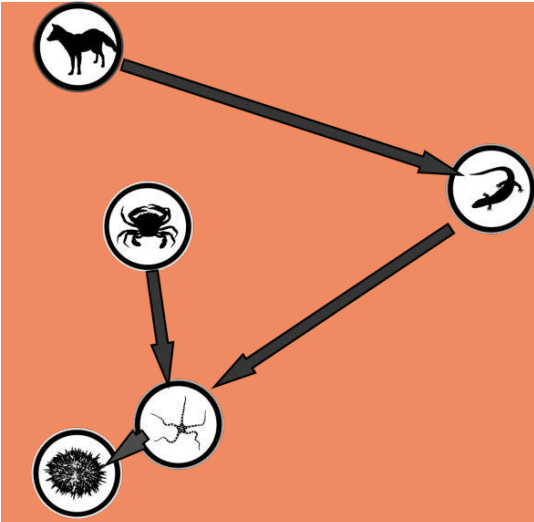
... Mas não houve o mesmo efeito na
abundância de *níveis tróficos*
superiores (predadores)

Comunidades estáveis (=mais ricas)
forneciam alimento de forma consistente
para herbívoros e refúgios contra
predadores

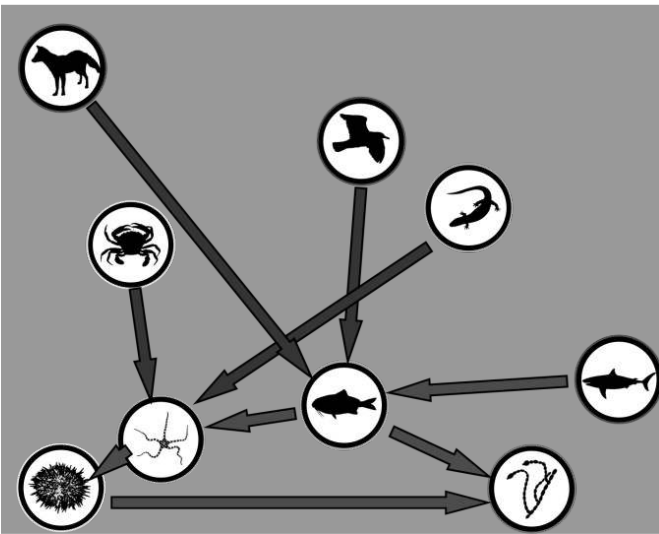


Experimento 120 (LTER) Cedar Creek, Minnesota

Consequências práticas



- Invasão biológica mais provável;
- Mesmo a remoção de uma *única* espécie pode ter consequências drásticas para comunidade.



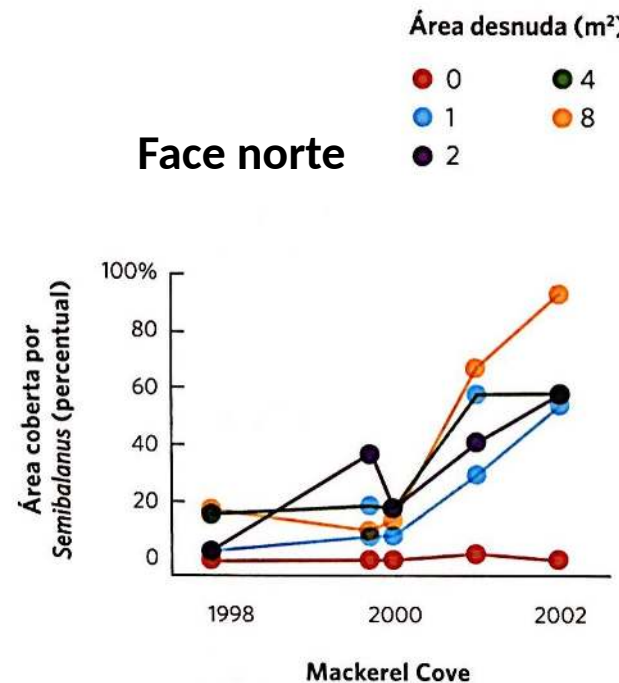
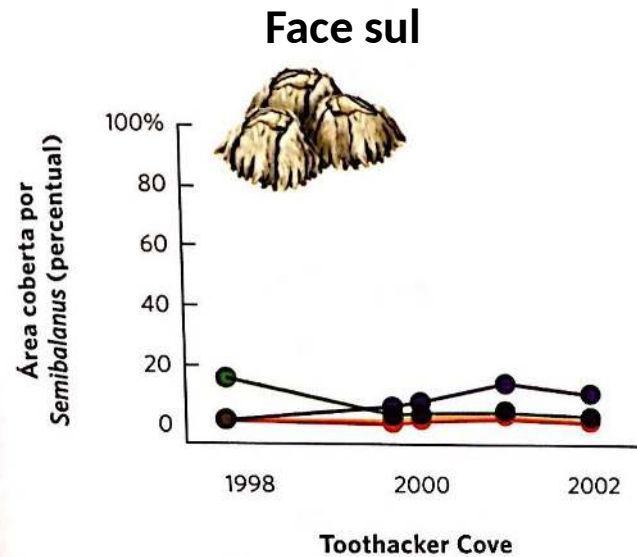
- Maior resistência a perturbações;
- Maior capacidade de recuperação (resiliência) após distúrbios.

Estados estáveis alternativos

Alternate stable states

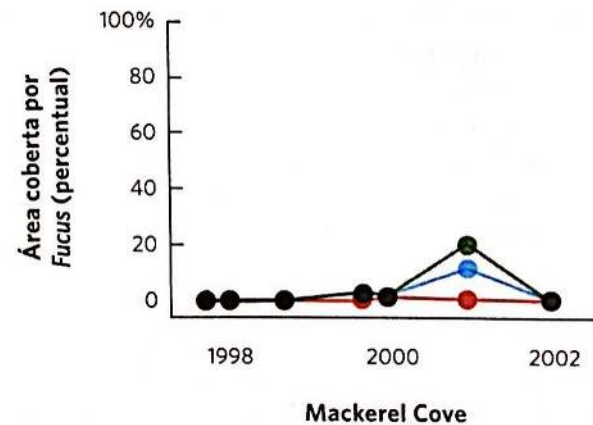
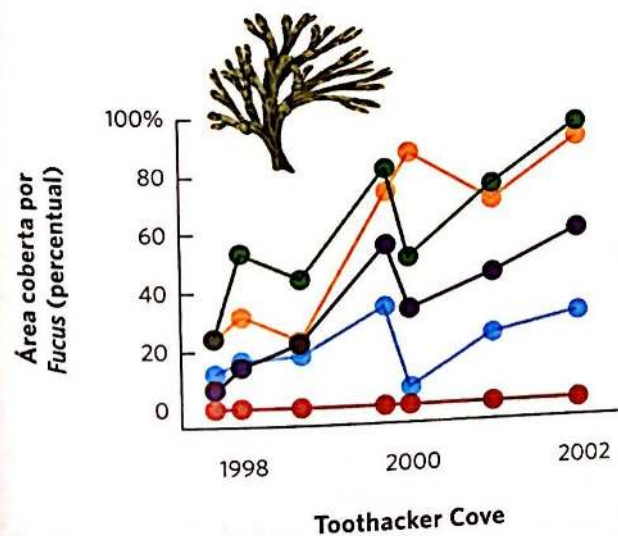
Conceito de estados alternativos

- Uma comunidade pode ser resiliente ou resistente à uma perturbação e retornar ao seu estado original com o tempo...
- ...ou mudar para um outro estado estável alternativo que será substancialmente diferente daquele original e resistente
- Esses estados alternativos podem representar comunidades com composição de espécie totalmente diferente daquele original, tanto sob o ponto de vista taxonômico (riqueza e abundância) quanto funcional (características dessas espécies)
- Precisa de uma grande perturbação, tal como perda de uma espécie chave



Área do costão raspada por gelo experimentalmente

Comunidades eram dominadas por alga-marrom antes do distúrbio



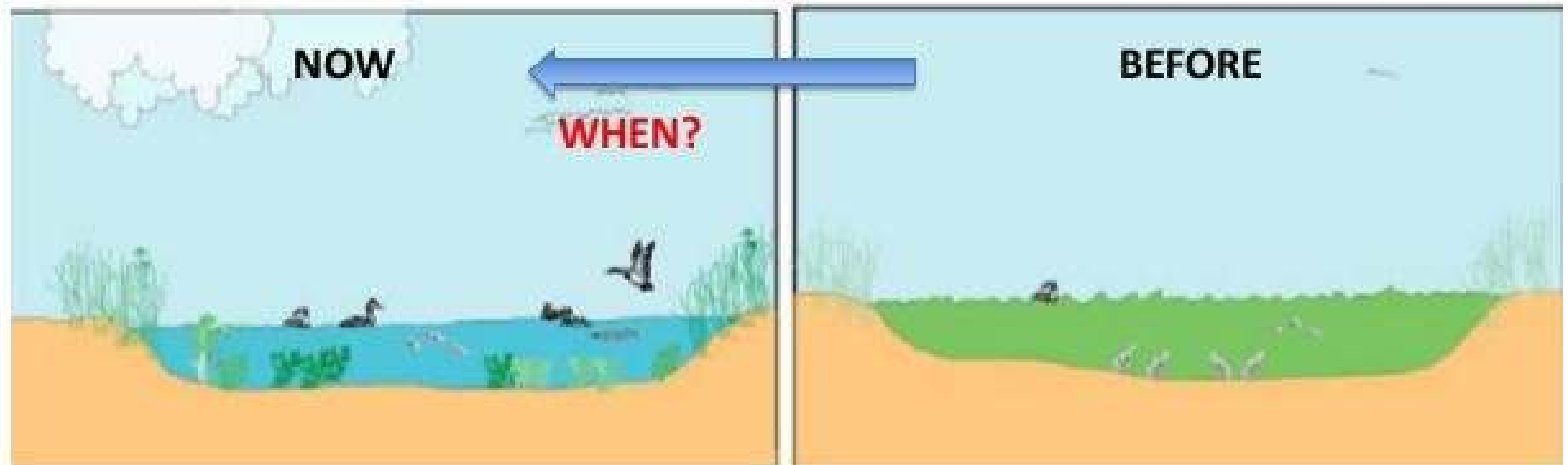
O efeito do distúrbio sobre as duas comunidades foi distinto devido às características das espécies colonizadoras

Alternative Equilibria in Shallow Lakes

The turbidity of lakes is generally considered to be a smooth function of their nutrient status. However, recent results suggest that over a range of nutrient concentrations, shallow lakes can have two alternative equilibria: a clear state domi-

M. Scheffer, S.H. Hosper, M-L. Meijer,
B. Moss and E. Jeppesen

Both states are
RESILIENT
Shifts associated to
DISTURBANCES



MACROPHYTES
(clear)

PHYTOPLANKTON
(turbid)

WHY?



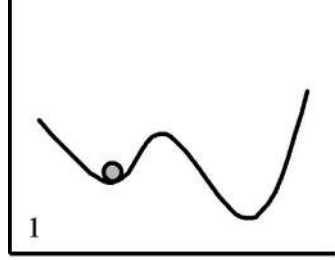
Andes • Ganges • Limpopo • Mekong • Nile • Volta

Volta

Consequências para manejo de ecossistemas

Consequências para manejo

- Se o "novo" estado estável não for "desejável" (e.g., lago oligotrófico tornado em um *bloom* de algas), pode ser difícil ou impossível reverter à situação anterior
- Imprevisibilidade do distúrbio causador



clear-water
lakes

coral-dominated
reefs

grassland

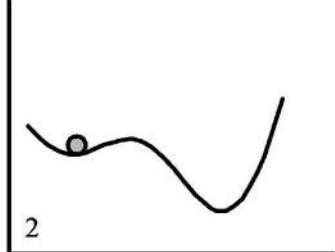
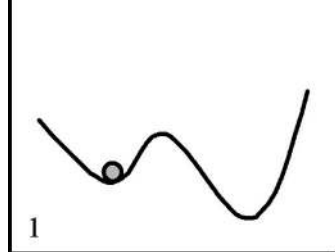
grassland

kelp forests

pine forest

seagrass beds

tropical lake with sub-
merged vegetation



clear-water
lakes

phosphorous accum-
ulation in agricultural
soil and lake mud

coral-dominated
reefs

overfishing, coastal
eutrophication

grassland

fire prevention

grassland

hunting of herbivores

kelp forests

functional elimination
of apex predators

pine forest

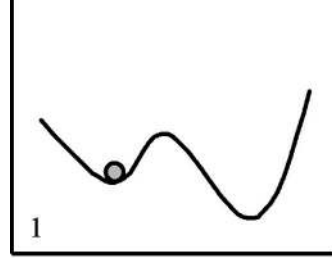
microclimate and soil
changes, loss of pine
regeneration

seagrass beds

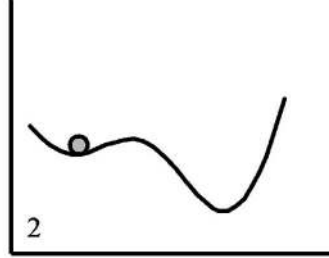
removal of grazers,
lack of hurricanes,
salinity moderation,
spatial homogenizatio

tropical lake with sub-
merged vegetation

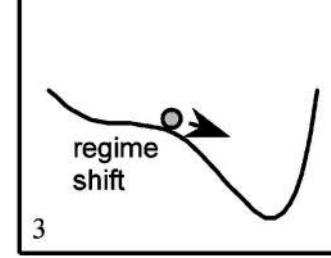
nutrient accumulation
during dry spells



clear-water
lakes



phosphorous accum-
ulation in agricultural
soil and lake mud



flooding, warming,
overexploitation
of predators

coral-dominated
reefs

overfishing, coastal
eutrophication

disease, bleaching
hurricane

grassland

fire prevention

good rains, continu-
ous heavy grazing

grassland

hunting of herbivores

disease

kelp forests

functional elimination
of apex predators

thermal event,
storm, disease,

pine forest

microclimate and soil
changes, loss of pine
regeneration

decreased fire
frequency, increased
fire intensity

seagrass beds

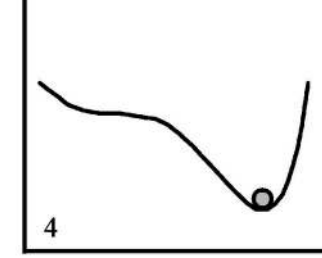
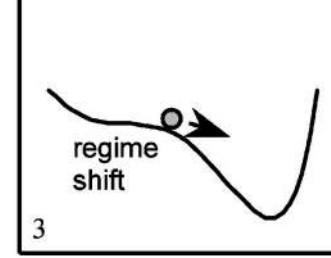
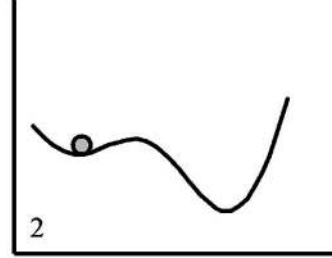
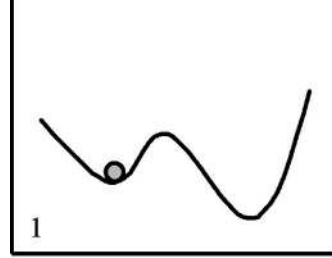
removal of grazers,
lack of hurricanes,
salinity moderation,
spatial homogenization

thermal event

tropical lake with sub-
merged vegetation

nutrient accumulation
during dry spells

nutrient release
with water table rise



clear-water
lakes

phosphorous accum-
ulation in agricultural
soil and lake mud

flooding, warming,
overexploitation
of predators

turbid-water
lakes

coral-dominated
reefs

overfishing, coastal
eutrophication

disease, bleaching
hurricane

algae-dominated
reefs

grassland

fire prevention

good rains, continu-
ous heavy grazing

shrub-bushland

grassland

hunting of herbivores

disease

woodland

kelp forests

functional elimination
of apex predators

thermal event,
storm, disease,

sea urchin
dominance

pine forest

microclimate and soil
changes, loss of pine
regeneration

decreased fire
frequency, increased
fire intensity

oak forest

seagrass beds

removal of grazers,
lack of hurricanes,
salinity moderation,
spatial homogenization

thermal event

phytoplankton
blooms

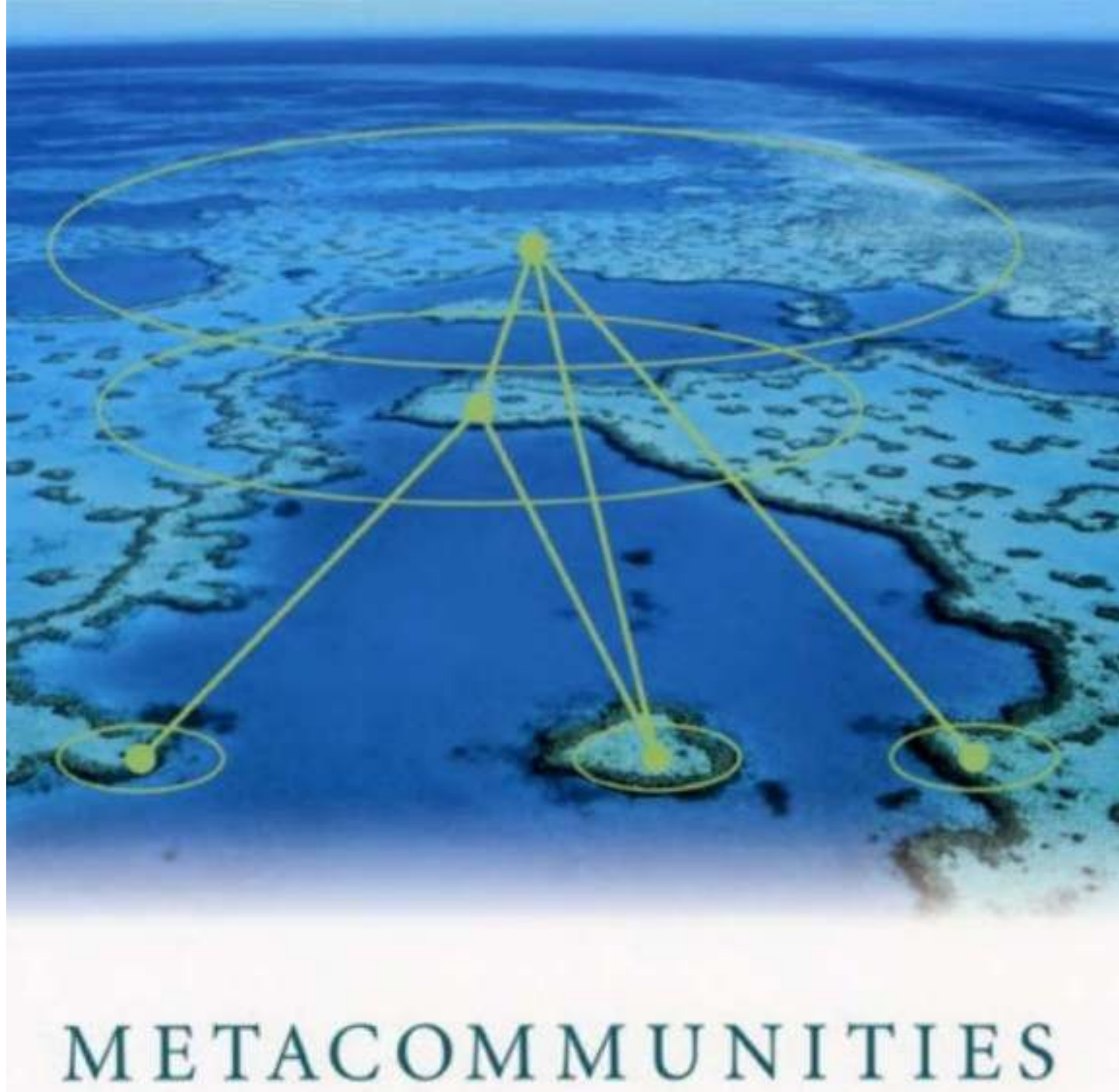
tropical lake with sub-
merged vegetation

nutrient accumulation
during dry spells

nutrient release
with water table rise

floating-plant
dominance

Fronteiras do conhecimento



Integração da escala
espacial nas análises
de redes de interação

REPORTS

18. H. E. Garcia, R. A. Locarnini, T. P. Boyer, J. I. Antonov, in *World Ocean Atlas 2005*, Vol. 3: Dissolved Oxygen, Apparent Oxygen Utilization, and Oxygen Saturation, S. Levitus, Ed. (National Oceanic and Atmospheric Administration Atlas National Environmental Satellite, Data, and Information Service 63, U.S. Government Printing Office, Washington, DC, U.S. Government, 2006), p. 1–342.
19. R. Schiller, <http://jco.amsi.edu> (2007).
20. Hydrobase (23) quality-controlled data augmented with recent repeat transects and available Argo float profiles within the areas shown (Fig. 2) were objectively mapped using correlation scales of 1 year and 50 m. To eliminate potential spatial bias due to recent sparser sampling, the meridional conductivity temperature depth and bottom sections used after 2000 were longitudinally ordered within each area. Inspection of data distributions

21. suggests that reported trends are not based on geographical shifts of data locations inside the investigation area or seasonal shifts as a function of time, except as noted in the text.
22. Suspect data for 1999 were removed from Fig. 2D (offset from the surface to 1000 m), for 1963 from Fig. 2E (locations only in the southern part of the box), and for 1986 from Fig. 2F (oxygen increased from 400 m to a maximum at 1000 m).
23. Linear trends and their 95% confidence intervals were estimated as in U73, using annual 300- to 700-m averages of the objectively mapped fields. Degrees of freedom for the confidence intervals were determined from integral line scales as in U47.
24. C. Wunsch, *The Ocean Circulation Inverse Problem* (Cambridge Univ. Press, Cambridge, 1996).

25. H. van Storch, F. W. Zwiers, *Statistical Analysis in Climate Research* (Cambridge Univ. Press, Cambridge, 1999), p. 734 (U.S.). Additional support was provided by the National Oceanic and Atmospheric Administration (NOAA) Office of Oceanic and Atmospheric Research (OAR) and NSF award no. 0223849. Conclusions in this article are those of the author and not necessarily those of the programs (www.argo.org).

6 December 2007; accepted
10.1126/science.115339

Le Normale Supérieure, 46 Rue d'Ulm, F-75230 Paris Cedex 5, France
5, 2008

Evolutionary emergence of size-structured food webs
Nicolas Loeuille* and Michel Loreau*
Laboratoire d'Ecologie, Unité Mixte de Recherche 5175, Centre National de la Recherche Scientifique, 63170 Levet, France

letters to nature

18. Gilinsky, N. L. in *Analytical Paleobiology* (eds Gilinsky, N. L. & Signor, P. W.) 157–174 (The Paleontological Society, Knoxville, Tennessee, 1991).
19. Cleveland, W. S. & McGill, B. The many faces of a scatterplot. *J. Am. Stat. Assoc.* **79**, 807–822 (1984).

Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

Acknowledgements

We are indebted to the late J. Sepkoski for his fossil databases and his encouragement, and we thank M. Foote and D. Erwin for comments on the manuscript. Our work was supported by grants from the University of California and the NSF to J.W.K. Correspondence and requests for materials should be addressed to J.W.K. (e-mail: kirschner@seismo.berkeley.edu).

Simple rules yield complex food webs

Richard J. Williams & Neo D. Martinez

two are from habitats at freshwater Bay and Ythan Estuary; and two are from Coachella Valley and the island of St Martin. Throughout this work, 'species' refers to trophic species and prey are functional groups of taxa that share the same predators and prey in a food web¹. 'Trophic species' is a widely accepted^{2,3,4,5,6,7,8} and sometimes criticized convention^{9,10} within structural food-web studies that reduces methodological biases in the data^{3,4,5}. A matrix with S rows and columns represents a food web with S species. Element a_{ij} is 1 if species j consumes species i and 0 if not. There are S^2 possible and L actual links. Directed connectance¹¹ (C) equals L/S^2 . In the random model^{12,13}, any link among S species occurs with the same probability (P) equal to C of the empirical web. This creates webs as free as possible from biological structuring while maintaining the observed S and C . The cascade model^{14,15} assigns each species a random value drawn uniformly from the interval $[0,1]$ and each species has probability $P = 2CS/(S-1)$ of consuming only species with values less than its own. This pecking order helps to explain species richness among trophic levels³ but underestimates inter-

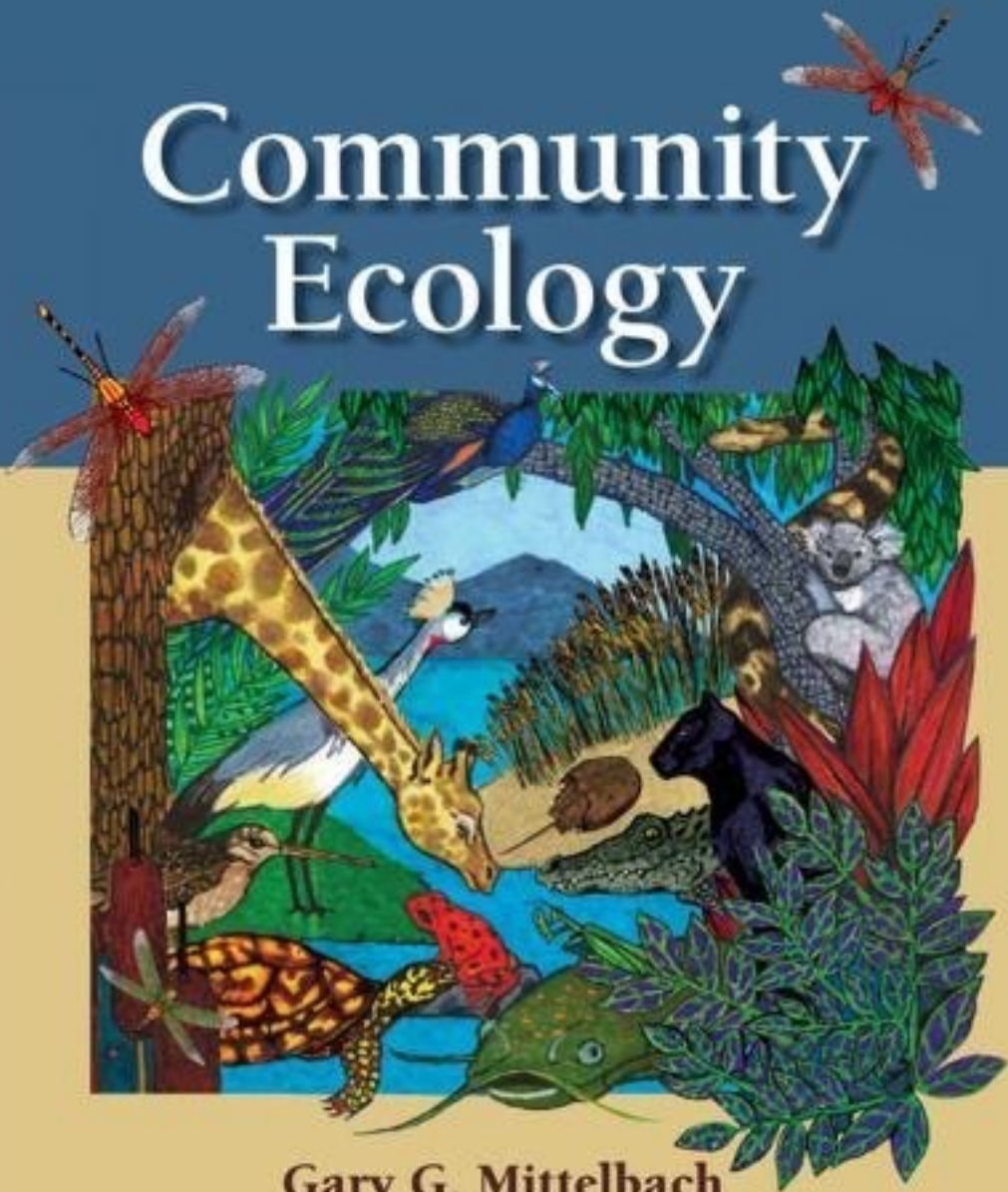
Modelos predictivos de estructura de redes

Size, foraging, and food web structure

Owen L. Petchey*†, Andrew P. Beckerman*, Jens O. Riede‡, and Philip H. Warren*

SEE COMMENTARY

Community Ecology



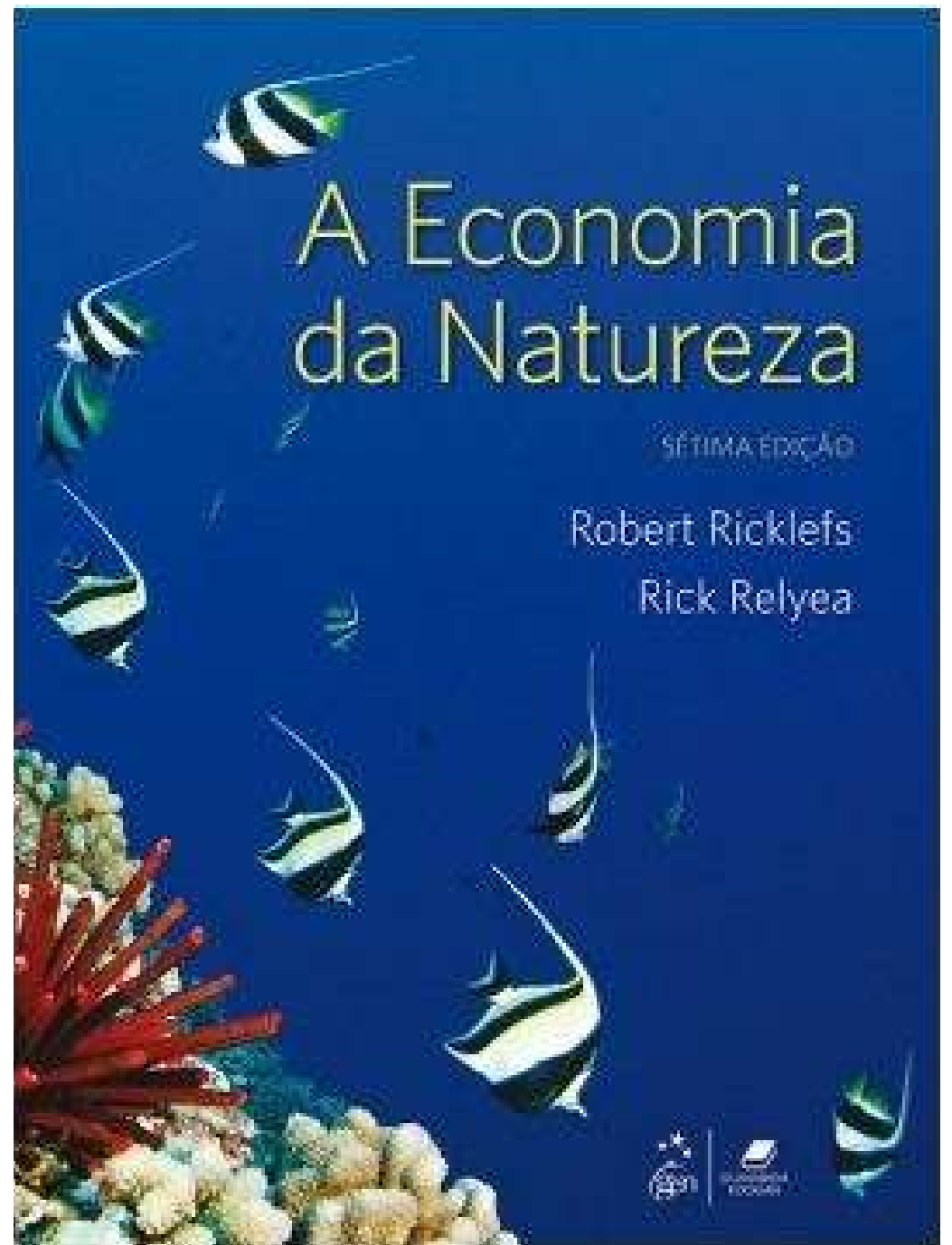
Gary G. Mittelbach

A Economia da Natureza

SÉTIMA EDIÇÃO

Robert Ricklefs

Rick Relyea



QUINTANA
TOURNAI