

# Escalas Locais e Regionais em Ecologia de Comunidades

A história oficial e algumas reflexões



# Escalas, História e Equilíbrio em Ecologia de Comunidades

## Conteúdo

O curso será organizado das teorias de equilíbrio e de montagem de comunidades através do nicho para teorias de não-equilíbrio e de montagem através de dispersão; da escala local para regional; e da individual para a ecossistêmica. Cada subtópico será contextualizado dentro de seu desenvolvimento histórico.

start [Ecologia de Comunidades] - Mozilla Firefox

os Ferramentas Ajuda

ologia.ib.usp.br/bie5778/doku.php

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ECOLOGIA DE COMUNIDADES

Alterações recentes Índice Autenticar-se

BIE-5778

Este é o site wiki de apoio a disciplina Ecologia de Comunidades do Programa de Pós Graduação em Ecologia da USP.

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[Laboratório de Ecologia Teórica](http://www.guilmaraes.bio.br/)
- Renata Pardini, IB - USP, Depto. de Zoologia

Colaboradores

- Paulo Guimarães Jr., IB - USP, Depto. de Ecologia  
<http://www.guilmaraes.bio.br/>
- Jason Moll, Pós-Doc EACH - USP

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Metodologia de Ensino

Discussões de artigos

Concluído

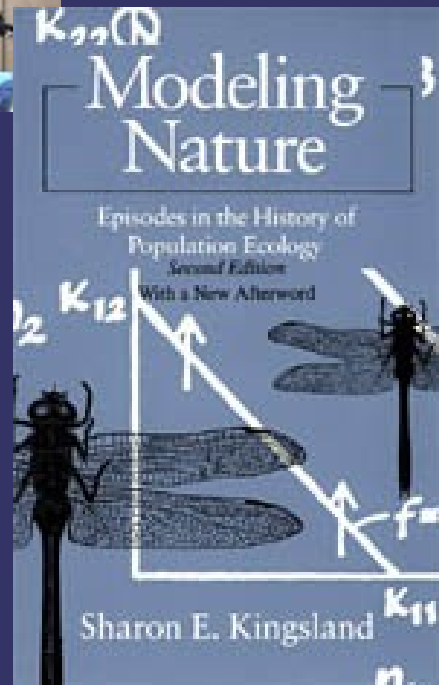
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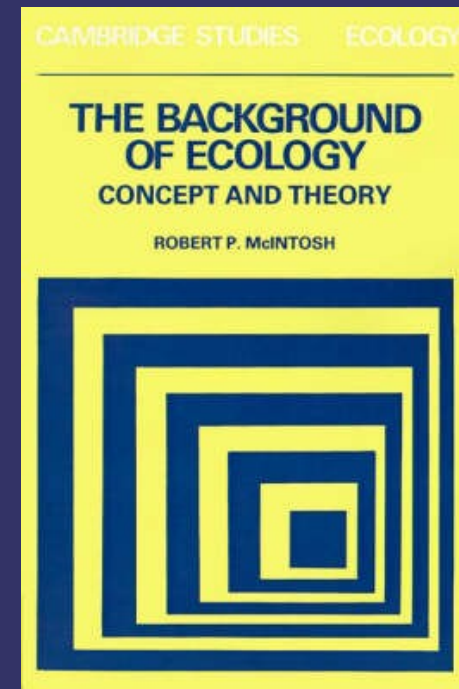
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# A HISTÓRIA



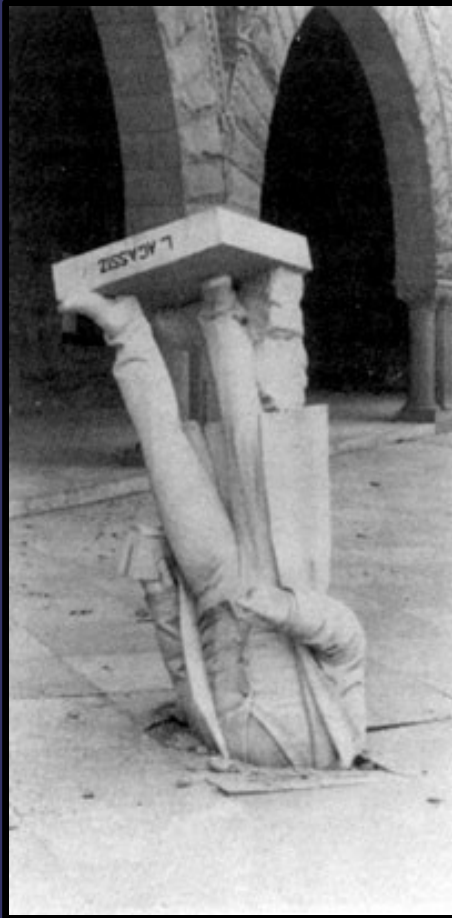
Chicago Univ. Press,  
1995



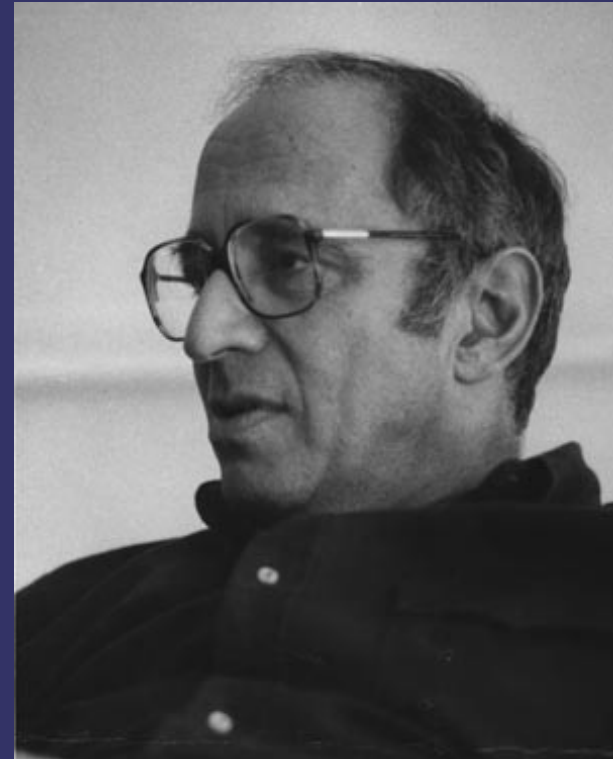
Cambridge Univ. Press,  
1986



# Paradigmas e Revoluções Científicas



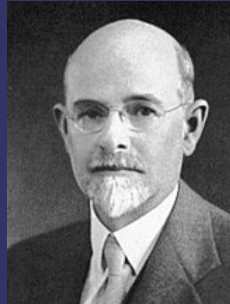
Estátua de Louis Agassiz  
em Standford,  
após terremoto de 1906



Thomas Kuhn  
1922 - 1996



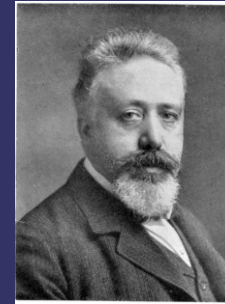
# Homenagem a Santa Rosália: Nasce um Paradigma



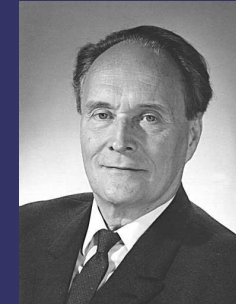
Grinnell



Lotka



Volterra



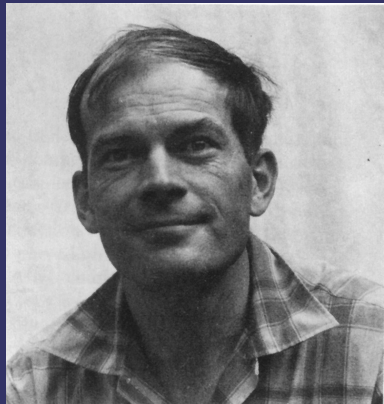
Gause



George E. Hutchinson  
1903-1991

- Competição como principal força estruturadora.
- Diferenças de nicho mediam coexistência.
- Leis e princípios que geram modelos matemáticos, derivados da dinâmica clássica.
- Sistemas saturados e em equilíbrio.





Robert MacArthur  
1930-1972

Kohn 1971. Limnology and Oceanography, Vol. 16

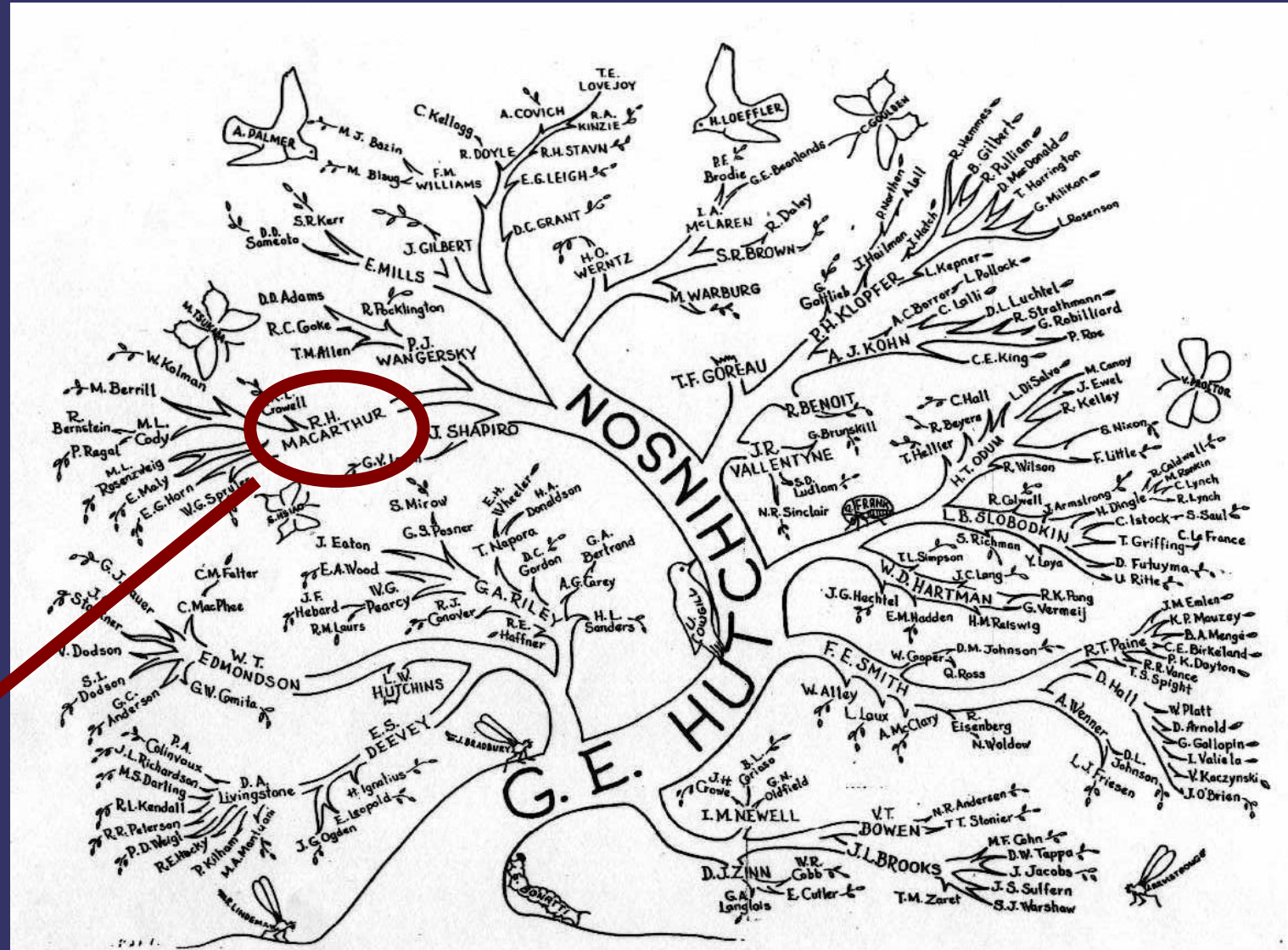
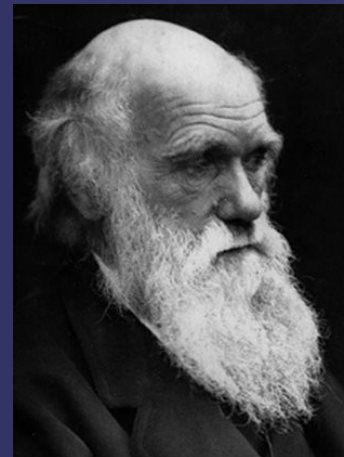
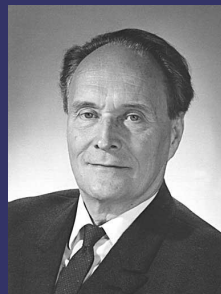
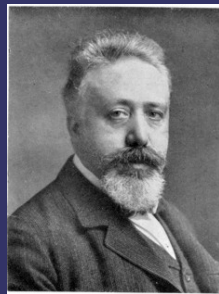
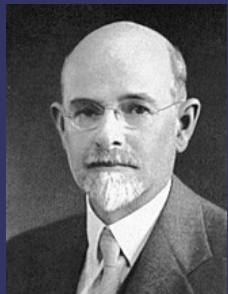


FIG. 9. Phylogenetic tree of intellectual descendants of G. E. Hutchinson, restricted to those possessing doctoral degrees. Main branches and capitalized names represent Hutchinson's own doctoral students. Secondary branches and twigs with lower-case names indicate second- and third-generation students. Terminal leaves indicate completed degrees, their absence means Ph.D. expected in 1971. The attendant fauna represent people who have done postdoctoral work with Hutchinson; their particular character and disposition were dictated by aesthetic considerations alone.

# As Cunhas de Darwin

*“Nature may be compared to a surface covered with ten-thousand sharp wedges, many of the same shape & many of different shapes representing different species, all packed closely together & all driven in by incessant blows: the blows being far severer at one time than at another; sometimes a wedge of one form & sometimes another being struck; the one driven deeply in forcing out others; with the jar and shock often transmitted very far to other wedges in many lines of direction: beneath the surface we may suppose that there lies a hard layer, fluctuating in its level, & which may represent the minimum amount of food required by each living being, & which layer will be impenetrable by the sharpest wedge.”*



# "Eclipse da História"\*

## Articles

### Community Diversity: Relative Roles of Local and Regional Processes

ROBERT E. RICKLEFS

The species richness (diversity) of local plant and animal assemblages—biological communities—balances regional processes of species formation and geographic dispersal, which add species to communities, against local processes of predation, competitive exclusion, adaptation, and stochastic variation, which may promote local extinction. During the past three decades, ecologists have sought to explain differences in local diversity by the influence of the physical environment on local interactions among species, interactions that are generally believed to limit the number of coexisting species. But diversity of the biological community often fails to converge under similar physical conditions, and local diversity bears a demonstrable dependence upon regional diversity. These observations suggest that regional and historical processes, as well as unique events and circumstances, profoundly influence local community structure. Ecologists must broaden their concepts of community processes and incorporate data from systematics, biogeography, and paleontology into analyses of ecological patterns and tests of community theory.

INTEREST IN NATURAL DIVERSITY HAS RISEN IN THE PUBLIC conscience recently with concern over the imminent extinction of thousands of species as a result of pollution and habitat destruction (1). Ecologists are unable to calculate the consequences of this havoc for natural resources of use to mankind and for the intrinsic stability of natural systems. But many consider these consequences to be potentially disastrous (2). If we are to predict change in system function after depauperization, we need to understand processes responsible for generating and maintaining diversity in biological communities. Indeed, the diversity issue may have two faces. Can one comprehend the ruin of natural systems without understanding how they are built?

Present-day ecological investigations are largely founded on the premise that local diversity—the number of species living in a small, ecologically homogeneous area—is the deterministic outcome of local processes within the biological community. As a general rule, community diversity parallels variation in local physical conditions. For example, on all continents, diversity tends to decrease with increasing distance north or south from the equator (3). But whether such patterns are mediated by competition between species, predation and disease, or patchworks of natural disturbances is intensely debated without any sign of resolution soon (4, 5).

Competition has been advocated strongly (6–8) because coexistence requires that each species has some corner on a limited resource market. If coexistence were precluded when ecological

similarity exceeded some limit, or if a species could not persist when its ecological niche were reduced below some minimum viable size, the number of species in a community would be determined in a manner analogous to the packing of balls in a box. Accordingly, one would expect to find regular spacing between the positions of species within ecological space. Equivocal evidence for such spacing (9) has prevented the "competition hypothesis" from completely sweeping the discipline.

Predation is ubiquitous. The fact that predators can manipulate the dynamic relations between competing prey species has attracted many to the position that predation may influence diversity (10). Disturbances to the uniform fabric of the community caused by storms, erosion, predation, and natural deaths of individuals increase the heterogeneity of the environment and increase the amount of ecological space available (11). Disturbance itself, by interrupting the return of systems to equilibrium, may retard competitive exclusion and thereby promote diversity (12).

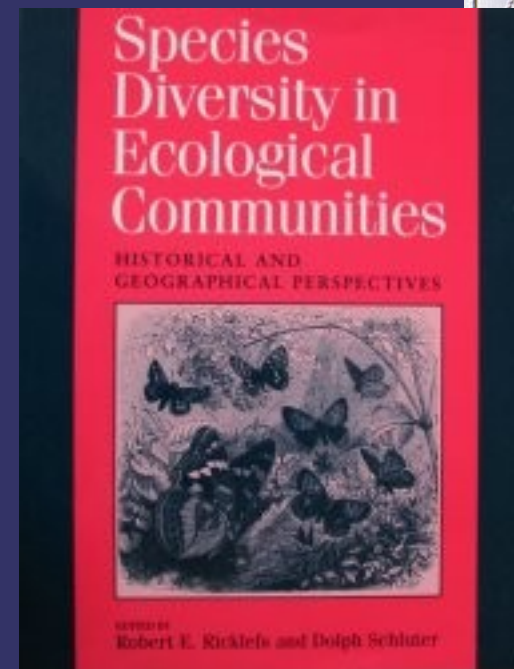
Almost certainly, these local factors influence local diversity. But a larger issue for ecologists is the degree to which they can explain local diversity solely by local processes, without considering the matrix of processes on larger spatial and temporal scales within which the community is imbedded. Ecologists are beginning to realize that local diversity bears the imprint of such global processes as dispersal and species production and of unique historical circumstance. These processes pose a challenge to community ecologists to expand the geographical and historical scope of their concepts and investigations.

#### Testing Predictions of Local-Process Theories

Regardless of the underlying mechanism, hypotheses that relate local diversity deterministically to local conditions make common predictions of (i) community convergence, (ii) resistance of the community to invasion, and (iii) independence of local and regional diversity. In two areas having different histories of biological development but similar physical conditions, adaptations of individuals and attributes of community structure and function should conform to limits imposed by local conditions. Although plant and animal form and function commonly converge in similar environments (13), accumulating counterexamples dispel belief that species diversity similarly converges (14, 15). Two examples will illustrate this important point. First, throughout the tropics, the boundary separating marine and terrestrial environments supports a mangrove-type vegetation consisting of species of trees uniquely (and convergently) adapted to the immersion of their roots in salt water. In the New World tropics and western Africa, mangrove communi-

The author is a professor in the Department of Biology, University of Pennsylvania, Philadelphia, PA 19104.

Robert Ricklefs



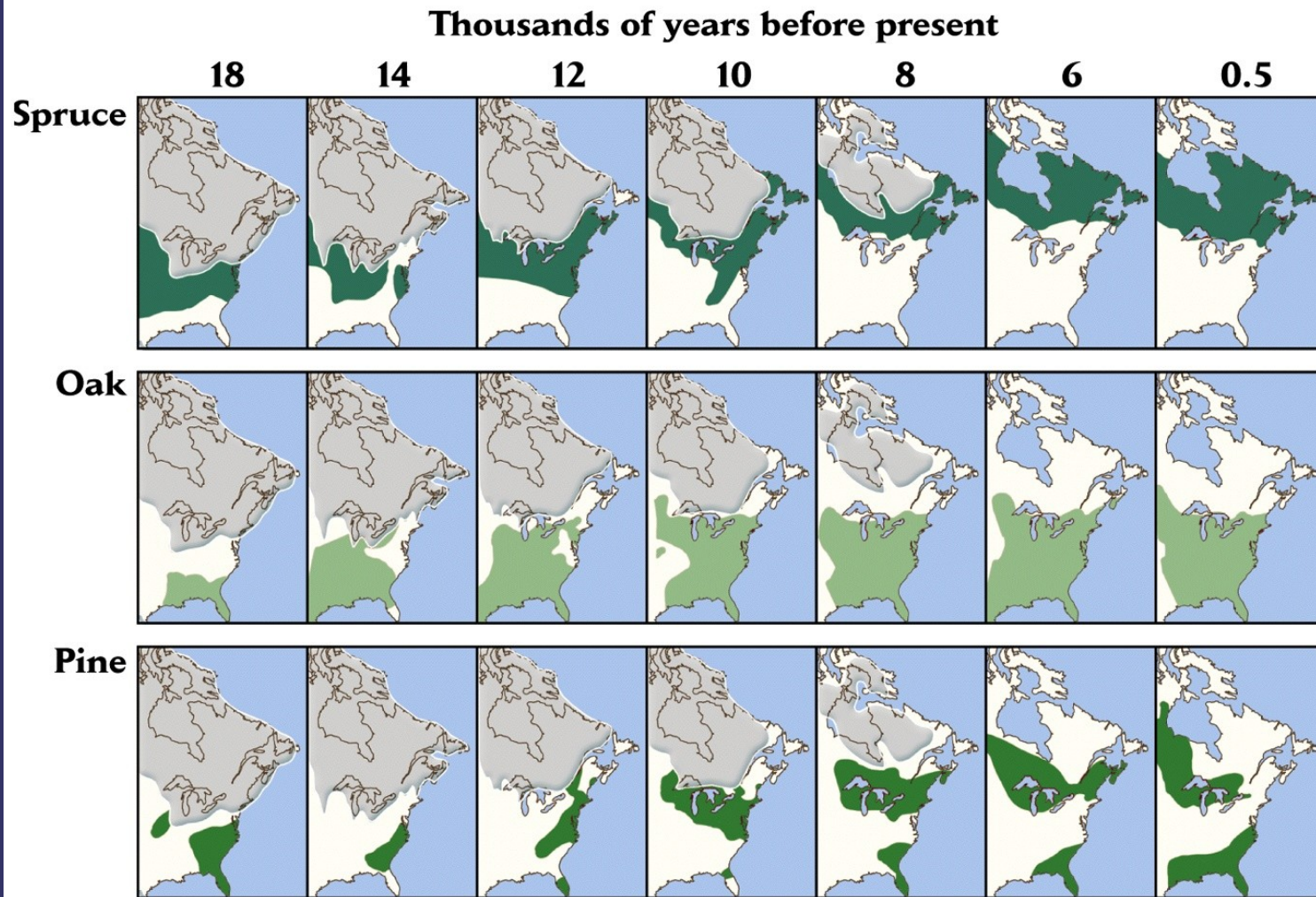
1993

Science, 1987

\* Expressão de Kingsland, 1986



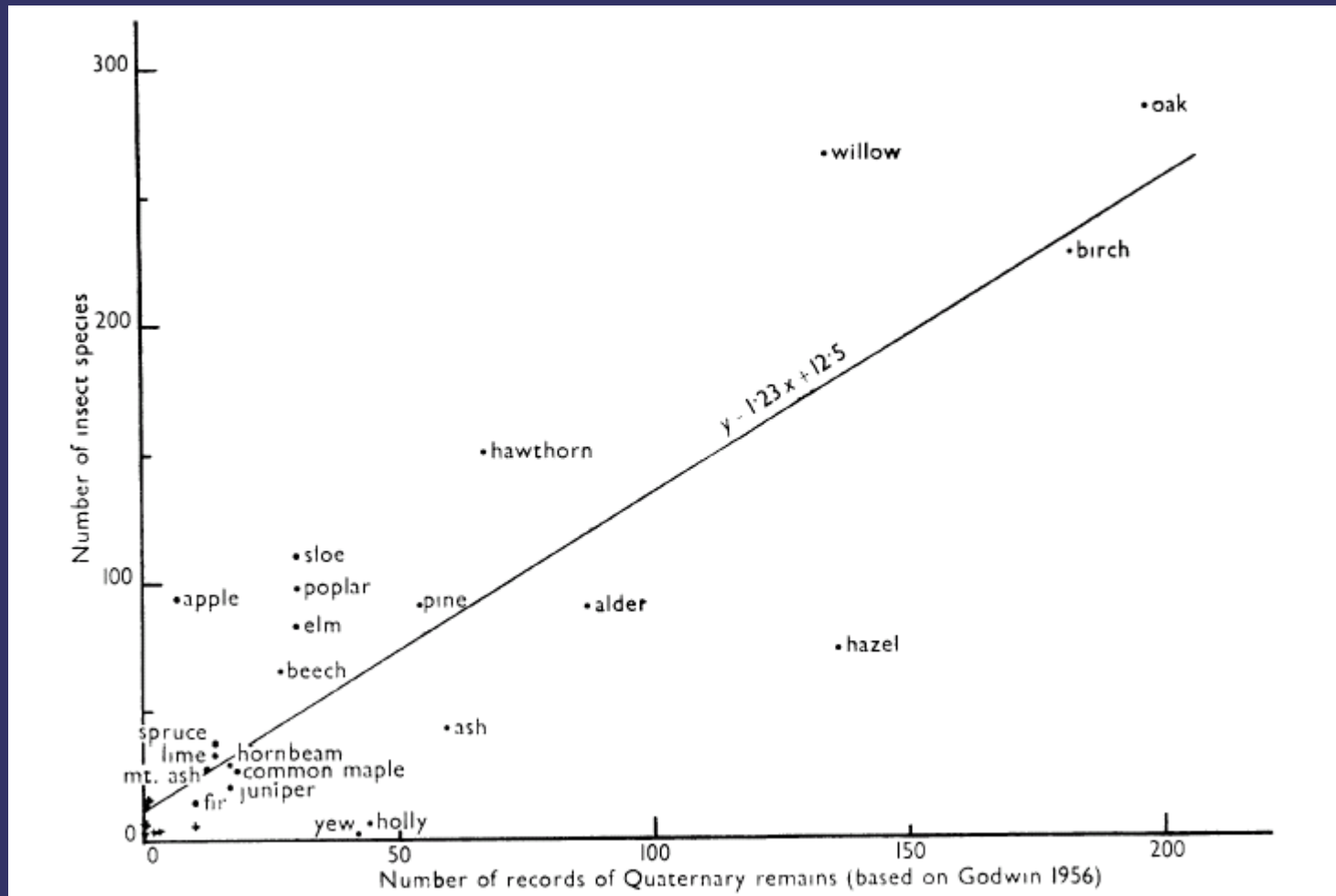
# O Papel da História



Distribuição geográfica de três espécies de árvores na costa leste da América do Norte, nos últimos 18 mil anos.

Jacobson et al. 1987, apud Ricklefs 2003.

# A Contribuição da Interação Inseto - Planta



Sir T. R. Southwood, FRS  
1931-2005

N de espécies de insetos herbívoros em árvores nas Ilhas Britânicas em função da frequência das espécies de árvores no registro fóssil quaternário.

# Pteridium e os Nichos Vagos de Lawton

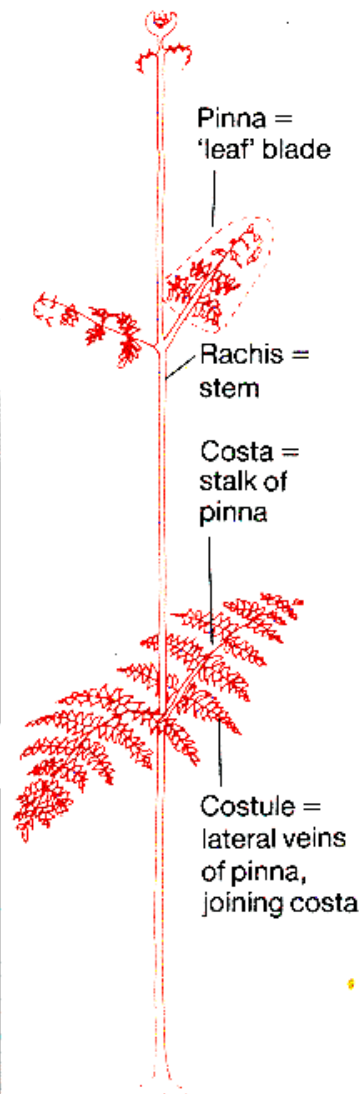
Feeding methods

Parts of plant—see diagram

(a)	Chew	Suck	Mine	Gall
Rachis		● ○		●
Pinna	●●●●●●●●	●●● ?	●●●○	●●
Costa		● ○	●	(● Rare)
Costule		●	●●	

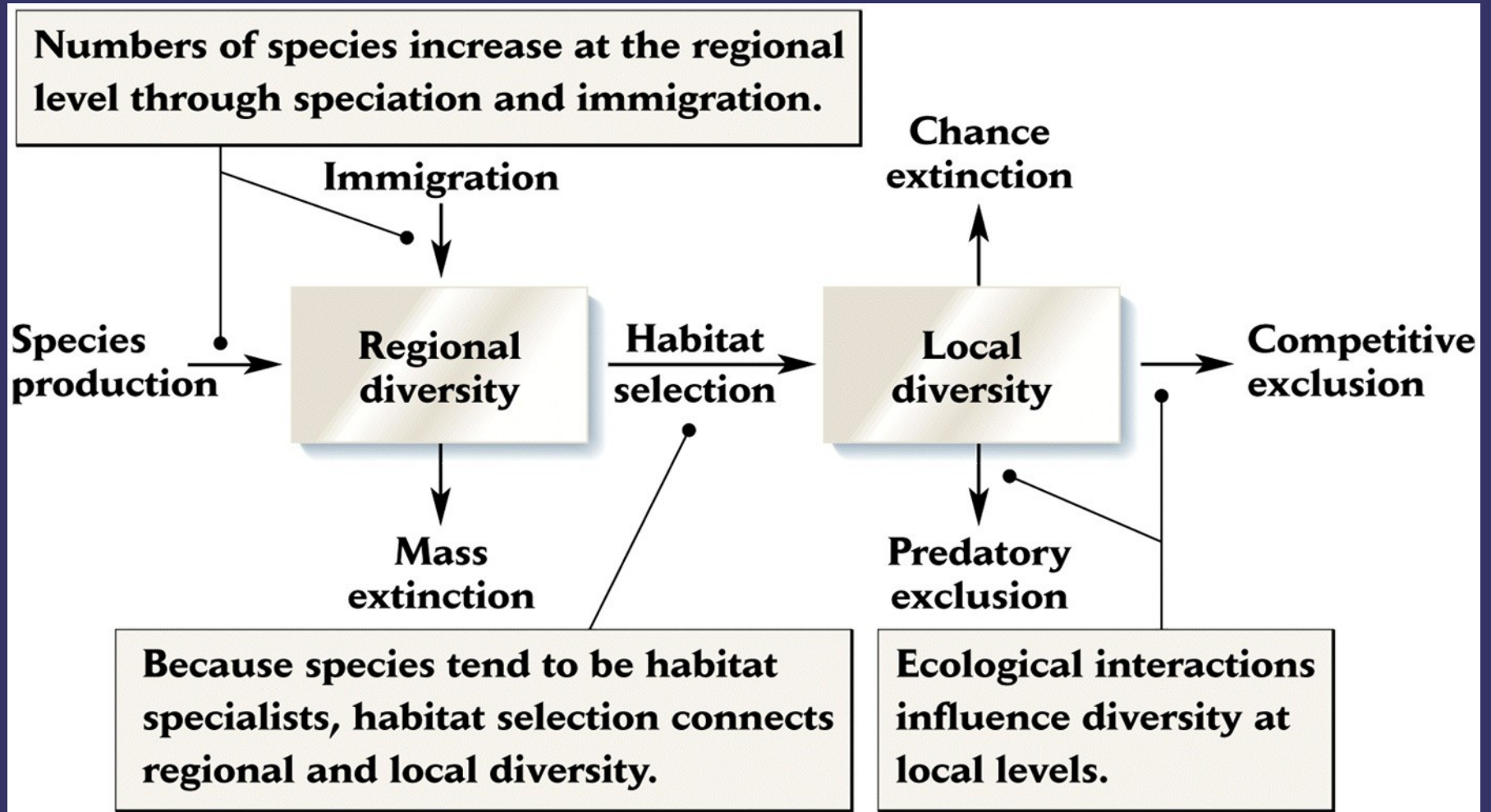
(b)	Chew	Suck	Mine	Gall
Rachis	●●		●●●●●●●●	●
Pinna	●●●	●●●●●●		
Costa			●●	
Costule			●	

(c)	Chew	Suck	Mine	Gall
Rachis				
Pinna	● ○	●●	○	
Costa				
Costule				



*Pteridium anquilinum* L.  
Scandinavian Ferns .  
Øllgaard & Tind, Rhodos, 1993

# O Modelo Conceitual de Ricklefs *et al.*



# O Eclipse da Escala Local?


VOL. 172, NO. 6 THE AMERICAN NATURALIST DECEMBER 2008

## Disintegration of the Ecological Community

American Society of Naturalists Sewall Wright Award Winner Address\*

Robert E. Ricklefs<sup>†</sup>

" I suggest that the distributions of species within a region reveal more about the processes that generate diversity patterns than does the co-occurrence of species at any given point. **The local community is an epiphenomenon that has relatively little explanatory power in ecology and evolutionary biology.**"

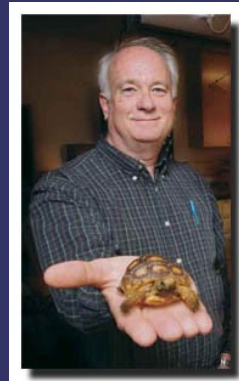


# Ecologia = Estudos de Caso?

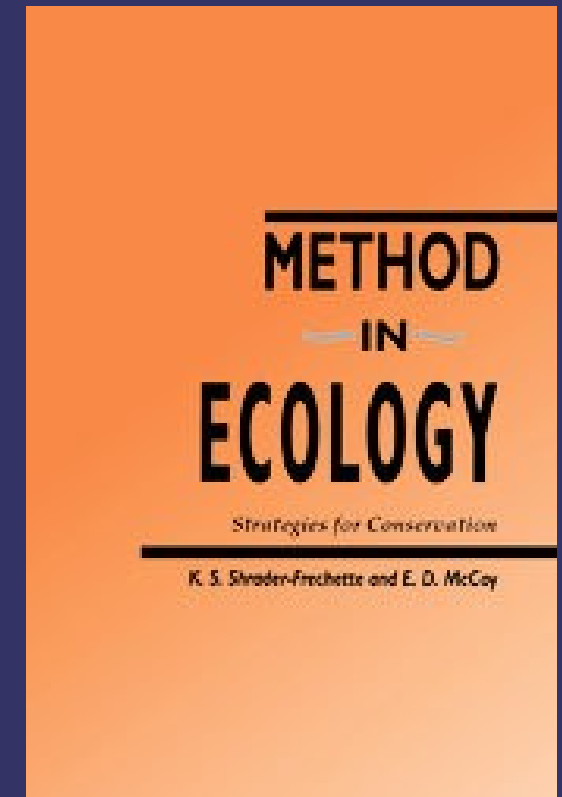
" When we wish to apply ecology to promote conservation or preservation our knowledge of particular taxa is more important than knowledge of general theory."



Kristin Shrader-Frechette



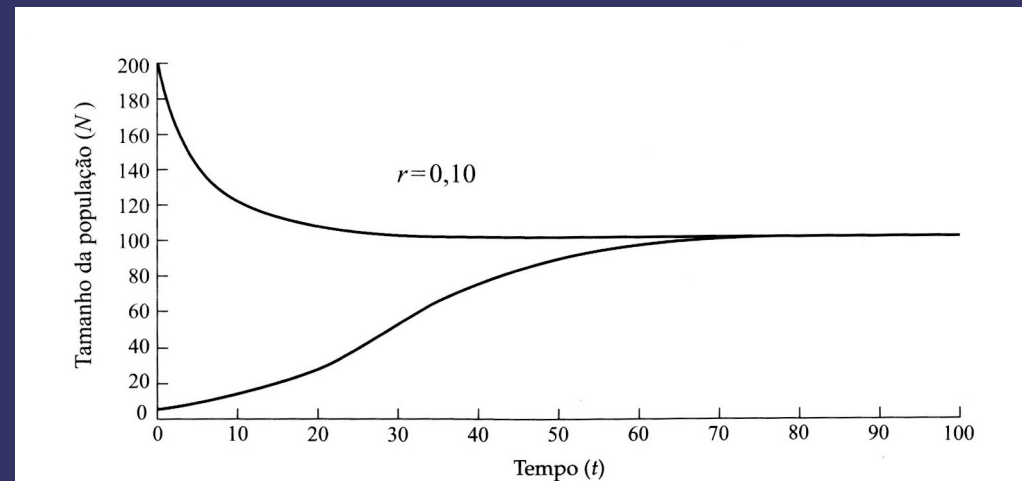
Earl McCoy



Cambridge Univ. Press,  
1993

# Algumas Considerações sobre Irreversibilidade, História e Evolução

$$\frac{dN}{dt} = r \cdot N \left( 1 - \frac{N}{K} \right)$$



**Figura 2.2** Curva de crescimento logístico. Quando o crescimento começa abaixo da capacidade de suporte, a trajetória de  $N$  em função do tempo descreve uma típica curva em forma de S. Acima da capacidade de suporte, a curva cai rapidamente para o equilíbrio. Neste exemplo,  $K = 100$ , e o tamanho inicial da população é 5 ou 200.

# Demônio de Laplace



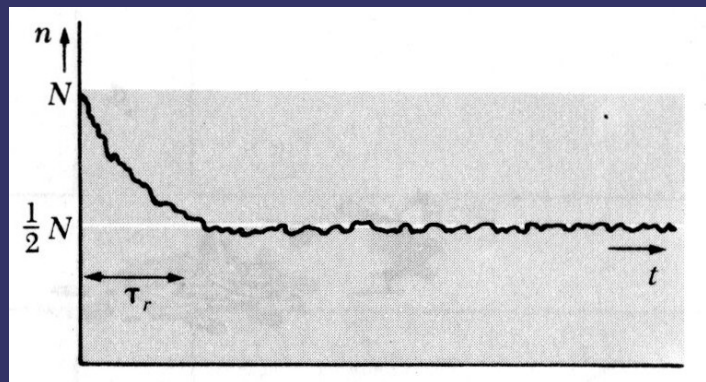
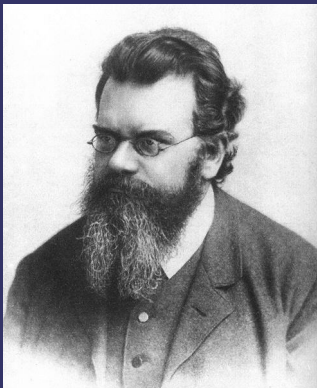
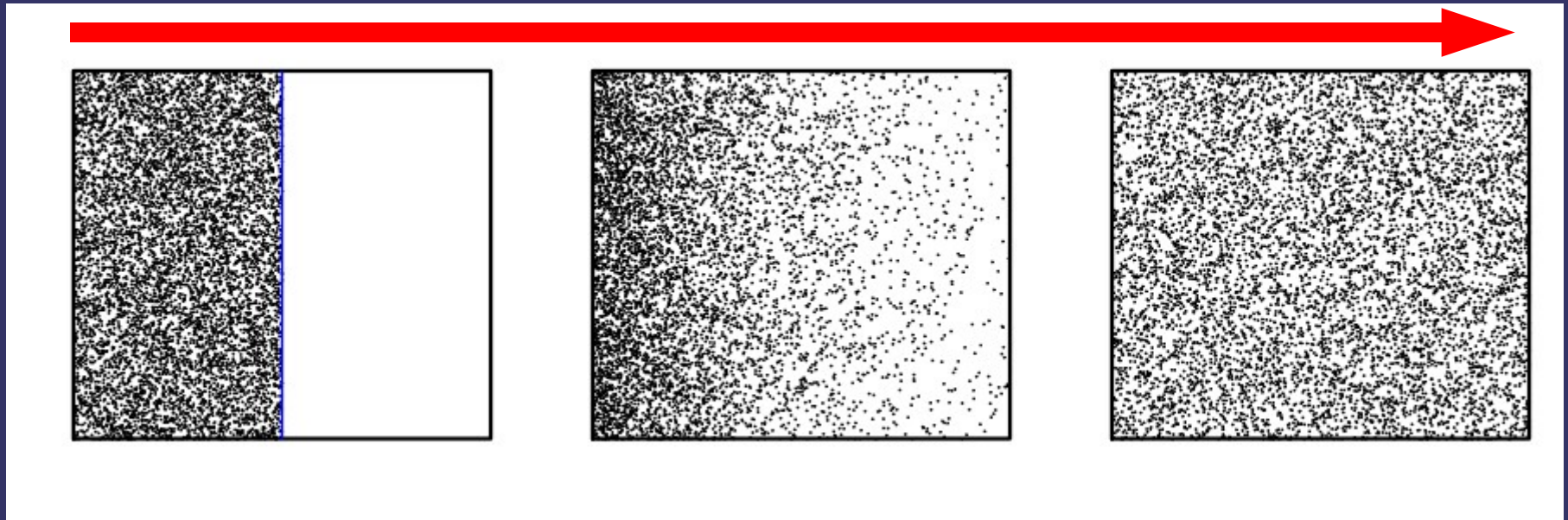
*“Se houvesse um intelecto que num dado momento conhecesse todas as forças que colocam a natureza em movimento, e todas as posições de seus elementos, e que também fosse vasto o suficiente para submeter esses dados à análise, **ele poderia abranger numa única fórmula** os movimentos dos maiores corpos celestes e do mais ínfimo átomo, e para ele nada seria incerto, e passado e futuro seriam o mesmo que o presente a seus olhos.”*

Marquês Pierre-Simon Laplace  
(1749-1827)





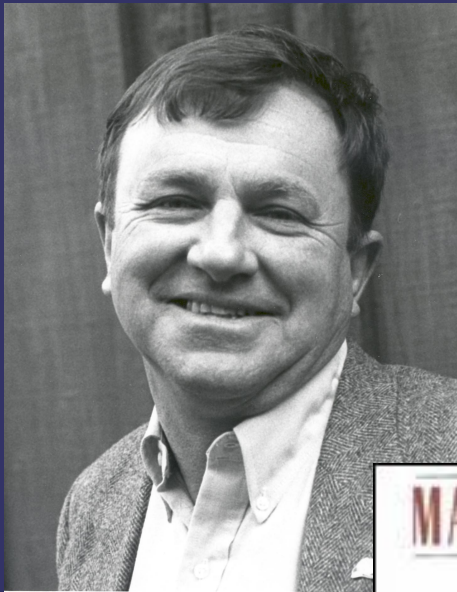
# A Seta do Tempo de Boltzmann



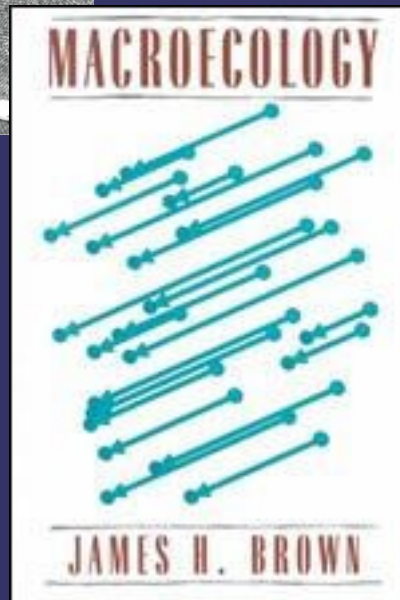
Propriedades macroscópicas do sistema evoluem para seu estado mais provável.

Ludwig Boltzmann  
1844 - 1906

# A Atávica Inveja da Física



James Brown

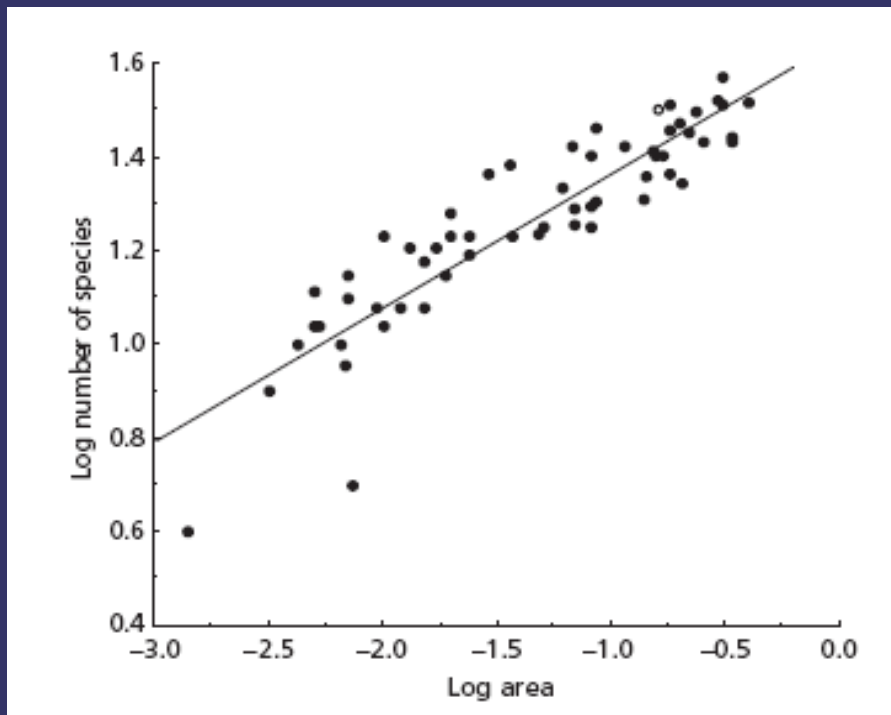


Chicago Univ. Press  
1995

" Macroecology is concerned with statistical distributions of variables among large numbers of ecological 'particles'. Usually these particles are either many individual organisms within species populations, or many species within local, regional or continental biotas. [...] In order to characterize and compare these distributions, it is desirable - but not always possible - to have samples of hundreds or thousands of particles. "

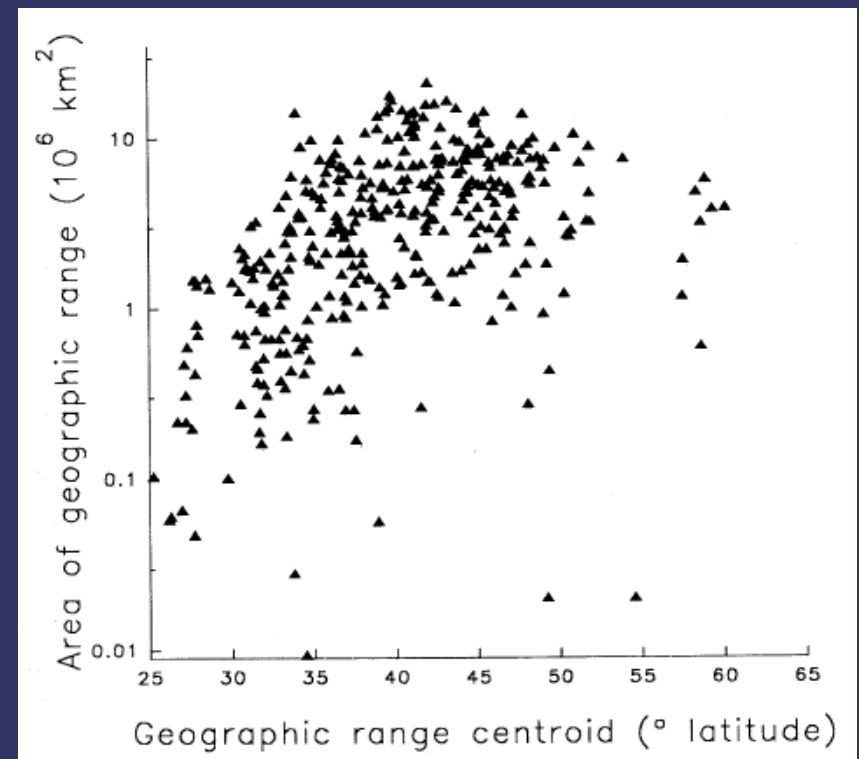
# Macroecologia: Dois Exemplos

## Relação Espécie x Área



Aves em ilhas britânicas,  
Gaston & Blackburn 2000

## Regra de Rapoport



Aves na América do Norte, Brown, 1995

# Basta uma Seta do Tempo?



- A irreversibilidade é a consequência macroscópica de nossa incapacidade de descrição do nível microscópico.
- Mesmo em termos macroscópicos, o sistema segue sempre para um mesmo estado de equilíbrio (determinismo).



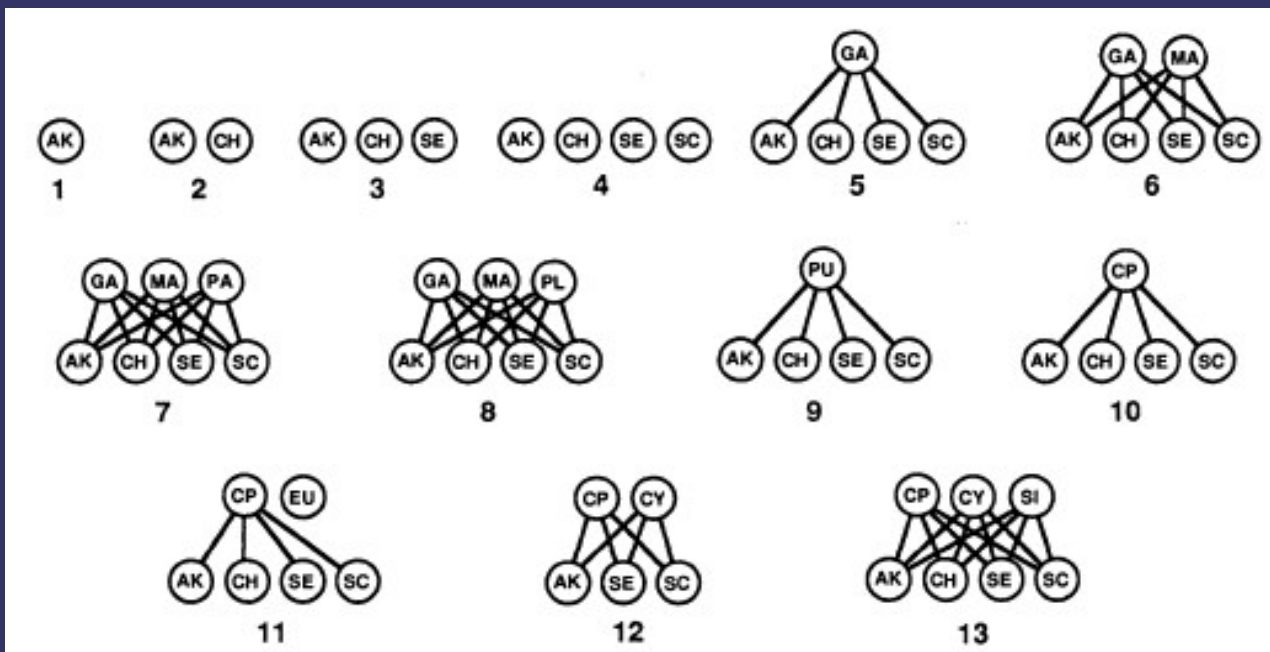
# O que define história?

- Além de irreversibilidade história exige:
  - **Acontecimento**: realização de um entre muitos estados possíveis.
  - **Contexto**: conjunto de condições que definem os acontecimentos possíveis, suas probabilidades, e seus efeitos no sistema.
  - **Coerência**: relações que definem o contexto como consequência de acontecimentos prévios.



Ilya Prigogine  
1917-2003  
Nobel em 1977

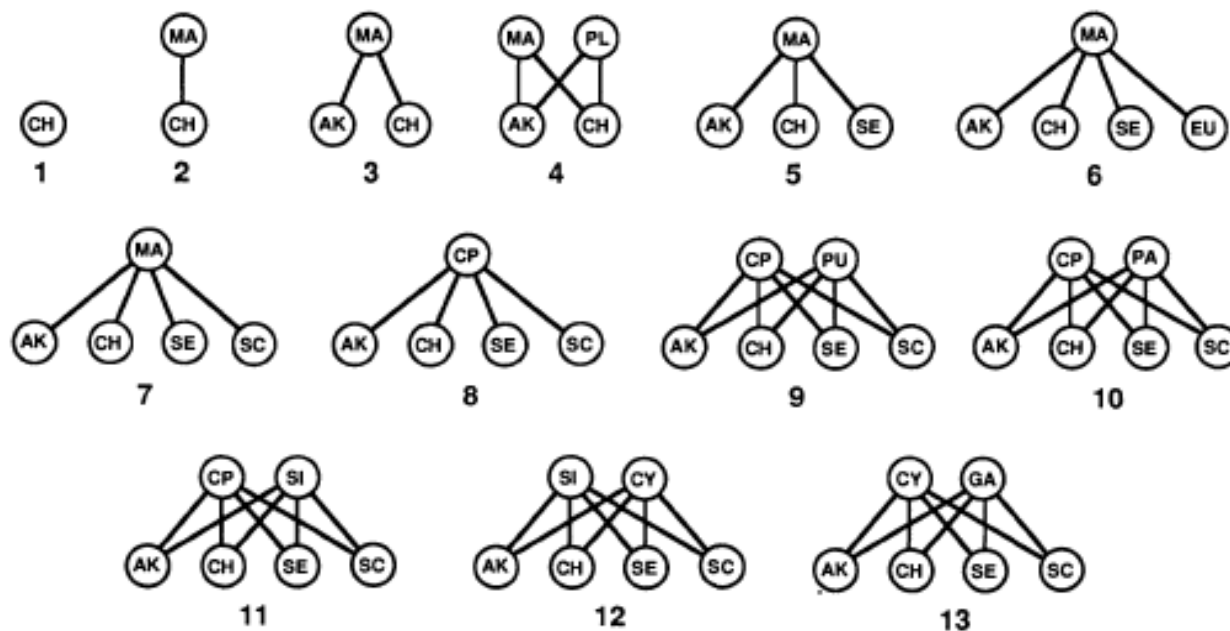
# Comunidades como Sistemas Históricos



Drake, 1991. Am. Nat

AK - *Ankistrodesmus falcatus*  
 CH - *Chlamydomonas reinhardtii*  
 CP - *Cypris*  
 CY - *Cyclops vernalis*  
 EU - *Euglena gracilis*  
 GA - *Gammarus lacustris*

MA - *Daphnia magna*  
 PA - *Paramecium multimicronucleatum*  
 PL - *Pleuroxus truncatus*  
 PU - *Daphnia pulex*  
 SC - *Scenedesmus quadricauda*  
 SE - *Selenastrum bibrium*



# Evolução de Sistemas Complexos



**Table 1** Results of species elimination

	Elimination method	
	Random	Natural selective
Maximum no. of eliminations required for homeostasis	50	29
Mean no. of eliminations required for homeostasis	46.7	25
Fraction of sample yielding a non-trivial homeostatic system	24%	100%
Fraction of feasible systems stable	100%	100%
Largest homeostatic system resulting	4	29
Smallest (non-trivial) homeostatic system resulting	2	21
Mean ratio of connectance in homeostatic set to that in random ensemble	0.80	0.99
Fraction of eliminated species which were consumers	0.50	0.826
Maximum fraction of consumers in a homeostatic system	0.33	0.25
Minimum fraction of consumers in a homeostatic system	0.00	0.11
Mean fraction of consumers in a homeostatic system	0.20	0.165
Ratio of mean no. of eliminations to initial no. of unfeasible species	1.82	0.99
Final range of values of $g$	0.88–1.25	0.33–0.39

# Complexidade sem Regras



- ✓ **Não** há limites claros
- ✓ **Não** há dinâmica interna coerente
- × **Há** relações simples com o contexto



Peter Taylor



Chicago Univ.  
Press, 2005



# Embebimento: Comunidades são Situações

"REGIONAL"



- ✓ **Não** há limites claros
- ✓ **Não** há dinâmica interna coerente
- ✓ **Não** há relações simples com o contexto

**A escala regional é ao mesmo tempo contexto e produto da escala local.**

# De quem a física tem inveja?

VOL. 8, 1922

*BIOLOGY: A. J. LOTKA*

147

## *CONTRIBUTION TO THE ENERGETICS OF EVOLUTION\**

BY ALFRED J. LOTKA

SCHOOL OF HYGIENE AND PUBLIC HEALTH, JOHNS HOPKINS UNIVERSITY

Communicated, May 6, 1922

It has been pointed out by Boltzmann<sup>1</sup> that the fundamental object of contention in the life-struggle, in the evolution of the organic world, is available energy.<sup>2</sup> In accord with this observation is the principle<sup>3</sup> that, in the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient<sup>4</sup> in directing available energy into channels favorable to the preservation of the species.

The first effect of natural selection thus operating upon competing

# NATURAL SELECTION AS A PHYSICAL PRINCIPLE\*

BY ALFRED J. LOTKA

SCHOOL OF HYGIENE AND PUBLIC HEALTH, JOHNS HOPKINS UNIVERSITY

Communicated May 6, 1922

In a paper presented concurrently with this, the principle of natural selection, or of the survival of the fittest (persistence of stable forms), is employed as an instrument for drawing certain conclusions regarding the energetics of a system in evolution.

Aside from such interest as attaches to the conclusions reached, the method itself of the argument presents a feature that deserves special note. The principle of natural selection reveals itself as capable of yielding information which the first and second laws of thermodynamics are not competent to furnish.

The two fundamental laws of thermodynamics are, of course, insufficient to determine the course of events in a physical system. They tell us that certain things cannot happen, but they do not tell us what does happen.

# Darwin Chegou Lá!

- Evolução por seleção natural:
    - **Acontecimento**: variação individual fenotípica, decorrente de genotípica.
    - **Contexto**: diferenças fenotípicas acarretam em diferentes probabilidades de reprodução e sobrevivência dos indivíduos.
    - **Coerência**: mudanças nas frequências dos genótipos na população fixam e eliminam fenótipos, o que por sua vez altera o contexto de seleção das gerações seguintes.
- 