群落组建机制

历史回顾与最新进展

张大勇

北京师范大学生态学研究所

2014年8月18日

生态学的核心是群落！

Ecology is the science of communities.

A study of the relations of a single species to the environment conceived without reference to communities and, in the end, unrelated to the natural phenomena of its habitat and community associations is not properly included in the field of ecology.

--- V. Shelford, 1929.

Victor Shelford

(1877-1968)

美国生态学会第一任会长，
Eugene Odum的老师

但群落生态学乱七八糟？

- Lawton (1999)： **“…community ecology is a mess, with so much contingency that useful generlisations are hard to find.”**

John Lawton
(b.1943 -)

Are there general laws in ecology?

John H. Lawton

Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177–192.

The dictionary definition of a law is: "Generalized formulation based on a series of events or processes observed to recur regularly under certain conditions; a widely observable tendency". I argue that ecology has numerous laws in this sense of the word, in the form of widespread, repeatable patterns in nature, but hardly any laws that are universally true. Typically, in other words, ecological patterns and the laws, rules and mechanisms that underpin them are contingent on the organisms involved, and their environment. This contingency is manageable at a relatively simple level of ecological organisation (for example the population dynamics of single and small numbers of species), and re-emerges also in a manageable form in large sets of species, over large spatial scales, or over long time periods, in the form of detail-free statistical patterns – recently called 'macroecology'. The contingency becomes overwhelmingly complicated at intermediate scales, characteristic of community ecology, where there are a large number of case histories, and very little other than weak, fuzzy generalisations. These arguments are illustrated by focusing on examples of typical studies in community ecology, and by way of contrast, on the macroecological relationship that emerges between local species richness and the size of the regional pool of species. The emergent pattern illustrated by local vs regional richness plots is extremely simple, despite the vast number of contingent processes and interactions involved in its generation. To discover general patterns, laws and rules in nature, ecology may need to pay less attention to the 'middle ground' of community ecology, relying less on reductionism and experimental manipulation, but increasing research efforts into macroecology.

群落生态学存在普适理论吗？

VOL. 163, NO. 6 THE AMERICAN NATURALIST JUNE 2004

Community Ecology: Is It Time to Move On?

(An American Society of Naturalists Presidential Address)*

Daniel Simberloff†

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996

Submitted August 29, 2003; Accepted January 9, 2004; Electronically published April 21, 2004

ABSTRACT: Because of the contingency and complexity of its subject matter, community ecology has few general laws. Laws and models in community ecology are highly contingent, and their domain is usually very local. This fact does not mean that community ecology is a weak science; in fact, it is the locus of exciting advances, with growing mechanistic understanding of causes, patterns, and processes. Further, traditional community ecological research, often local, experimental, and reductionist, is crucial in understanding and responding to many environmental problems, including those posed by global changes. For both scientific and societal reasons, it is not time to abandon community ecology.

Keywords: community ecology, general laws, introduced species, kelp, longleaf pine, red-cockaded woodpecker.

There are three separate issues here. First, does community ecology really not have general laws? Second, is the worth of community ecology as a science determined by the degree to which communities adhere to general laws? Third, whether community ecology has or will ever have general laws, we must study communities because understanding them is crucial to dealing with many key conservation and environmental issues.

Science and the Importance of General Laws

The first issue of whether community ecology has general laws can be dispensed with quickly. Except for very high-level laws, such as those of thermodynamics, that are so basic as to be ecologically uninteresting, I concede Lawton's point: the "general laws" of community ecology consist of relatively few fuzzy generalizations. Some of these, for example, the frequent top-down governance of ecosystems by large carnivores, have been gleaned from excellent scientific research and may be enormously useful

Simberloff, 2004

悲观主义者

Biol Philos
DOI 10.1007/s10539-009-9164-z

Is there a general theory of community ecology?

Joan Roughgarden

Roughgarden, 2009

中间派

Received: 3 June 2008 / A

Abstract Community ecology entered the 1970s with the belief that niche theory would supply a general theory of community structure. The lack of wide-spread empirical support for niche theory led to a focus on models specific to classes of communities such as lakes, intertidal communities, and forests. Today, the needs of conservation biology for metrics of "ecological health" that can be applied across types of communities prompts a renewed interest in the possibility of general theory for community ecology. Disputes about the existence of general patterns in community structure trace at least to the 1920s and continue today almost unchanged in concept, although now expressed through mathematical modeling. Yet, a new framework emerged in the 1980s from findings that community composition and structure depend as much on the processes that bring species to the boundaries of a community as by processes internal to a community, such as species interactions and co-evolution. This perspective, termed "supply-side ecology", argued that community ecology was to be viewed as an "organic earth science" more than as a biological science. The absence of a general theory of the earth would then imply a corresponding absence of any general theory for the communities on the earth, and imply that the logical structure of theoretical community ecology would consist of an atlas of models special to place and geologic time. Nonetheless, a general theory of community ecology is possible similar in form to the general theory for evolution if the processes that bring species to the boundary of a community are analogized to mutation, and the processes that act on the species that arrive at a community are analogized to selection. All communities then share some version of this common narrative, permitting general theorems to be developed pertaining to all ecological communities. Still, the desirability of a general theory of community ecology is debatable because the existence of a general theory suppresses diversity of thought

J. Roughgarden (✉)
Department of Biological Sciences, Stanford University, Stanford, CA 94305, USA
e-mail: joan.roughgarden@stanford.edu; joan@joandistrict6.com

Published online: 30 April 2009 Springer

VOLUME 85, NO. 2 THE QUARTERLY REVIEW OF BIOLOGY JUNE 2010

CONCEPTUAL SYNTHESIS IN COMMUNITY ECOLOGY

MARK VELLEND
Departments of Botany and Zoology, and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada, V6T 1Z4
E-MAIL: MVELLEND@INTERCHANGE.UBC.CA

KEYWORDS
dispersal, drift, community ecology, population genetics, selection, speciation

ABSTRACT
Community ecology is often perceived as a "mess," given the seemingly vast number of processes that can underlie the many patterns of interest, and the apparent uniqueness of each study system. However, at the most general level, patterns in the composition and diversity of species—the subject matter of community ecology—are influenced by only four classes of process: selection, drift, speciation, and dispersal. Selection represents deterministic fitness differences among species, drift represents stochastic changes in species abundance, speciation creates new species, and dispersal is the movement of organisms across space. All theoretical and conceptual models in community ecology can be understood with respect to their emphasis on these four processes. Empirical evidence exists for all of these processes and many of their interactions, with a predominance of studies on selection. Organizing the material of community ecology according to this framework can clarify the essential similarities and differences among the many conceptual and theoretical approaches to the discipline, and it can also allow for the articulation of a very general theory of community dynamics: species are added to communities via speciation and dispersal, and the relative abundances of these species are then shaped by drift and selection, as well as ongoing dispersal, to drive community dynamics.

Vellend, 2010

乐观主义者

群落学历史上的三次大论战

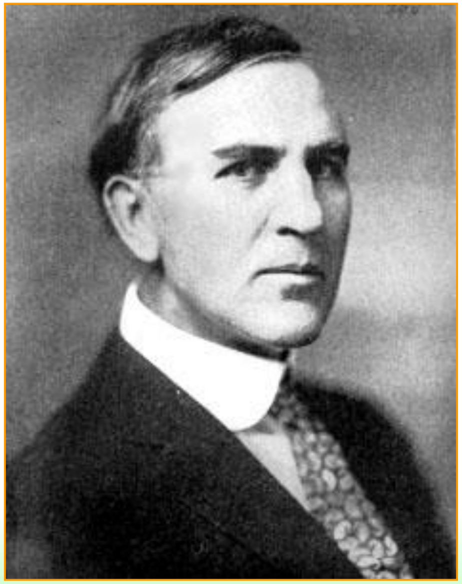
- 第一次（~1920年）：群落的本质
- 第二次（~1980年）：群落模式的真实性
- 第三次（~2000年）：局域与区域; 确定与随机

群落学历史上的三次大论战

- 第一次（~1920年）：群落的本质
- 第二次（~1980年）：群落模式的真实性
- 第三次（~2000年）：局域与区域; 确定与随机

群落的本质：机体论与个体论

- 群落是一个“有机的整体”还是“一盘散沙”？或者说，生物相互作用到底有多重要？

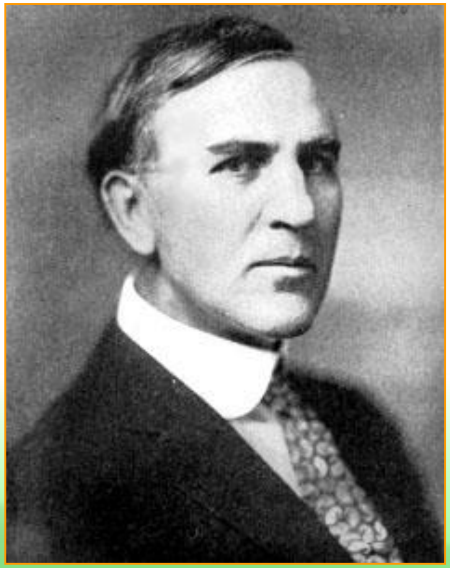


Federick Clements
(1874-1945)

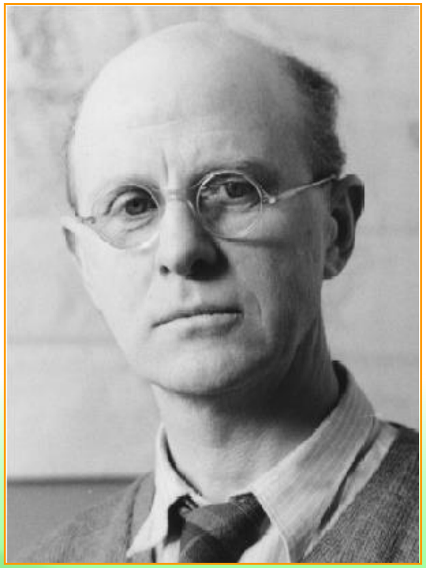
Henry A. Gleason
(1872-1975)

群落的本质：机体论与个体论

- 机体论：群落是高度有组织的物种组合体，边界清楚，可象物种那样进行自然的分类；高度强调种间相互作用的重要性；演替被类比为个体发育；
- 代表人物：**Clements**（植物）**– Elton**（动物）



Federick Clements
(1874-1945)



Charles S. Elton
(1900～1991)

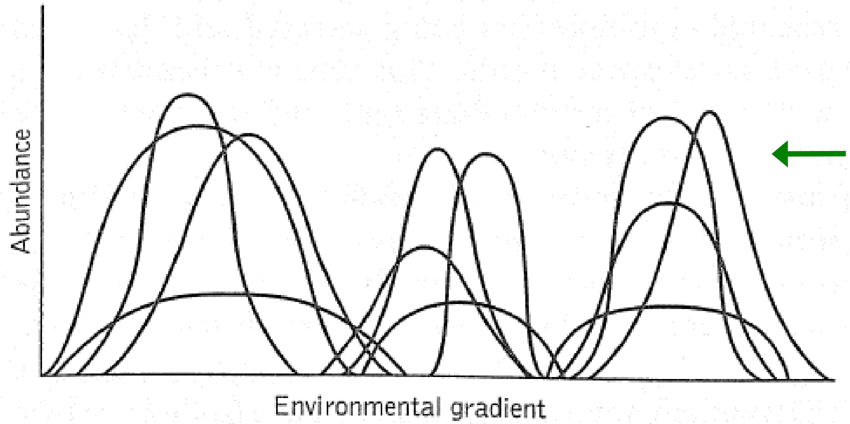
群落的本质：机体论与个体论

- 个体论：与机体论相反，各个物种独立的出现与消失而非紧密连锁在一起，群落无明确的边界，不能进行分类（而应排序）；否定种间相互作用在群落构建中的作用；演替不可以比拟为个体发育
- 代表人物：**Gleason (植物) – Andrewartha (动物；参与少)**

Henry A. Gleason
(1872-1975)

Herbert G Andrewartha
(1907-1992)

群落的本质：沿环境梯度的分布

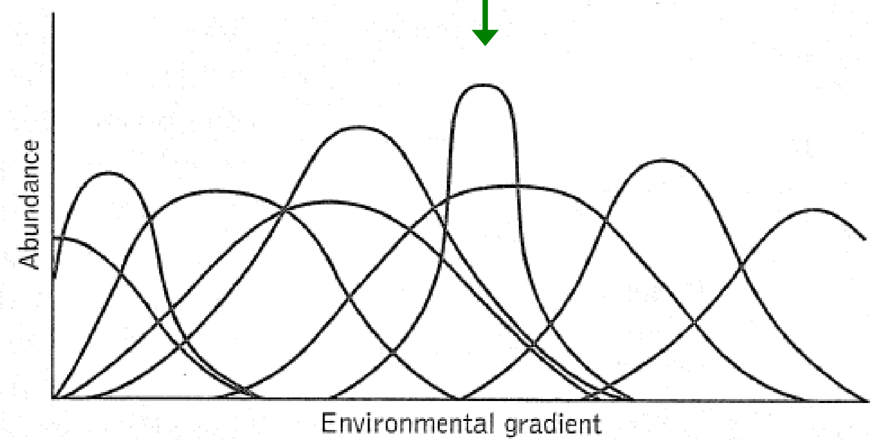


(a)

←机体论

Fig. 5.1 Diagrammatic representation of two models of vegetation.
(a) The model of Clements in which species' requirements coincide, leading to the separation of distinct 'communities'.

个体论
↓



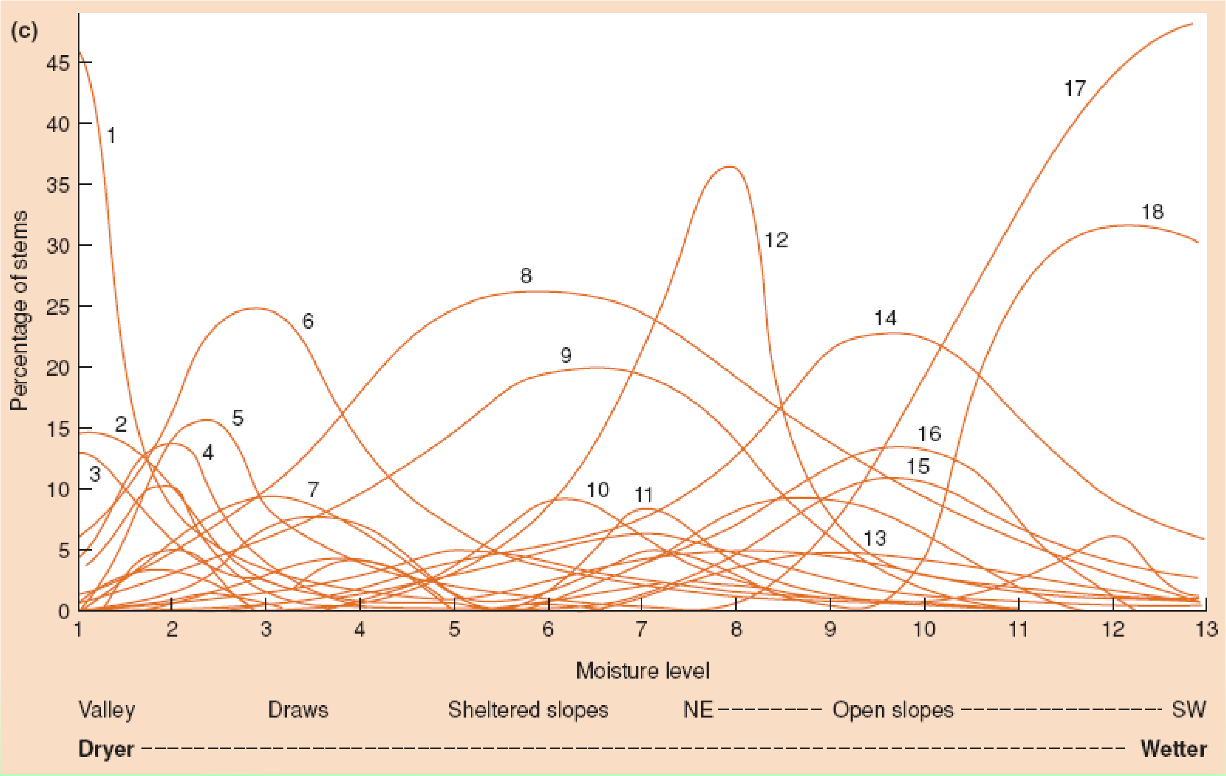
(b)

(b) The 'individualistic' model of Gleason in which each species is distributed independently and no clear 'communities' are apparent.

群落的边界问题

群落的本质：沿环境梯度的分布

- 植被分布数据支持Gleason的个体论！



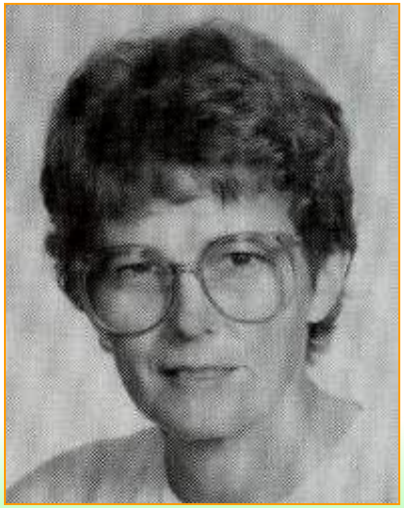
ROC, red oak–chestnut forest; S, spruce forest; SF, spruce–fir forest; WOC, white oak–chestnut forest. Major species: 1, *Halesia monticola*; 2, *Aesculus octandra*; 3, *Tilia heterophylla*; 4, *Betula alleghaniensis*; 5, *Liriodendron tulipifera*; 6, *Tsuga canadensis*; 7, *B. lenta*; 8, *Acer rubrum*; 9, *Cornus florida*; 10, *Carya alba*; 11, *Hamamelis virginiana*; 12, *Quercus montana*; 13, *Q. alba*; 14, *Oxydendrum arboreum*; 15, *Pinus strobus*; 16, *Q. coccinea*; 17, *P. virginiana*; 18, *P. rigida*. (After Whittaker, 1956.)

Robert H. Whittaker
(1920-1980)

孢粉学证据支持个体论

- 北美森林冰期后恢复：不同物种共进退？还是物种的组合被完全打破、各个物种分别独立的对气候变化做出响应？

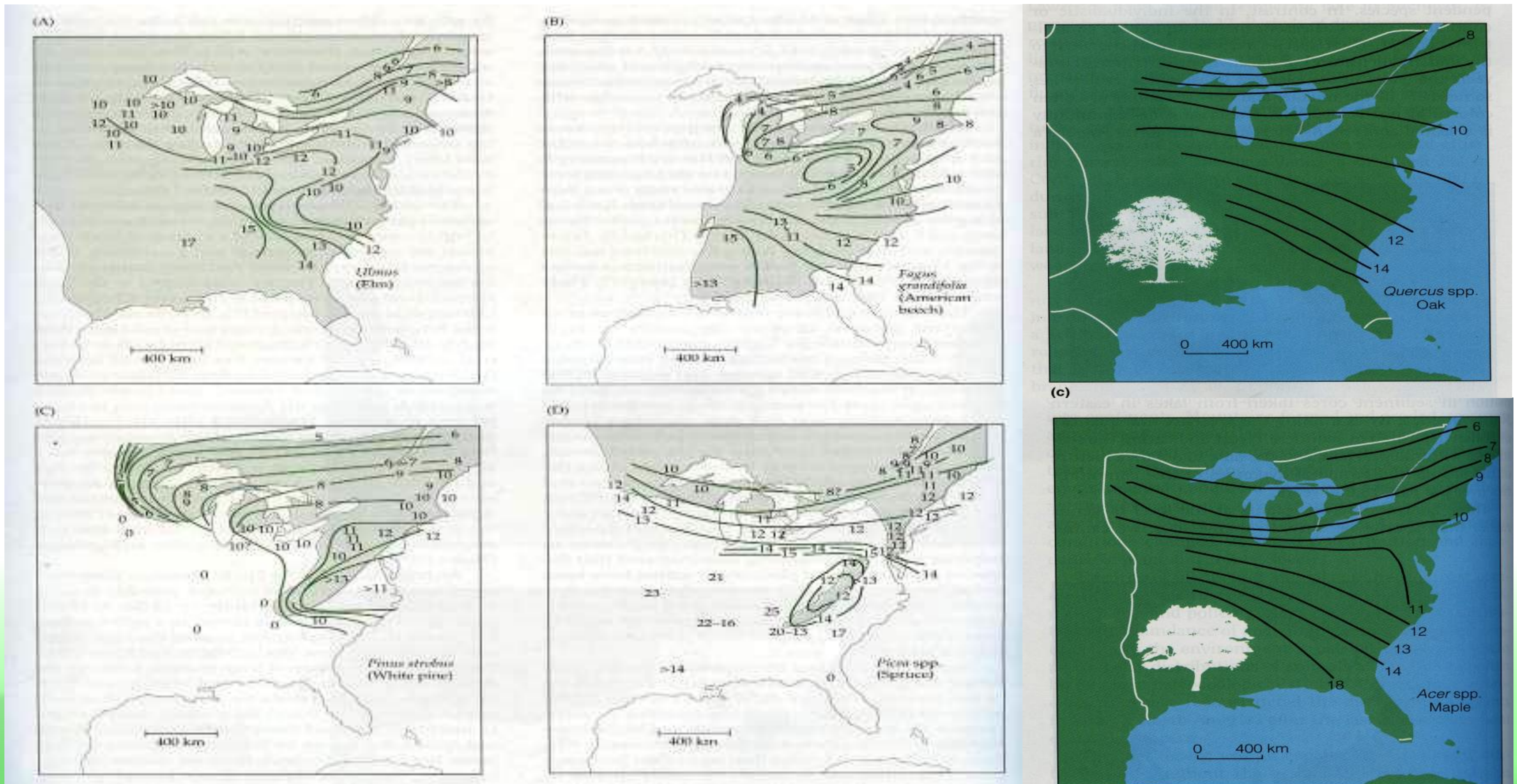
Lucy Brown
(1889-1971)



Margaret Davis
(b. 1931-)

孢粉学证据支持个体论

- 现时植物群落的各个物种是末次冰期后从不同地点、在不同时期回迁来的，并非紧密连结的“共进退”



亲缘地理学与物种分布模型

- 基本假设：各个物种独立地对环境变化作出反应，即Gleason范式
  - 忽略了生物相互作用对物种分布的影响
  - 忽略了扩散限制的作用

PROCEEDINGS OF THE ROYAL SOCIETY B

FirstCite e-publishing

Proc. R. Soc. B
doi:10.1098/rspb.2009.1272
Published online

Review

Refugia revisited: individualistic responses of species in space and time

John R. Stewart[1], Adrian M. Lister[1], Ian Barnes[2] and Love Dalén[2,*,†]

[1]*Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK*
[2]*School of Biological Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK*

Climate change in the past has led to significant changes in species' distributions. However, how individual species respond to climate change depends largely on their adaptations and environmental tolerances. In the Quaternary, temperate-adapted taxa are in general confined to refugia during glacials while cold-adapted taxa are in refugia during interglacials. In the Northern Hemisphere, evidence appears to be mounting that in addition to traditional southern refugia for temperate species, cryptic refugia existed in the North during glacials. Equivalent cryptic southern refugia, to the south of the more conventional high-latitude polar refugia, exist in montane areas during periods of warm climate, such as the current interglacial. There is also a continental/oceanic longitudinal gradient, which should be included in a more complete consideration of the interaction between species ranges and climates. Overall, it seems clear that there is large variation in both the size of refugia and the duration during which species are confined to them. This has implications for the role of refugia in the evolution of species and their genetic diversity.

REVIEW

The evolutionary consequence of the individualistic response to climate change

J. R. STEWART

Department of Palaeontology, Natural History Museum, London, UK

Keywords:
climate change;
coevolution;
Gleasonian;
nonanalogue ecology (no-analogue);
quaternary.

Abstract

The Quaternary fossil record has abundant evidence for ecologically non-analogue communities made up of combinations of modern taxa not seen in sympatry today. A brief review of the literature detailing these nonanalogue communities is given with a discussion of their various proposed causes. The individualistic, Gleasonian, response of species to climate and environmental change is favoured by many. The degree to which communities are nonanalogue appears to increase with greater time depth, and this progressive process is a necessary outcome of the individualistic response of species to climate change through time. In addition, it is noted that populations within species, as well as the species as a whole, respond individualistically. This paper proposes that many elements of nonanalogue communities are extinct populations, which may explain their environmentally anomalous combinations. These extinct populations are, by definition, lineages without descendents. It is further proposed that the differential extinction of populations, as a result of continuous ecological reassembly, could amount to a significant evolutionary phenomenon.

群落的本质：争论仍在继续

- 大多数生态学家走中间路线：一方面承认群落不是有机体，另一方面又认为种间相互作用制约着生物的分布与多度！
- 集成群落(Integrated Community)
- 根深蒂固的信念：种间互作对群落结构具有重要影响，即：

整体大于部分之和！

Rethinking plant community theory

Christopher J. Lortie, Rob W. Brooker, Philippe Choler, Zaal Kikvidze, Richard Michalet, Francisco I. Pugnaire and Ragan M. Callaway, Division of Biological Sciences, University of Montana, Missoula, MT, 59812, USA (chris@onepoint.ca).

Plant communities have traditionally been viewed as either a random collection of individuals or as organismal entities. For most ecologists however, neither perspective provides a modern comprehensive view of plant communities, but we have yet to formalize the view that we currently hold. Here, we assert that an explicit re-consideration of formal community theory must incorporate interactions that have recently been prominent in plant ecology, namely facilitation and indirect effects among competitors. These interactions do not support the traditional individualistic perspective. We believe that rejecting strict individualistic theory will allow ecologists to better explain variation occurring at different spatial scales, synthesize more general predictive theories of community dynamics, and develop models for community-level responses to global change. Here, we introduce the concept of the integrated community (IC) which proposes that range from highly natural plant communities individualistic to highly interdependent depending on synergism among: (i) stochastic processes, (ii) the abiotic tolerances of species, (iii) positive and negative interactions among plants, and (iv) indirect interactions within and between trophic levels. All of these processes are well accepted by plant ecologists, but no single theory has sought to integrate these different processes into our concept of communities.

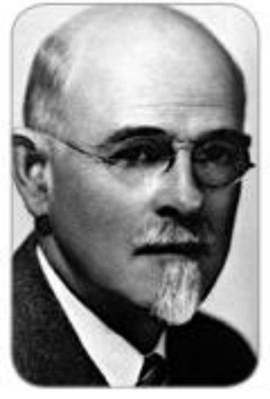
Gleason clearly presents modern misinterpretations of his ideas but does not conclude with a call to an appropriate definition of individualistic theory (Nicholson and McIntosh 2002).

While it is tempting to dismiss this legacy as ancient history and argue that we have moved beyond this, the bottom line is that although modern experiments are much more multifactorial and often consider many species within a community, there is still a bias in plant ecology to structure research and interpret results from an individualistic perspective. Certainly, the study of individualistic attributes such as physiological tolerance or competitive ability has led to very successful research on the importance of the environment and competition as factors structuring plant communities. Also without question, facilitation and its importance has also been clearly demonstrated (Bruno et al. 2003). Nonetheless, both processes are still interpreted primarily in the

Lortie C.J. et al. 2004. Oikos, 107:433-438

生态位理论的兴起

- 生态学家强调种间相互作用（如竞争）的重要性，导致了生态位概念的产生及其理论的兴起
- 竞争排除法则：占有相同生态位的物种不能共存



Joseph Grinnell
(1877-1939)

Charles S. Elton
(1900-1991)

G. Evelyn Hutchinson
(1903-1991)

不同物种占据不同生态位?

MacArthur, R. H. 1958. Population ecology of some warblers of north-eastern coniferous forests. *Ecology* 39:599-619.

MacArthur's warbler

极限相似性

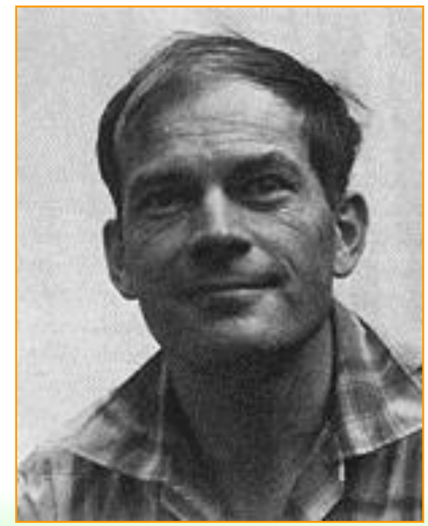
- 以”竞争排斥法则”为基础，**Hutchinson** 和**MacArthur**进一步提出了“极限相似性”的概念，即物种间的生态学相似性存在一个上限，超过这个阈值物种不能共存

Vol. 101, No. 921 The American Naturalist September–October, 1967

THE LIMITING SIMILARITY, CONVERGENCE, AND DIVERGENCE OF COEXISTING SPECIES

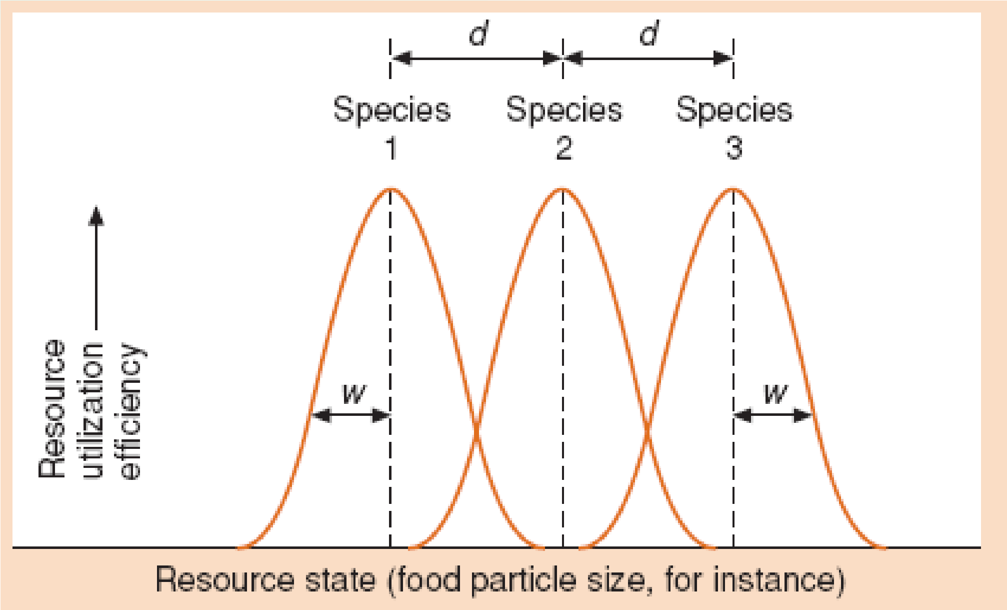
ROBERT MACARTHUR AND RICHARD LEVINS*

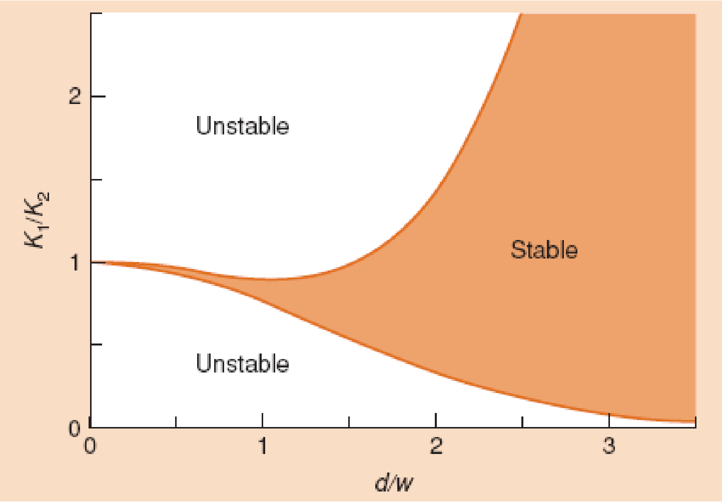
Department of Biology, Princeton University, Princeton, New Jersey, and



Robert H. MacArthur (1930-1972)

极限相似性





d/w≈1?

极限相似性预测群落饱和？

Robert M. May (b.1936)

Robert H. MacArthur (1930-1972)

生态位理论与群落模式

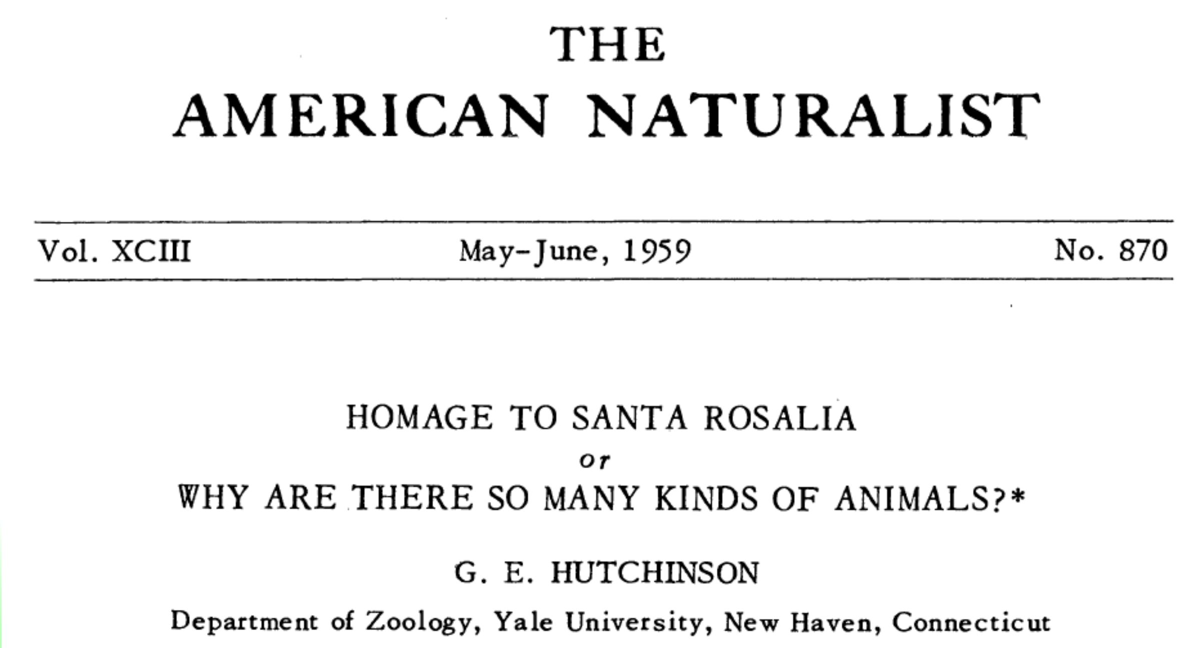
- 假设竞争塑造群落结构（合理性不证自明?），那么在极限相似性原理基础上，可对群落水平上物种分布模式给出若干预测，如：

  - Hutchinson动物体型大小比率
  - 特征替代
  - 群落装配规则

群落模式 —— 体型大小比率

- 体型大小—**Hutchinson**比率

——长度比为1.3：1；重量比则为2：1



THE

AMERICAN NATURALIST

Vol. XCIII   May–June, 1959   No. 870

HOMAGE TO SANTA ROSALIA

or

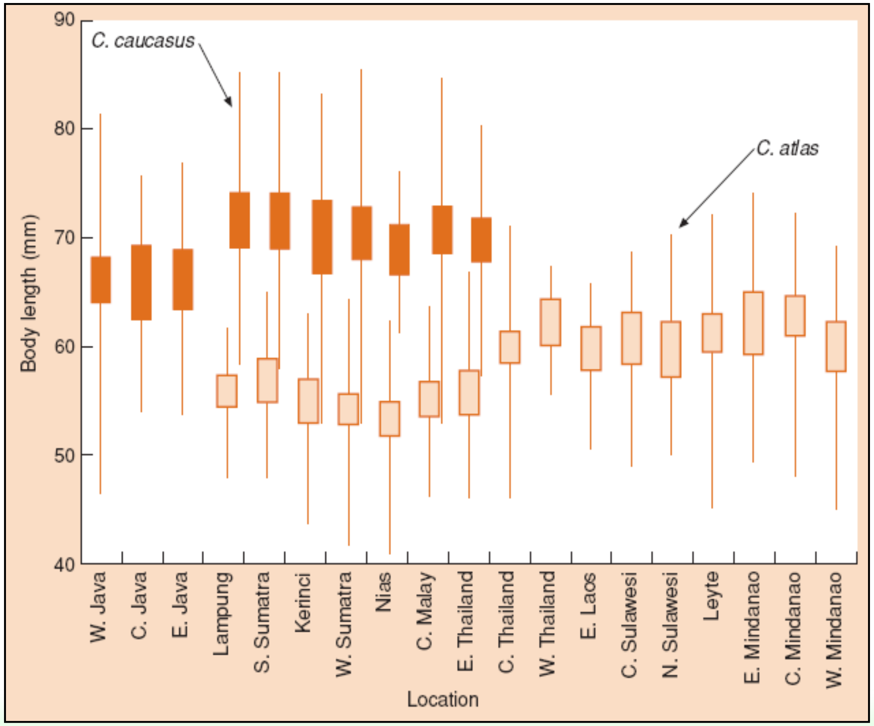
WHY ARE THERE SO MANY KINDS OF ANIMALS?*

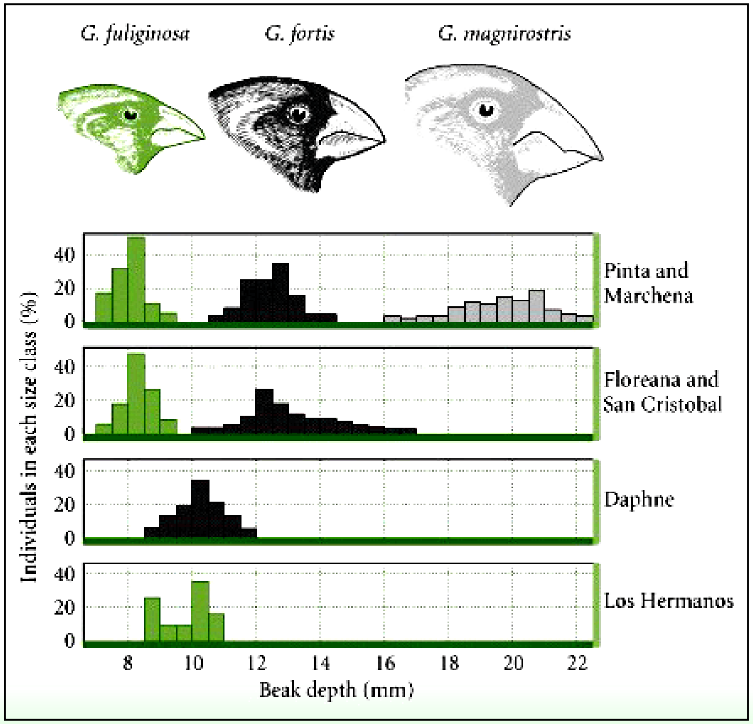
G. E. HUTCHINSON

Department of Zoology, Yale University, New Haven, Connecticut

G. Evelyn Hutchinson (1903-1991)

群落模式 —— 特征替代





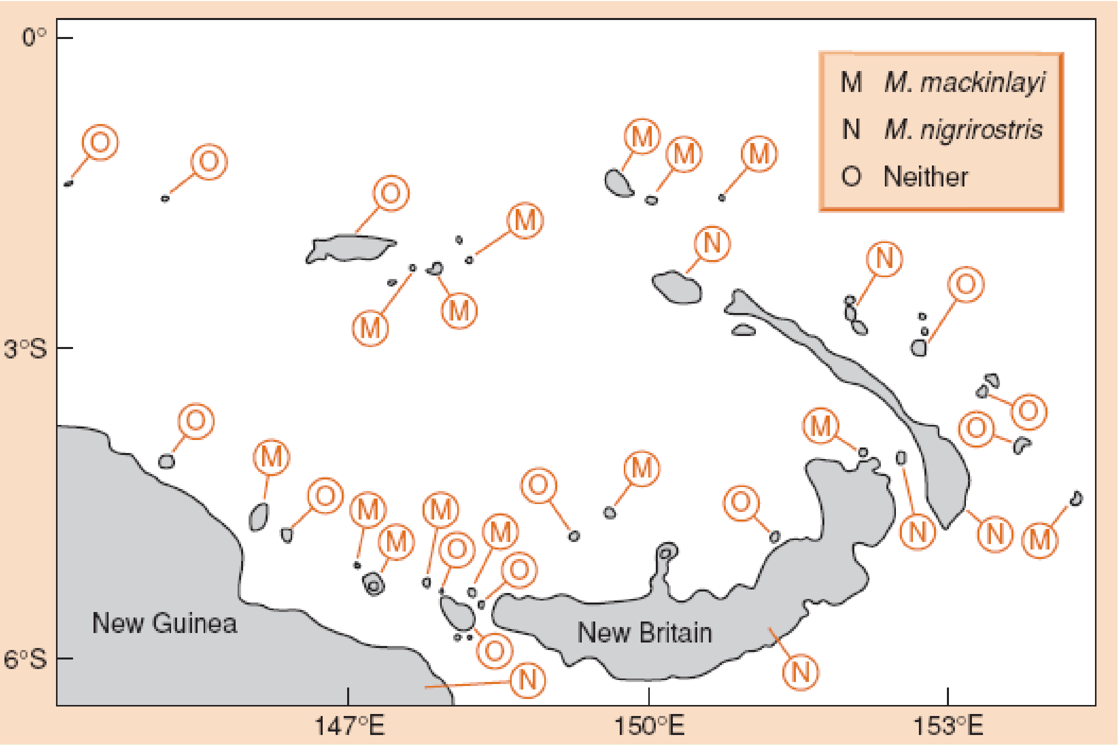
Giant rhinoceros beetles in Southeast Asia

Galápagos ground finches

群落模式 —— 装配规则

物种分布问题

群落装配规则之一是某些鸟类物种对从不共同出在同一岛屿，或者说，如果出现在一起，那么其中一个种将会竞争排斥另一个种(Diamond 1975)



两个近缘鸟类种的棋盘分布模式

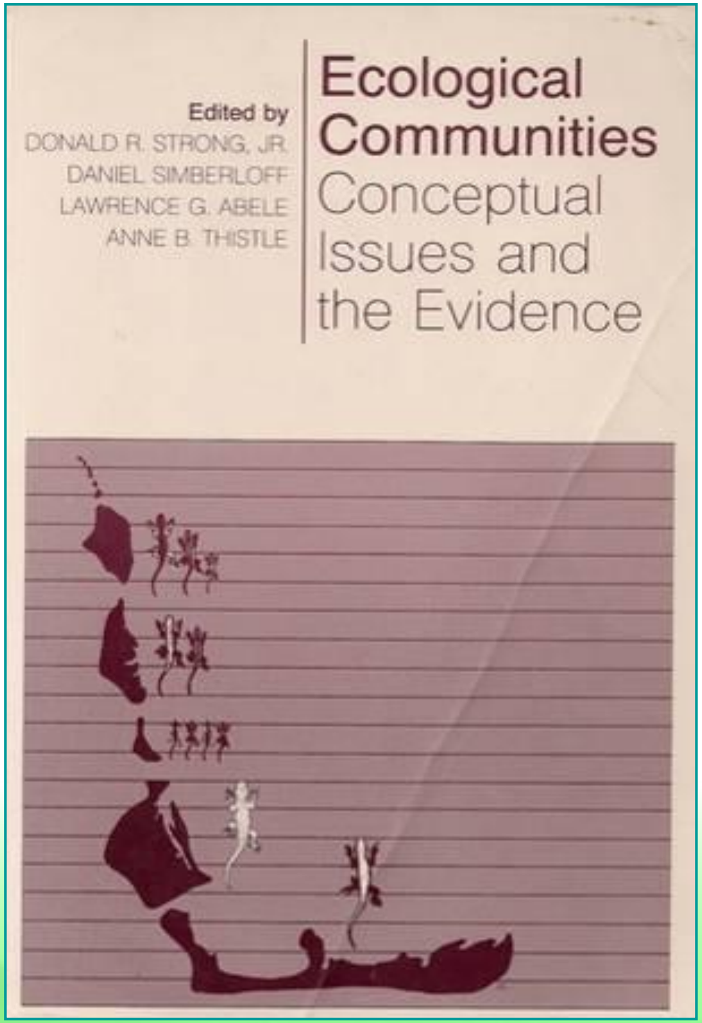
群落学历史上的三次大论战

- 第一次（~1920年）：群落的本质
- 第二次（~1980年）：群落模式的真实性
- 第三次（~2000年）：局域与区域; 确定与随机

群落的模式与过程：统计检验

- 与生态位理论相关的模式和过程并没有进行严格的统计检验；这些模式是否真正存在，所设想的内在过程是否确实起作用，要打个问号“ ？ ”

- 鉴定模式与过程的真实性，在1980年左右引发了一次激烈的争论！



群落的模式与过程：统计检验

- **体型大小－Hutchinson比率**

Simberloff & Boecklen构造了零假设进行统计检验，发现原来文献中声称获得了Hutchinson 1.3 比率的工作只有1/3达到统计显著

Daniel Simberloff

Evolution, 35(6), 1981, pp. 1206–1228

SANTA ROSALIA RECONSIDERED: SIZE RATIOS AND COMPETITION

DANIEL SIMBERLOFF AND WILLIAM BOECKLEN
Department of Biological Science, Florida State University, Tallahassee, Florida 32306

Received July 11, 1980. Revised January 14, 1981

"When Prof. Buckland, the eminent osteologist and geologist, discovered that the relics of St. Rosalia at Palermo, which had for ages cured diseases and warded off epidemics, were the bones of a goat, this fact caused not the slightest diminution in their miraculous power."

A. D. White, 1896, p. 29

Hutchinson's (1959) seminal paper, "Homage to Santa Rosalia *or* Why are

chel, 1975; Hespenheide, 1975; Robison, 1975; Inouye, 1977, 1978; Uetz, 1977; May, 1978; Pearson and Mury, 1979; Edwards and Emberton, 1980).

2) Three or more ecologically similar coexisting species tend to have constant size ratios between species adjacent in a size-ranking, though the constant

群落的模式与过程：统计检验

- 物种分布问题－群落装配规则

Connor & Simberloff 提出，Diamond 所观察到的棋盘分布也可以通过异域物种分化和扩散限制所得出，并非一定是竞争所致

Ecology, 60(6), 1979, pp. 1132–1140

THE ASSEMBLY OF SPECIES COMMUNITIES: CHANCE OR COMPETITION?[1]

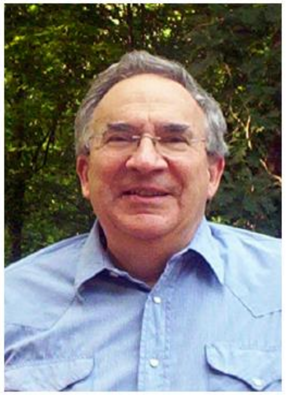
EDWARD F. CONNOR[2,3]
Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22903 USA

AND

DANIEL SIMBERLOFF
Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306 USA

Eminent Ecologist Award
Daniel Simberloff

Daniel Simberloff is not only eminent in ecology today: for many years, he has been the quintessential ecological iconoclast.



Any undergraduate student who has ever had an ecology class is familiar with Dan Simberloff's work. His experimental island biogeography papers with E.O. Wilson are textbook classics, elegant experimental studies that appeared to beautifully confirm the emerging theory of island biogeography. Simberloff rigorously tested a nascent body of theory, which won him the Mercer Award with Wilson in 1971. If he had done nothing else, this work would have assured him lasting prominence. But many ecologists were dismayed by his 1976 *Science* paper, in which he threw stones at his own glass house, arguing that most of the insect turnover in this assemblage was ephemeral and did not therefore confirm the predictions of the theory. Few ecologists among us have the courage to publicly challenge our own paradigm in this way, particularly once it has become widely accepted. As society began to embrace island biogeography and extend it to designing nature reserves, Simberloff was further cast as a *bete noire* when he argued (backed by plenty of empirical data) that large reserves are not always the best conservation option.

In the late 1970's and early 1980's, Dan Simberloff took on the MacArthurian paradigm of competitively structured communities, championing the null models approach in community ecology. In so doing, he forever changed the face of our field. The shock waves from this debate still ripple through ecology. His work forced ecologists to ask: what would these patterns look like if mechanism *x* were not in operation? Boiled down to its essence, his arguments have been summarized as "rely on the data to tell you how nature operates; don't simply find the patterns that you're supposed to find."

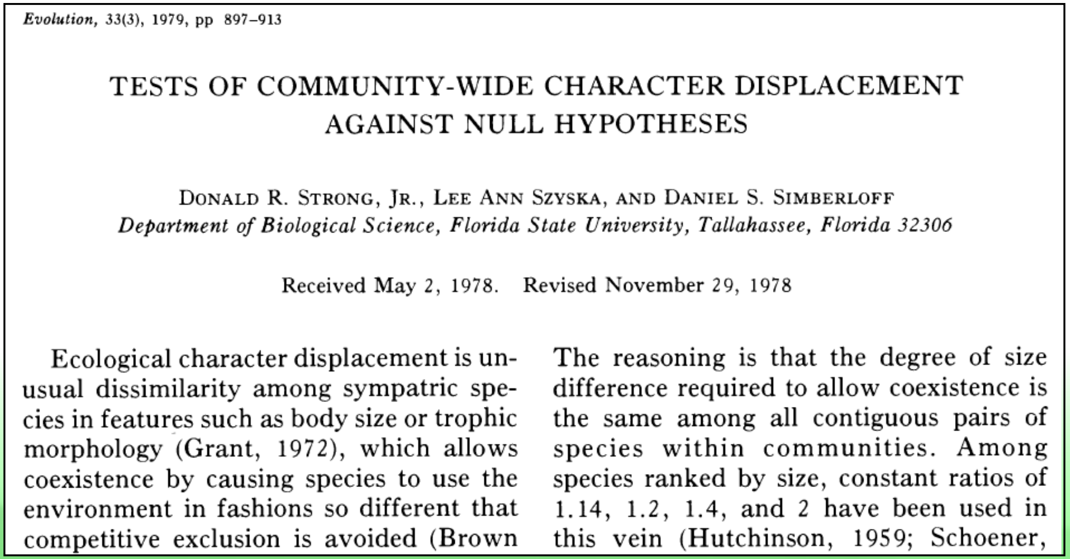
His more recent work has been equally notorious. He has written pointed and controversial critiques about the wisdom of biological control, calling attention to the threats imposed by invasive species and raising the specter of "invasional meltdown." His criticisms of biological control gone bad (and his data to support those criticisms) are slowly reaching land managers and the general public. He has become a world expert on the threats imposed by invasive species.

These are just the highlights. In almost every aspect of his research program, he has been a leader and has demanded rigorous tests and critical interpretations of data. His approach — know your organisms, ask interesting questions, and deal with the data rigorously — has been an example for countless numbers of ecologists and has made ecology a better, more quantitative science.

群落的模式与过程：统计检验

- **特征替代问题**

Strong et al. (1979) 发现，所谓的特征替代都不能和与从物种库中随机挑选组装得到的结果有显著差异


Evolution, 33(3), 1979, pp 897–913

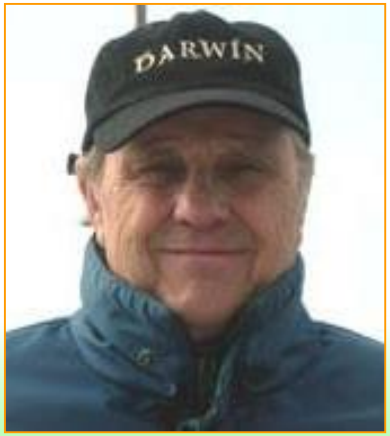
TESTS OF COMMUNITY-WIDE CHARACTER DISPLACEMENT AGAINST NULL HYPOTHESES

DONALD R. STRONG, JR., LEE ANN SZYSKA, AND DANIEL S. SIMBERLOFF
Department of Biological Science, Florida State University, Tallahassee, Florida 32306

Received May 2, 1978. Revised November 29, 1978

Ecological character displacement is unusual dissimilarity among sympatric species in features such as body size or trophic morphology (Grant, 1972), which allows coexistence by causing species to use the environment in fashions so different that competitive exclusion is avoided (Brown

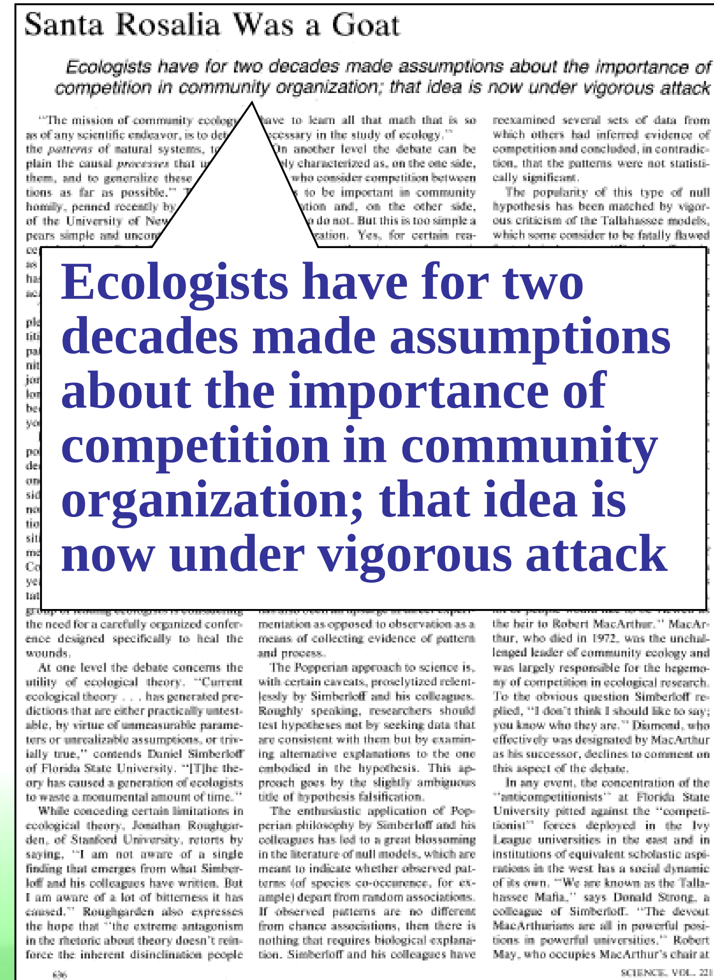
The reasoning is that the degree of size difference required to allow coexistence is the same among all contiguous pairs of species within communities. Among species ranked by size, constant ratios of 1.14, 1.2, 1.4, and 2 have been used in this vein (Hutchinson, 1959; Schoener,



Donald Strong
Ecology现任主编

群落的模式与过程：统计检验

- 模式的识别，以及判断产生模式的内在过程，都需要建立零模型，进而形成零假设，进行统计检验；
- 如果未能拒绝零假设，群落是随机组装的吗？
- 竞争是否存在？



本次争论的一个显著特点是植物学家基本没有参与!

群落学历史上的三次大论战

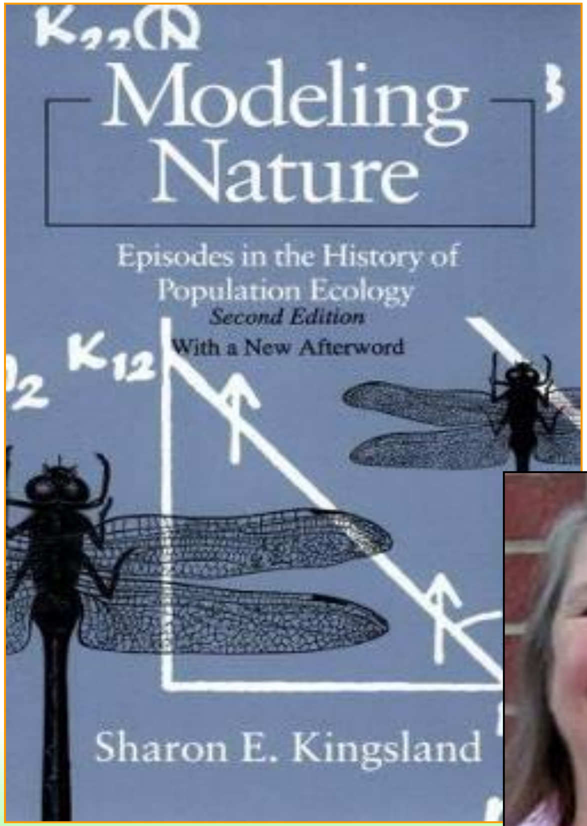
- 第一次（~1920年）：群落的本质
- 第二次（~1980年）：群落模式的真实性
- 第三次（~2000年）：局域与区域; 确定与随机

生态位理论面临的问题

- 由“竞争过程”预测的一些群落模式其真实性受到了挑战（统计检验）
- 浮游生物悖论：环境条件非常均一的几毫升水体内共存着至少30种以上的浮游藻类
- 群落看作为封闭系统，忽视了区域过程和特定历史事件的作用（历史的湮没）
- 无法解释一些宏观群落结构（如物种相对多度模式、种-面积关系等）

局域决定论与历史的湮没

- 经典生态位理论预测局域生态过程（竞争、捕食和干扰等）塑造了群落结构，而区域和历史过程的影响可以忽略！
- Kingsland称为“历史的湮没”(Eclipse of history)



Sharon E. Kingsland

区域过程在群落构建中的作用

- 如果局域的种间相互作用完全决定了群落结构，可以预测：
  - 在相似生境条件下群落结构应该趋于相同
  - 区域种多样性与局域(群落)种多样性相互独立
  - 群落对物种入侵具有抵抗力

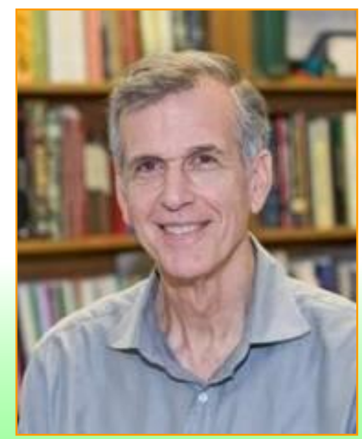
Community Diversity: Relative Roles of Local and Regional Processes

1987 Science

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

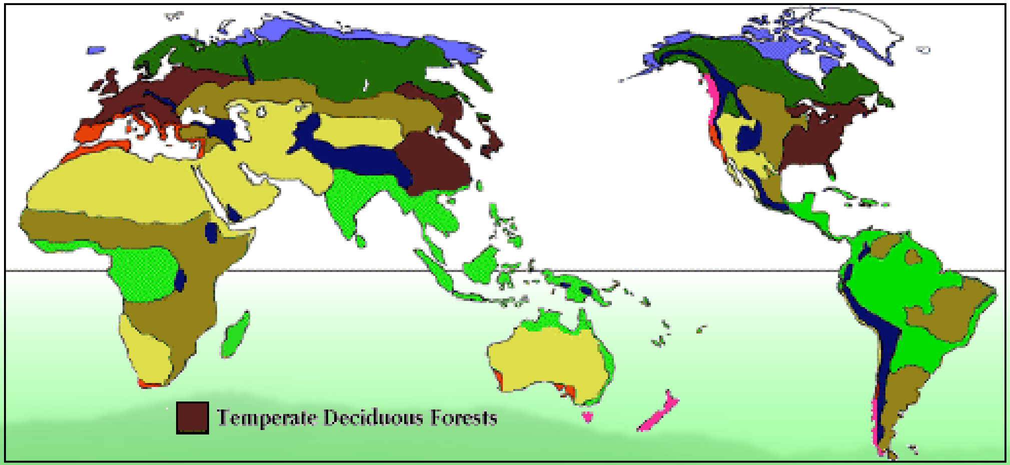
similarity exceeded some limit, or if a species could not persist when its ecological niche were reduced below some minimum viable size, the number of species in a community would be determined in a manner analogous to the packing of balls in a box. Accordingly, one would expect to find regular spacing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



Robert Ricklefs (1943-)

温带森林的多样性异常

- 相似生境的群落往往具有显著不同的物种多样性；温带森林：欧洲(120万km^2；124种)、东亚(120万km^2；729种)、北美东部(180万km^2；253种)



局域多样性与区域多样性相关

- 生态位理论预测局域饱和，与实际数据不符！

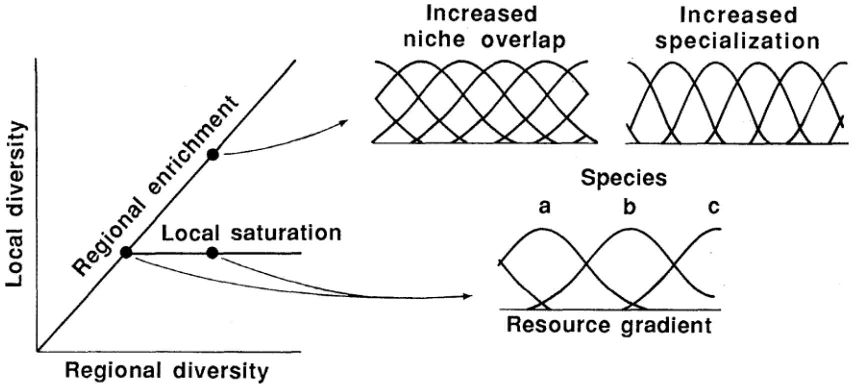
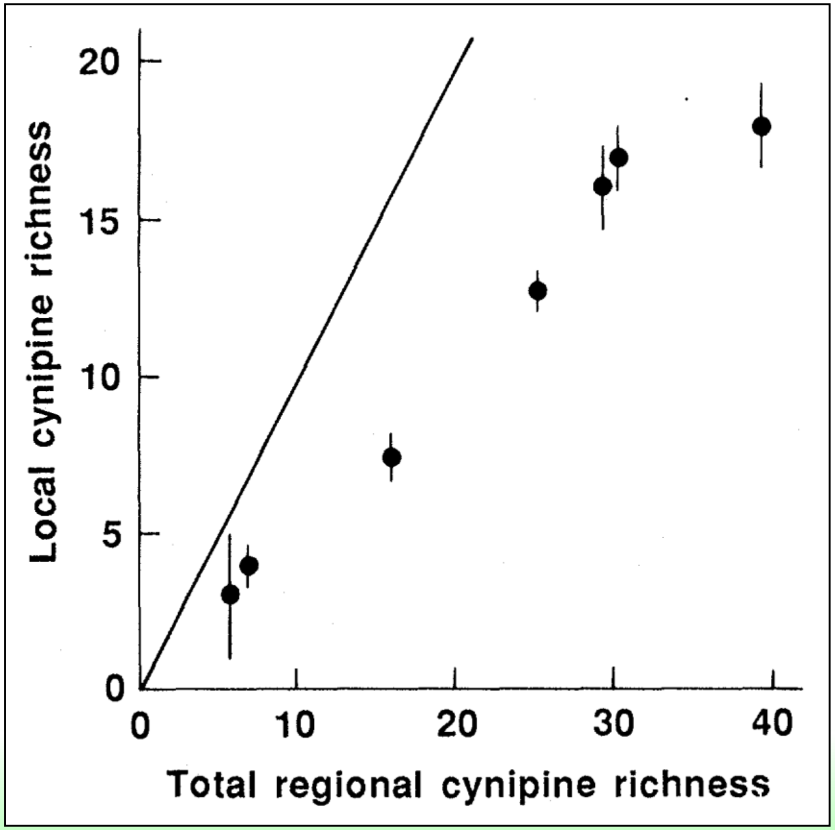
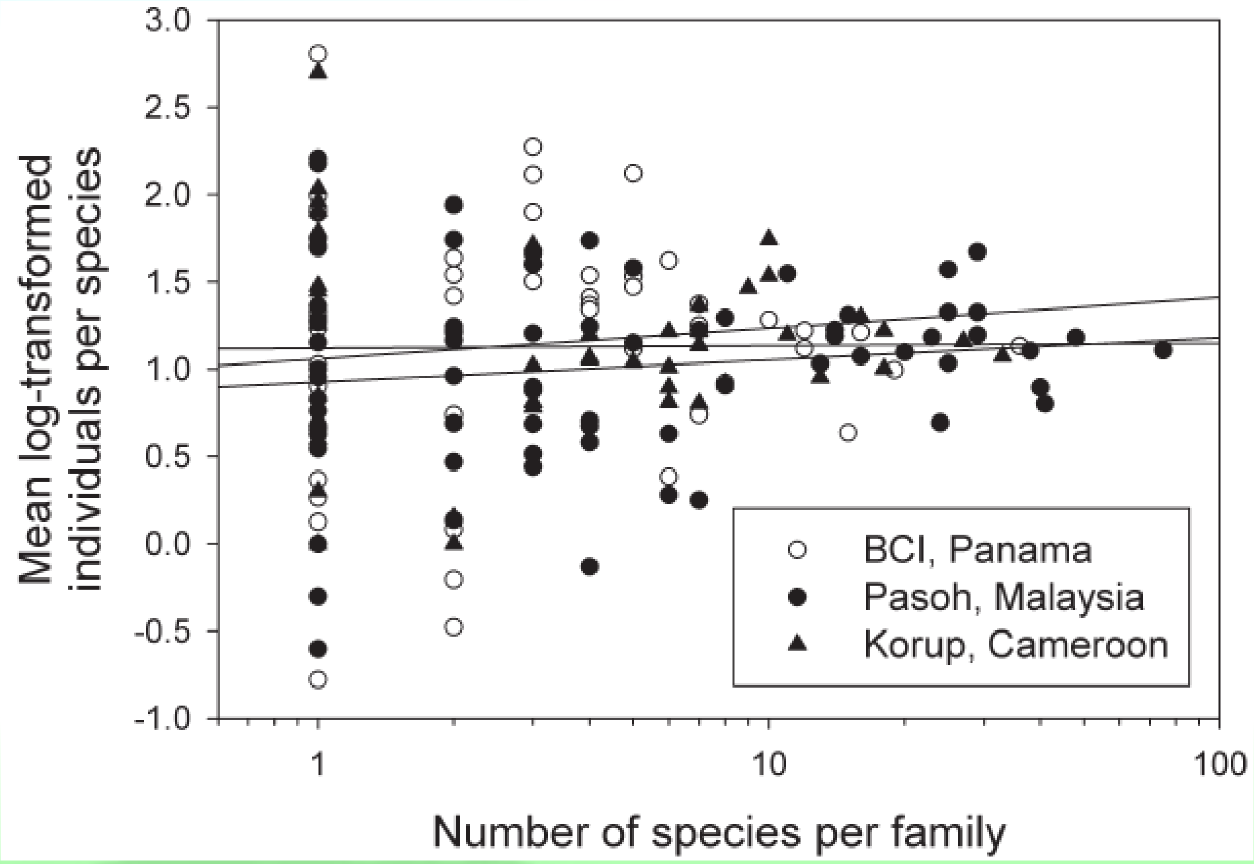


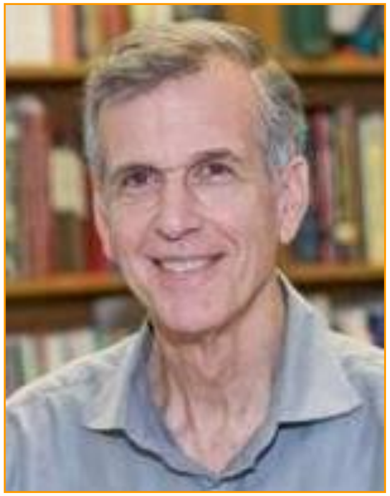
Fig. 1. Two models of the relation between local species richness and regional diversity. According to the saturation model, the coexistence of



Cornell, H.V. 1985. Local and regional richness of cynipine gall wasps on California oaks. *Ecology* 66: 1247-1260.

类群内物种数与多度/分布的关系？



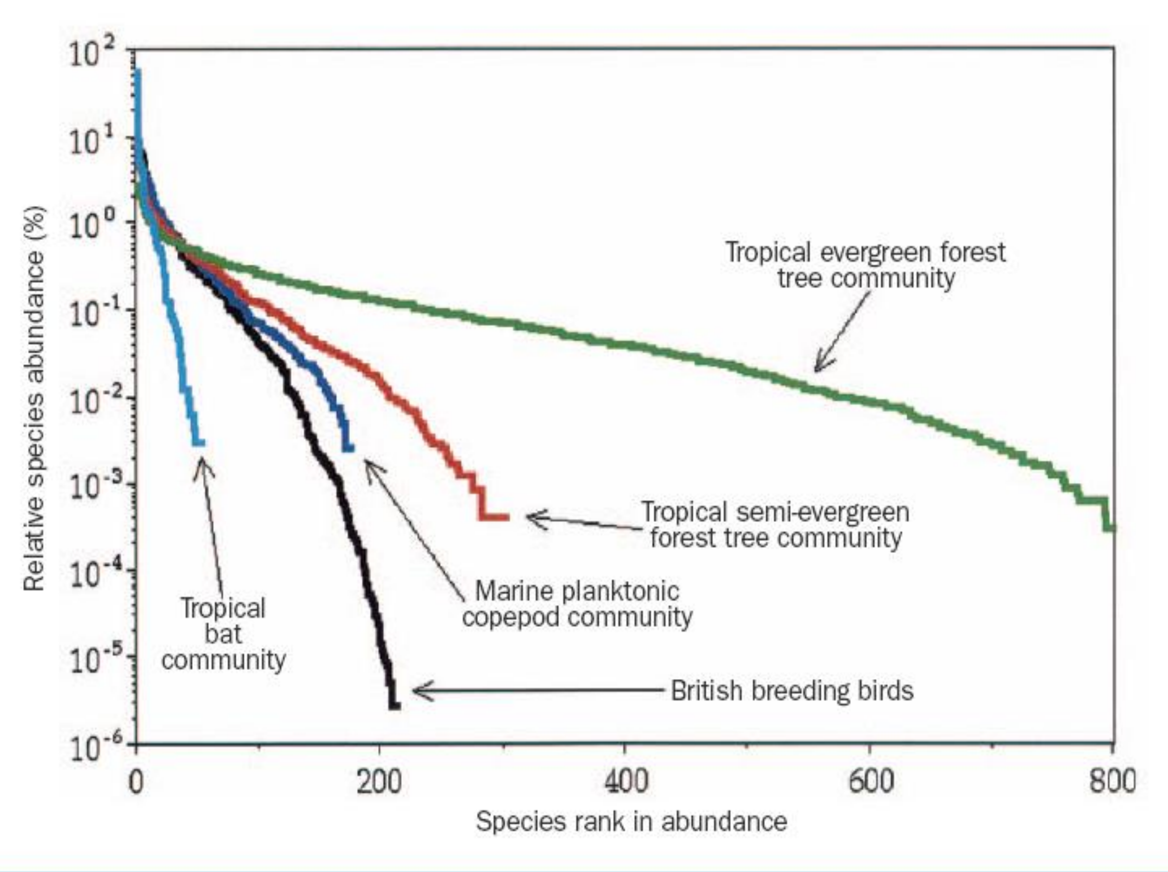


Robert E. Ricklefs (b. 1943)

Ricklefs R. 2012. Naturalists, Natural History, and the Nature of Biological Biodiversity. American Naturalist, 179:423-435.

生态位理论不能说明群落结构

对数正态分布是最常见的物种相对多度分布，适用于许多不同类型的群落。



不同类型的生物群落表现出相同的物种多度分布模式，是否意味着生物学细节是无关紧要的？

生态位理论的关键证据很少

Ecology, 91(11), 2010, pp. 3153–3164

生态位分化必然导致“稀有种优势”！

即如果群落内任何一种变得特别稀少，那么该种数量将会表现出增加趋势！

On the evidence for species coexistence: a critique of the coexistence program

Adam M. Siepielski and Mark A. McPeek[1]

Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA

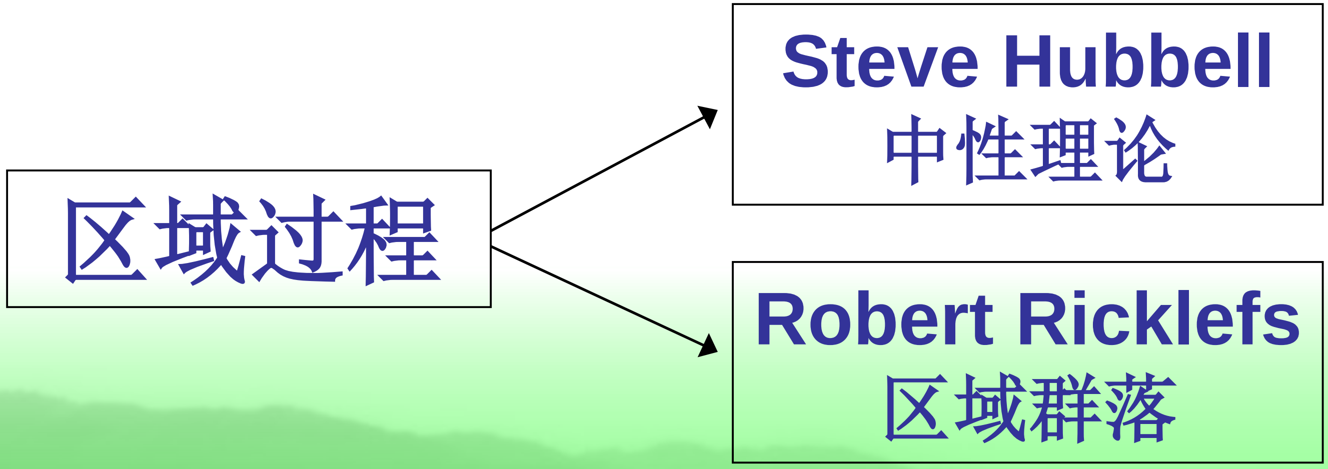
Abstract. A major challenge in ecology is to understand how the millions of species on Earth are organized into biological communities. Mechanisms promoting coexistence are one such class of organizing processes, which allow multiple species to persist in the same trophic level of a given web of species interactions. If some mechanism promotes the coexistence of two or more species, each species must be able to increase when it is rare and the others are at their typical abundances; this invasibility criterion is fundamental evidence for species coexistence regardless of the mechanism. In an attempt to evaluate the level of empirical support for coexistence mechanisms in nature, we surveyed the literature for empirical studies of coexistence at a local scale (i.e., species found living together in one place) to determine whether these studies satisfied the invasibility criterion. In our survey, only seven of 323 studies that drew conclusions about species coexistence evaluated invasibility in some way in either observational or experimental studies. In addition, only three other studies evaluated necessary but not sufficient conditions for invasibility (i.e., negative density dependence and a trade-off in performance that influences population regulation). These results indicate that, while species coexistence is a prevalent assumption for why species are able to live together in one place, critical empirical tests of this fundamental assumption of community structure are rarely performed. These tests are central to developing a more robust understanding of the relative contributions of both deterministic and stochastic processes structuring biological communities.

Key words: coexistence; density dependence; empirical evidence; invasibility; phenotypic trade-offs; species diversity.

“稀有种优势”的经验证据很少

开放群落：区域过程的重要性

- 传统的生态位理论：群落是一个封闭系统，只关注局域过程
- 物种库的形成：影响物种库大小的因素包括物种分化速率，灭绝速率，扩散等



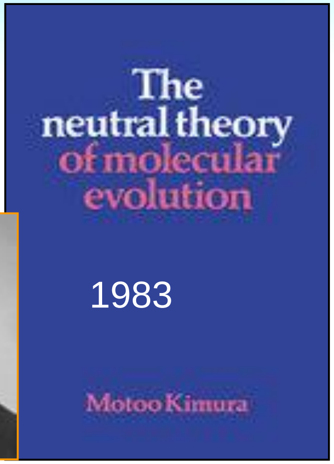
群落生态学的发展趋势

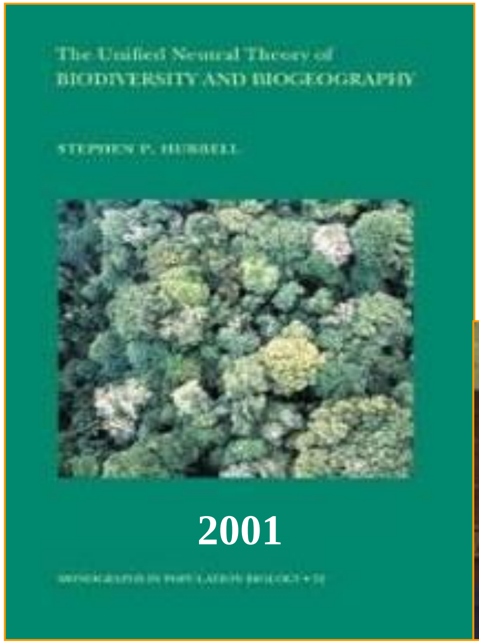
从局域到区域（**local→regional**）

1. 中性理论：承认竞争存在，但结局是随机的。迁入与竞争结局的随机性（漂变）共同作用决定了局域群落结构。不承认物种差异有任何作用

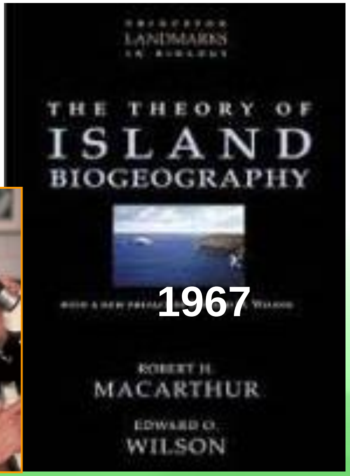
2. 区域群落理论：区域过程彻底决定了（局域）群落结构；局域群落内生态过程（如竞争）的作用被迁入过程所彻底掩盖。承认物种差异的作用

中性理论





Steve Hubbell
（b.1943）



中性理论承认竞争存在，
但否认其竞争排斥作用！

中性理论10周年

2001 - 2011

Review

Cell PRESS

The Unified Neutral Theory of Biodiversity and Biogeography at Age Ten

James Rosindell[1,2], Stephen P. Hubbell[3,4] and Rampal S. Etienne[5,6]

[1] Institute of Integrative and Comparative Biology, University of Leeds, Leeds, UK, LS2 9JT
[2] Institute of Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, ID 83844, USA
[3] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA
[4] Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, Repu
[5] Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Gro
11103, 9700 CC Groningen, The Netherlands
[6] Department of Soil and Physical Sciences, Faculty of Agriculture and Life Sciences, Lincoln University, Box 84, L
Christchurch, New Zealand

A decade has now passed since Hubbell published *The Unified Neutral Theory of Biodiversity and Biogeography*. Neutral theory highlights the importance of dispersal limitation, speciation and ecological drift in the natural world and provides quantitative null models for assessing the role of adaptation and natural selection. Significant advances have been made in providing methods for understanding neutral predictions and comparing them with empirical data. In this review, we describe the current state-of-the-art techniques and ideas in neutral theory and how these are of relevance to ecology. The future of neutral theory is promising, but its concepts must be applied more broadly beyond the current focus on species–abundance distributions.

The mystery of biodiversity

Glossary

Beta-diversity: also known as distance-decay; the probabili
distance between two individuals that they will be of the sa
Coalescence: a technique developed in population genetics
analytically solving properties of a sample of individual
ancestry back to their common ancestors.
Dispersal kernel: a statistical distribution describing stochast
by giving the probability of dispersal as a function of distar
Dispersal limitation: a process that causes the location of a
restricted in some sense by the location of its parent.
application of neutral models to tropical forest trees, this co
'seed limitation'. It has been further noted that 'recruitment li
a better term because only individuals of adult reproductiv
modelled. In the context of the spatially implicit neutral
limitation is given by parameter *m*, which measures the rela
regional dispersal processes from the metacommunity co
processes of birth and death in the local community [17].
Fat-tailed distribution: a statistical distribution favouring rar
very far from the mean. Mathematically, the tails of a 'fa
kernel have power-law decay (rather than exponential decay

Opinion

Cell PRESS

The case for ecological neutral theory

James Rosindell[1,2,3], Stephen P. Hubbell[4,5], Fangliang He[6,7], Luke J. Harmon[2,8] and Rampal S. Etienne[9]

[1] Institute of Integrative and Comparative Biology, University of Leeds, Leeds, LS2 9JT, UK
[2] Institute of Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, ID 83844, USA
[3] Division of Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5 7PY, UK
[4] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA
[5] Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, Republic of Panama
[6] Department of Renewable Resources, University of Alberta, Edmonton, Alberta, T6G 2H1, Canada
[7] SYSU-Alberta Joint Lab for Biodiversity Conservation, State Key Laboratory of Biocontrol, Sun Yat-sen University, Guangzhou 510275, China
[8] Department of Biological Sciences, University of Idaho, Moscow, ID 83844, USA
[9] Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Box 11103, 9700 CC Groningen, The Netherlands

Ecological neutral theory has elicited strong opinions in recent years. Here, we review these opinions and strip away some unfortunate problems with semantics to reveal three major underlying questions. Only one of these relates to neutral theory and the importance of ecological drift, whereas the others involve the link between pattern and process, the tradeoff between simplicity and complexity in modeling, and the role of stochasticity and drift in ecology. We explain how neutral theory cannot be simultaneously used both as a null hypothesis and as an approximation. However, we also show how neutral theory always has a valuable use in one of these two roles, even though the real world is not neutral.

There are many different interpretations of what 'neutral theory' really is (Box 1), and this led both proponents and opponents to 'debate' without being clear what they were debating about. A formal debate requires a well-defined motion and this has been lacking in the discussions so far. We propose the following: 'Neutral theory, an ensemble of different neutral models of community assembly, is useful in ecological research' (Box 1). The usefulness of neutral theory inevitably depends on the context of use. Indeed, even the critics have often 'made use of neutral theory' by producing interesting ecological findings directly through arguing against it [17–19]. Finding data that are unexplained by neutrality [20,21] is a valuable application of neutral theory, not a triumph over it. We feel obliged to

区域群落概念

区域群落 vs. 局域群落

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

Disintegration of the Ecological Community

American Society of Naturalists Sewall Wright Award Winner Address*

Am. Nat. 2008

Robert E. Ricklefs†

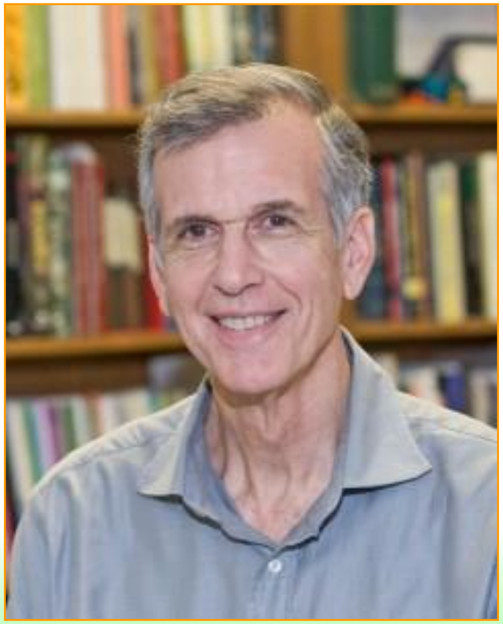
Department of Biology, University of Missouri, St. Louis, Missouri 63121

ABSTRACT: In this essay, I argue that the seemingly indestructible concept of the community as a local, interacting assemblage of species has hindered progress toward understanding species richness at local to regional scales. 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. Local coexistence cannot provide insight into the ecogeographic distributions of species within a region, from which local assemblages of species derive, nor can local communities be used to test hypotheses concerning the origin, maintenance, and regulation of species richness, either locally or regionally. Ecologists are moving toward a community concept based on interactions between populations over a continuum of spatial and temporal scales within entire regions, including the population and evolutionary processes that produce new species.

Keywords: biodiversity, biogeography, community ecology.

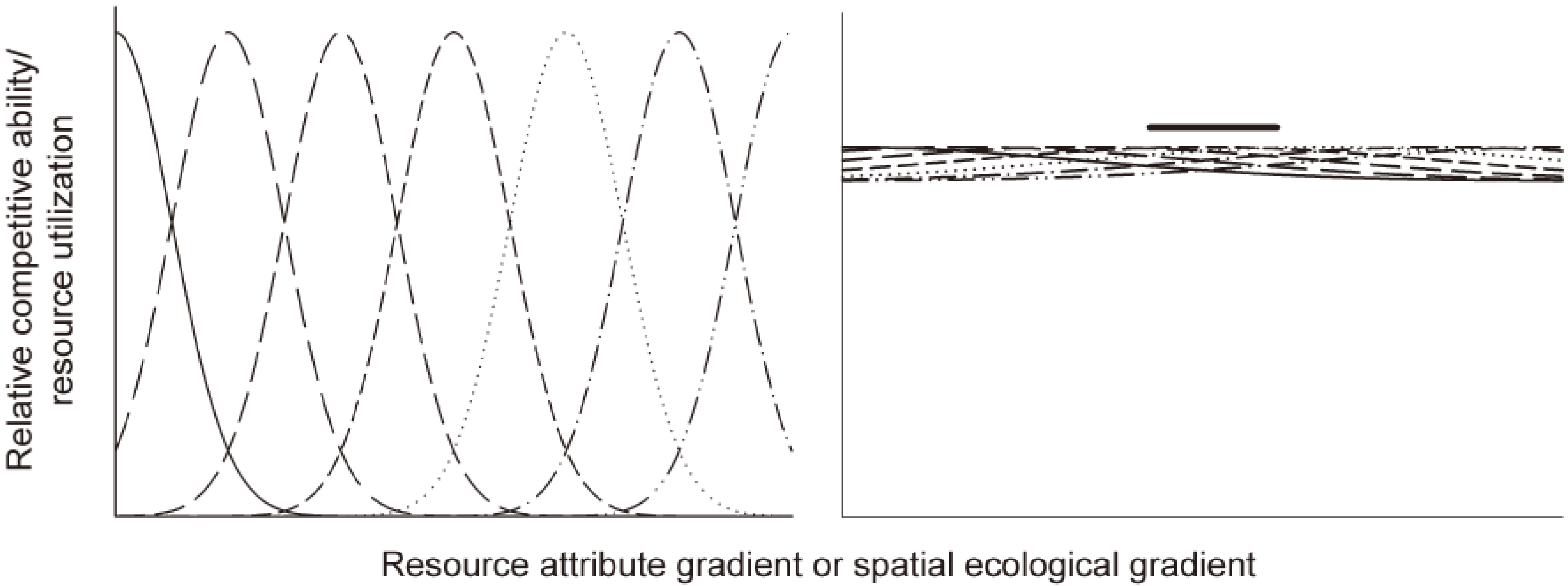
linked as it is to such disparate issues as global climate change and molecular phylogenetics, has stimulated ecologists to consider with more interest the history of the environment and the historical and geographic contexts of ecological systems (Latham and Ricklefs 1993*a*; Wiens and Donoghue 2004; Jaramillo et al. 2006; Ricklefs et al. 2006). We appear to be in the midst of a major synthesis in ecology (Lawton 1999), comparable to the maturation of ecosystem perspectives during the 1950s (McIntosh 1985) and population perspectives during the 1960s (MacArthur 1972; Kingsland 1985).

Despite these developments, however, ecologists, for the most part, continue to regard local communities as ecological units with individual integrity (Harrison and Cornell 2008). Empirical and experimental studies, including recent analyses of food webs and mutualistic networks (Jordano et al. 2003; Lewinsohn et al. 2006), circumscribe populations and communities locally (Morin 1999; Chase and Leibold 2003). Spatial scale rarely appeared in "community" theory until recently (Ives and May 1985; Brown et al. 2000; Leibold et al. 2004; McCann et al. 2005), and where it does appear, it is generally limited to the influence of dispersal limitation and population aggregation on local



Robert Ricklefs
(b. 1943~)

区域群落概念



传统生态位观点　　　　区域群落观点

Ricklefs R. 2012. Naturalists, Natural History, and the Nature of Biological Biodiversity. American Naturalist, 179:423-435.

中性理论 vs.区域群落理论

- 中性理论和区域群落理论都对生态位理论（局域决定论）发出了挑战，均强调区域过程的重要性
- 中性理论强调随机性，而区域群落理论强调确定性过程（尤其是寄主与病原体的互作）的作用，
- 中性理论强调扩散限制，而区域群落理论则强调扩散的有效性（模糊了局域与区域的差别）
- 预测力：中性理论 > 区域群落理论

调和中性假设与物种差异

1、扩散限制；2、生活史权衡

Functional Ecology 2005
19, 166–172

FORUM

Neutral theory in community ecology and th
functional equivalence

STEPHEN P. HUBBELL*

Ecology, 87(6), 2006, pp. 1387–1398
© 2006 by the Ecological Society of America

NEUTRAL THEORY AND THE EVOLUTION OF
ECOLOGICAL EQUIVALENCE

STEPHEN P. HUBBELL[1]

The Unified Neutral Theory of
BIODIVERSITY AND BIOGEOGRAPHY

STEPHEN P. HUBBELL

MONOGRAPHS IN POPULATION BIOLOGY • 32

扩散限制导致中性动态？

J. theor. Biol. (1995) **176,** 1–12

The Consequences of Recruitment Limitation: Reconciling Chance, History and Competitive Differences Between Plants

GEORGE C. HURTT AND STEPHEN W. PACALA

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, *U.S.A.*

(*Received on* 19 *October* 1993, *Accepted in revised form on* 23 *March* 1995)

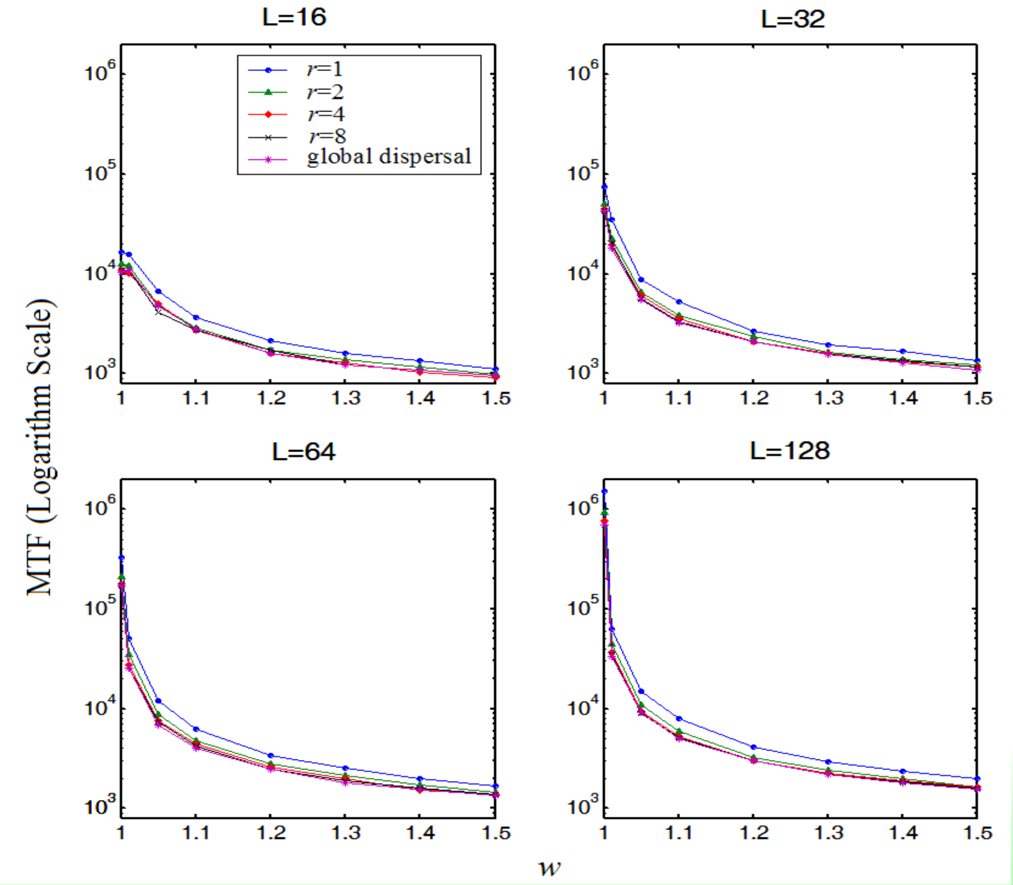
Plant competition for space is studied using analytical and simulation models. Here, the interaction is viewed as a local competition between juveniles of different species for environmentally variable sites vacated by the random deaths of adults. Because plants are sedentary and have finite fecundity, often only a subset of species will compete for an available site. When a dominant species is recruitment limited, inferior competitors will win some sites by forfeit. It is shown that recruitment limitation allows "winning-by-forfeit" which lessens the effect of competitive asymmetries and slows population and community dynamics. Moreover, since recruitment limitation is likely to be most pronounced in highly diverse communities because of the rarity of many species, it is suggested that there is no conflict between the hypothesis that species-rich plant communities are more influenced by chance and history than regulated by competition, and observations of strong interspecific differences among plants.

- 本文的前提假设是物种已经具有生态位分化！
- 如果不存在生态位分化，…
- **Google Scholar 引用358次！**

扩散限制导致中性动态？

- 种间竞争能力差异和扩散限制对物种共存时间的影响。随着群落大小的增加，共存时间随竞争能力差异加大而下降幅度更大。

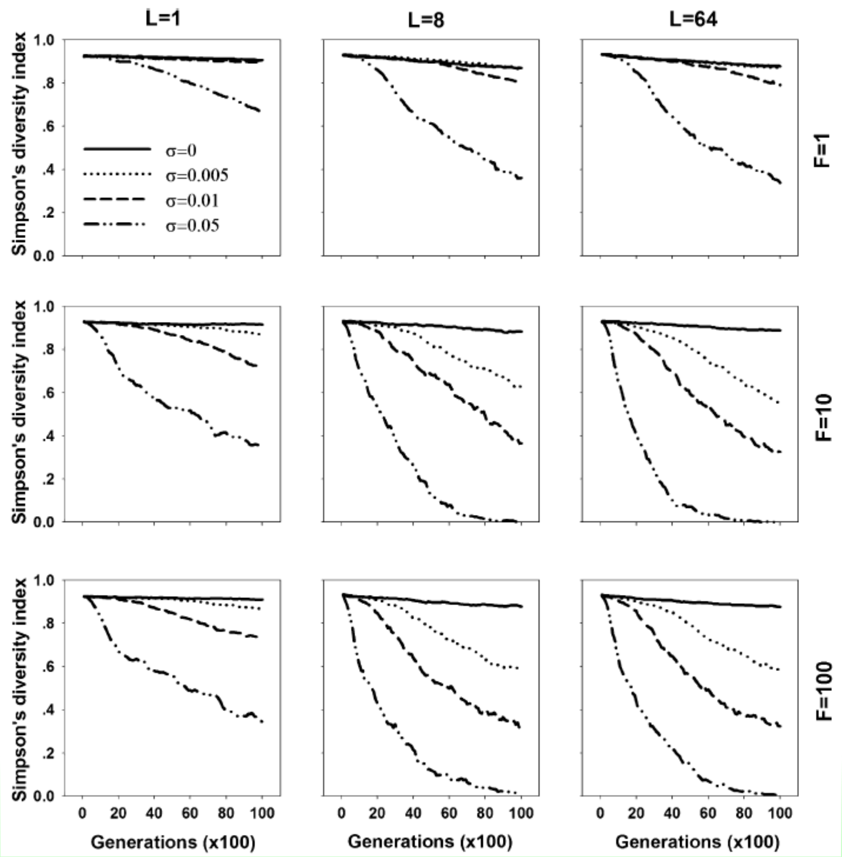
- 扩散限制对竞争共存的影响非常有限！



Zhou S-R & Zhang D-Y, 2008. Ecology, 89:248-258

扩散限制导致中性动态？

- 扩散限制与更新限制对非中性物种共存的影响很有限，并且方式有所不同！
- 扩散限制的作用非常有限！
- 更新限制对共存的影响相对更大！



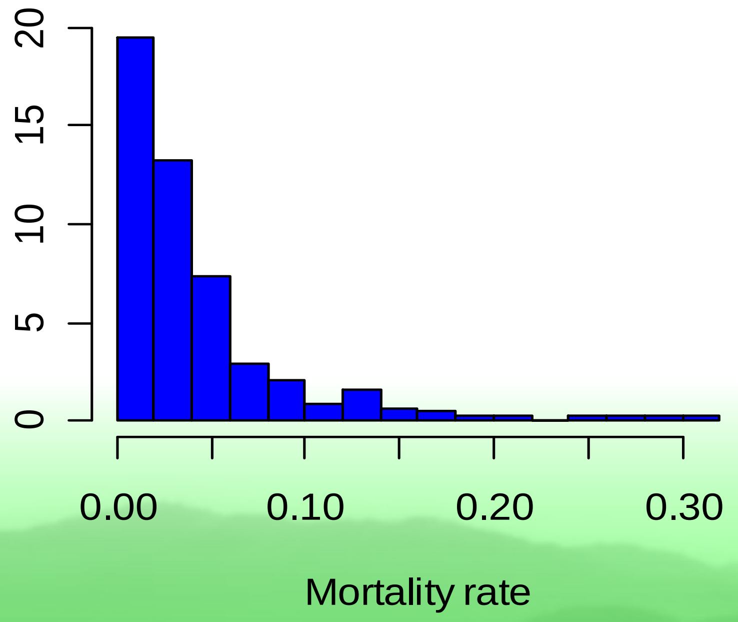
Peng, Zhou & Zhang, 2012. J. Pl. Ecol., 5:89-96

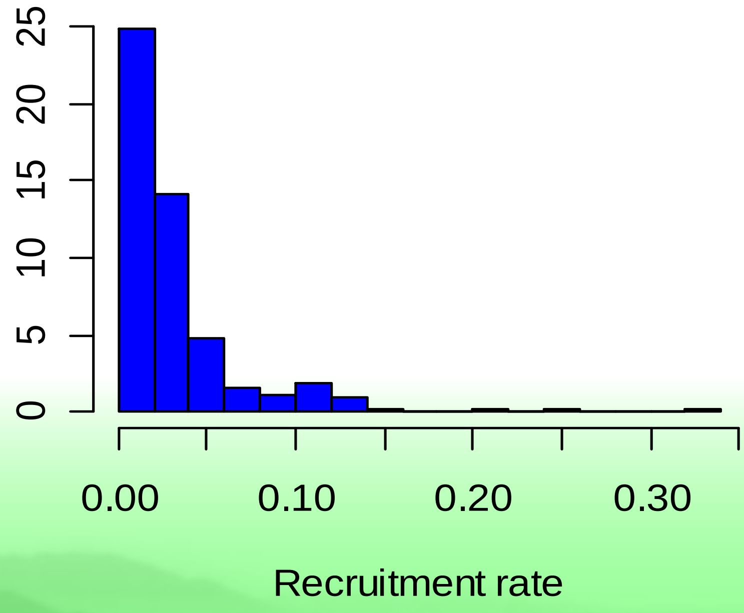
扩散限制导致中性动态？

不能！

生活史权衡导致中性动态?

- 自然群落内物种之间存在明显的生活史性状差异
- **BCI**大样地中树种的死亡率与更新率频度分布图，说明各个物种在关键生活史参数上是明显不同的！





生活史权衡导致中性动态？

- 生活史权衡普遍存在！
- 权衡使得物种之间的竞争能力差异减小，是一种均等化共存机制！

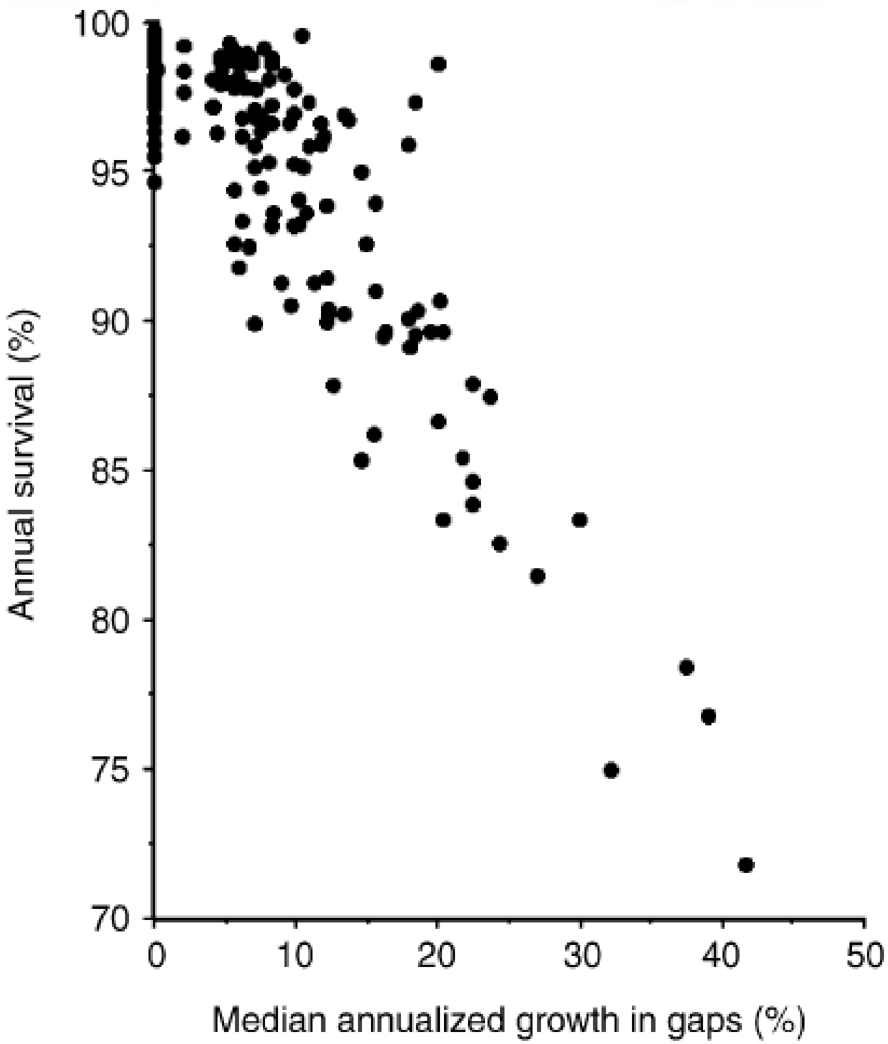


Fig. 1. Principal axis of life history differentiation among BCI tree species is in relation to light availability. Each dot represents the mean phenotype of a single species. Species at the upper left are shade-tolerant species with high annual percentage survival in understorey shade but low annual relative growth rate in full sun, measured as a percentage of initial stem diameter. Species at the lower right are light-demanding, gap-dependent species that exhibit high mean relative growth rates in full sun, but low mean annual survival rates in understorey shade. Note the concentration of species at the shade-tolerant end of the manifold. Data such as this are usually interpreted as evidence for a trade-off between survival and growth rate. However, these mean phenotype points mask significant within-species variation in survival and growth performance (see Fig. 4). After Hubbell & Foster (1992).

生活史权衡导致中性动态？

- 只要各个物种的竞争能力或适合度相同，不需要方方面面都相同；
- 在零和假设（群落饱和）条件下，出生率与死亡率的比值可以作为合适的适合度指标；出生率－存活率的权衡可以导致物种等同，即中性

Ecology, 90(1), 2009, pp. 31–38

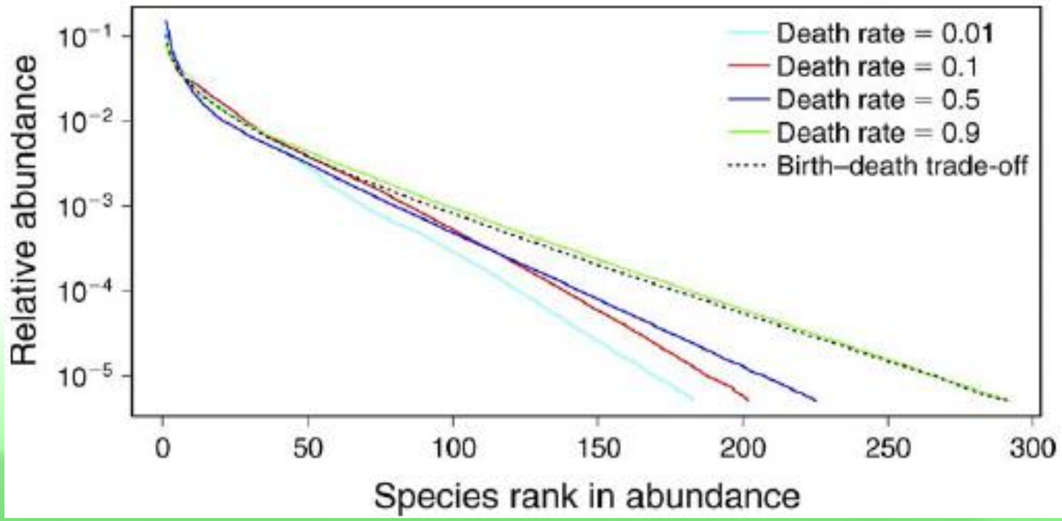
Demographic trade-offs in a neutral model explain death-rate–abundance-rank relationship

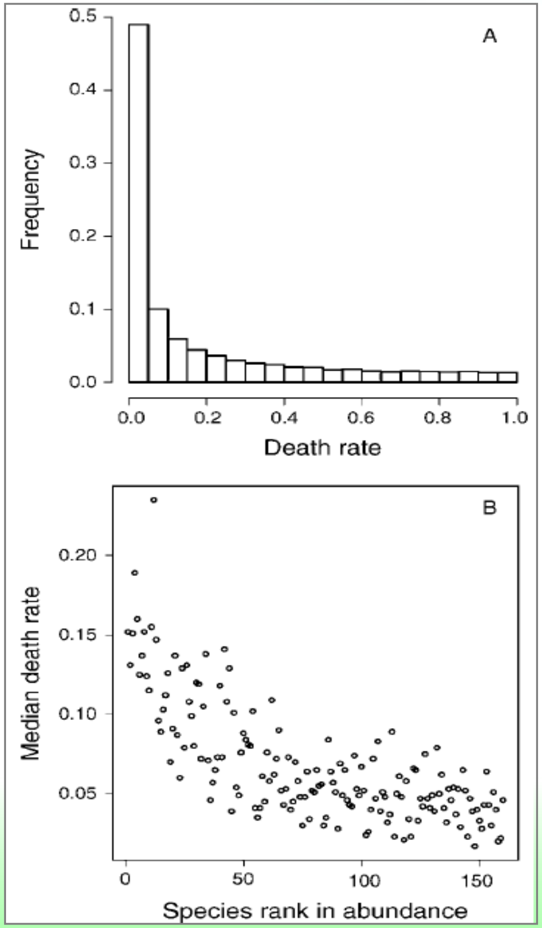
Kui Lin,[1] Da-Yong Zhang,[1,3] and Fangliang He[1,2]

[1]*State Key Laboratory of Earth Surface Processes and Resource Ecology and MOE Key Laboratory of Biodiversity Sciences and Ecological Engineering, Beijing Normal University, Beijing 100875 China*
[2]*Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2H1 Canada*

生活史权衡导致中性动态?

- 严格的生活史权衡可导致物种竞争能力等同;
- 相同的物种多度分布 – 对数级数分布
- 过滤效应 – 稀有种具有相对较低的死亡率





Lin *et al*. 2009. Ecology
Zhang *et al*. 2012. J. Plant Ecol.

生活史权衡导致中性动态？

- 生活史权衡可使物种竞争能力趋于等同，但无法保证绝对相等！
- 如果权衡之后物种竞争能力不完全等同，那么群落动态不可能是中性的，群落内的生活史性状变异也无法维持！

Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2010 doi: 10.1111/j.1365-2656.2010.01738.x

Different but equal: the implausible assumption at the heart of neutral theory

Drew W. Purves[1]* and Lindsay A. Turnbull[2]

生活史权衡导致中性动态？

不能！

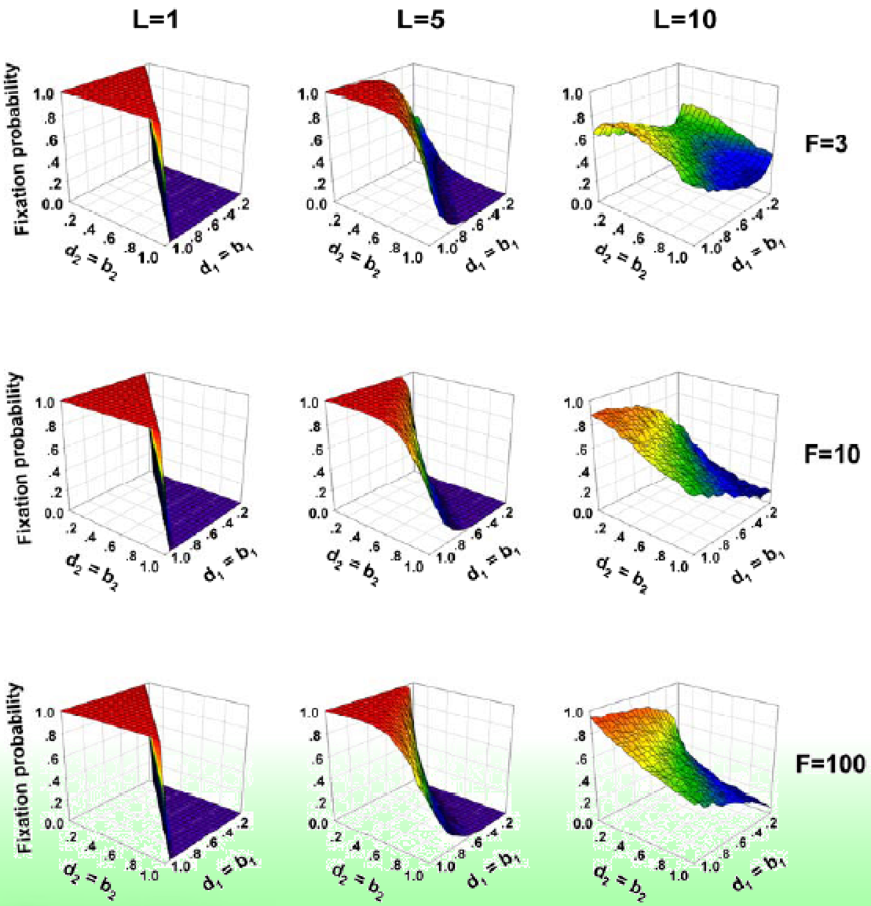
权衡与扩散限制的结合导致中性？

$$1+1=2?$$

- 生活史权衡和扩散限制都可使物种竞争能力趋于等同，二者联合作用是否可使得群落动态更接近于中性动态？
- 如果同时考虑扩散限制和生活史权衡，群落动态更加偏离于中性！

权衡+扩散限制 ＝ 中性？

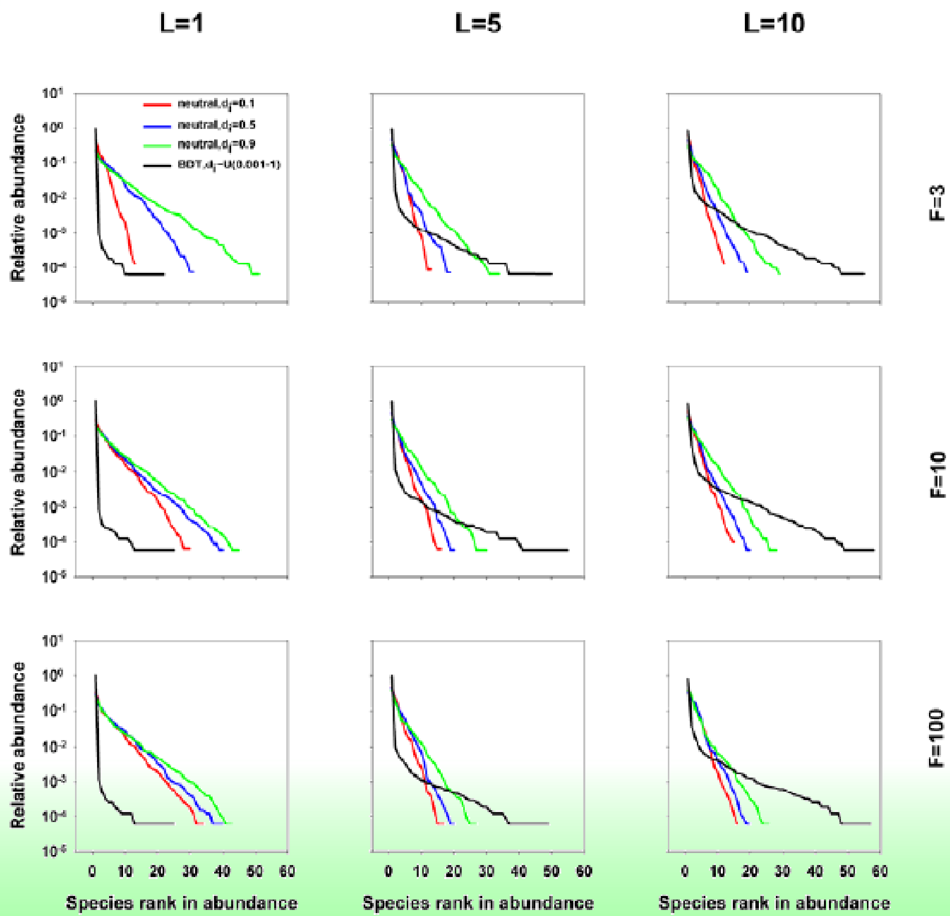
- 在扩散限制条件下，权衡中性无法达到！
- 扩散限制对高出生率（高死亡率）物种有利！



Zhou S-R, Peng Z. & Zhang D.-Y.
Am Nat, in revision

权衡+扩散限制 = 中性？

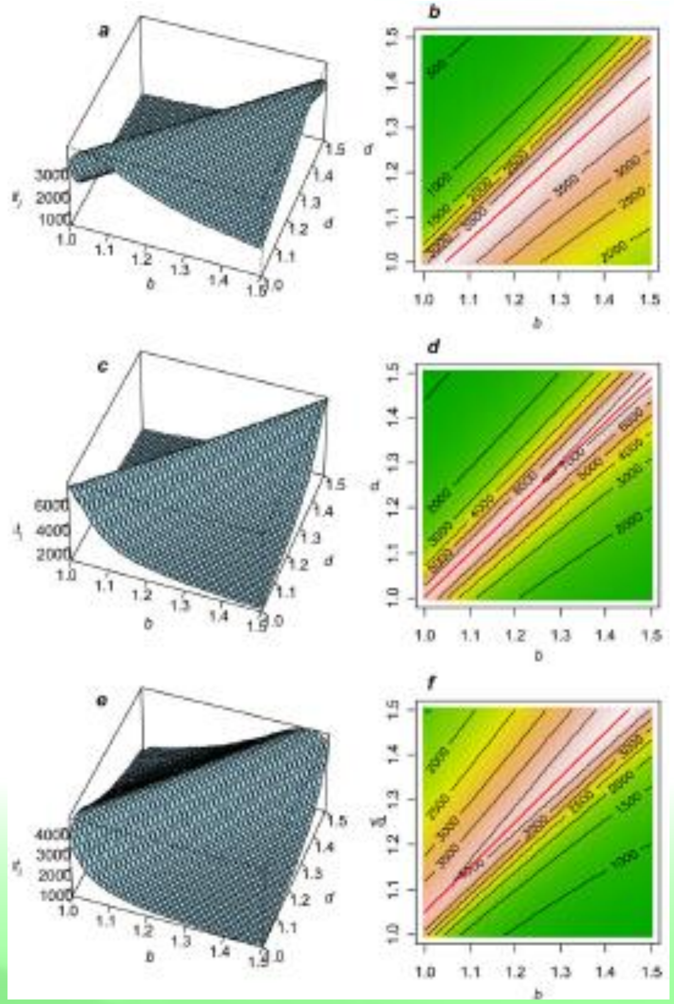
- 虽然非中性，但生活史权衡比中性（所有物种具有相同的出生率、死亡率）能维持更高的物种数量！
- 近中性群落物种相对多度分布的均匀度下降
- 扩散限制似乎对稀有种生存有利！



Zhou S-R, Peng Z. & Zhang D.-Y.
Am Nat, in revision

近中性取代中性？

- 自然界不存在严格中性的动态！
- 生活史权衡的物种（即使竞争能力不同）也有可能比中性物种（具有相同的出生率、死亡率）共存更长的时间！



Journal of
Plant Ecology

VOLUME 5, NUMBER 1,
PAGES 72–81

MARCH 2012

doi: 10.1093/jpe/rtr040

available online at
www.jpe.oxfordjournals.org

Coexistence of nearly neutral species

Fangliang He[1,2,], Da-Yong Zhang[3] and Kui Lin[3]*

[1] Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada T6G 2H1
[2] SYSU-Alberta Joint Lab for Biodiversity Conservation, State Key Laboratory of Biocontrol, Sun Yat-sen

近中性取代中性？

选择与漂变都很重要！

但不一定需要生态位！

Ecology, 89(1), 2008, pp. 248–258

A NEARLY NEUTRAL MODEL OF BIODIVERSITY

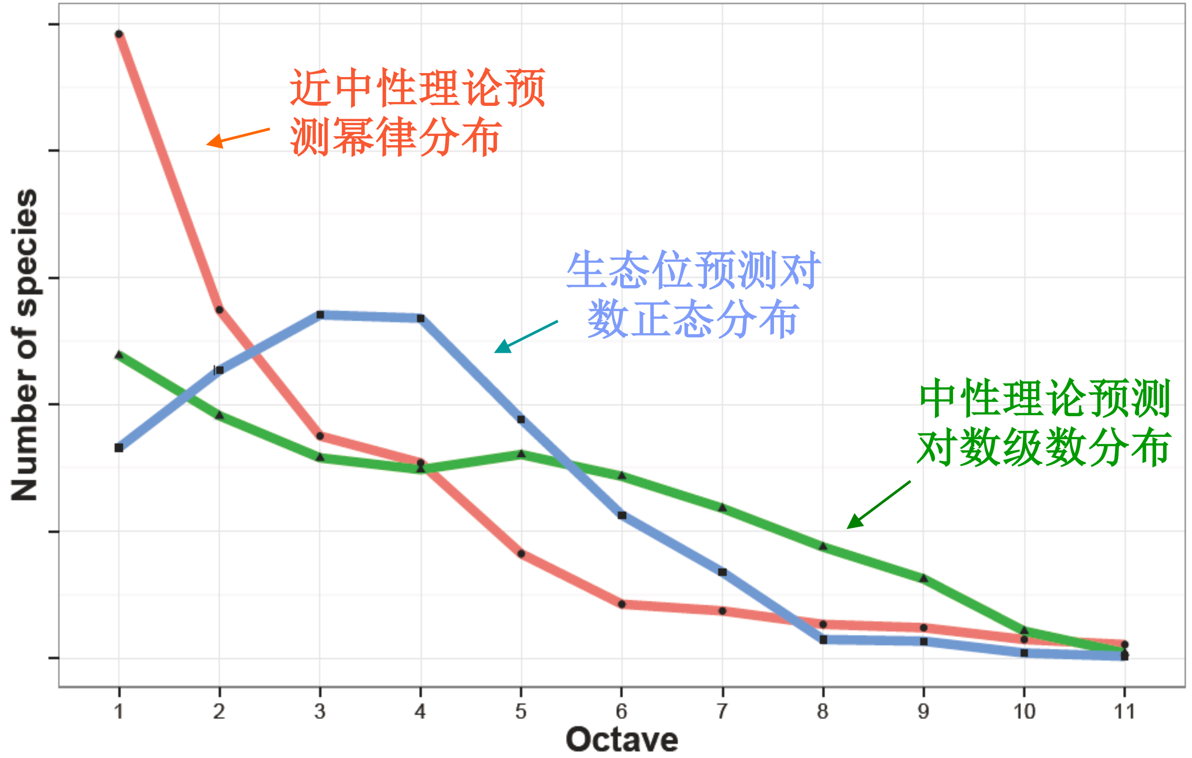
SHU-RONG ZHOU[1,2] AND DA-YONG ZHANG[1,3]

[1]*State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, Beijing 100875, China*
[2]*Laboratory of Arid and Grassland Ecology under the Ministry of Education, School of Life Sciences, Lanzhou University, Lanzhou 730000, China*

Abstract. S. P. Hubbell's unified neutral theory of biodiversity has stimulated much new thinking about biodiversity. However, empirical support for the neutral theory is limited, and several observations are inconsistent with the predictions of the theory, including positive correlations between traits associated with competitive ability and species abundance and correlations between species diversity and ecosystem functioning. The neutral theory can be extended to explain these observations by allowing species to differ slightly in their competitive ability (fitness). Here, we show that even slight differences in fecundity can greatly reduce the time to extinction of competitors even when the community size is large and dispersal is spatially limited. In this case, species richness is dramatically reduced, and a markedly different species abundance distribution is predicted than under pure neutrality. In the nearly neutral model, species co-occur in the same community not because of, but in spite of, ecological differences. The more competitive species with higher fecundity tend to have higher abundance both in the metacommunity and in local communities. The nearly neutral perspective provides a theoretical framework that unites the sampling model of the neutral theory with theory of biodiversity affecting ecosystem function.

Key words: coexistence; competitive asymmetries; dispersal limitation; metacommunity; nearly neutral model; species diversity.

近中性取代中性？



幂律分布：

$$f(n) = \frac{e^{-\beta n}}{n^{\alpha}}$$

是广义伽马分布

近中性取代中性？

Oikos 119: 1149–1155, 2010
doi: 10.1111/j.1600-0706.2009.18236.x

Subject Editor: Tim Benton. Accepted 3 November 2009

Research

A meta-analysis of species–abundance distributions

Werner Ulrich, Marcin Ollik and Karl Inne Ugland

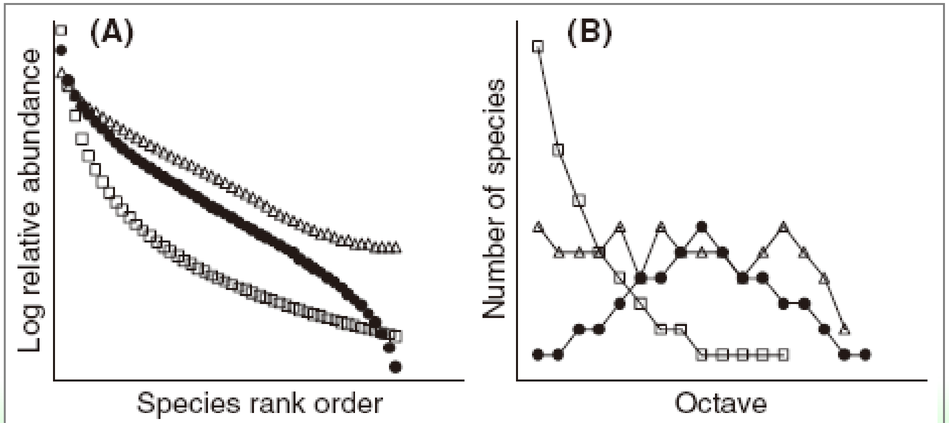


Figure 1. Basic shapes of species–abundance distributions in Whittaker (A) and Preston plots (B). Black dots: lognormal shape; open triangles: logseries; open squares: power law.

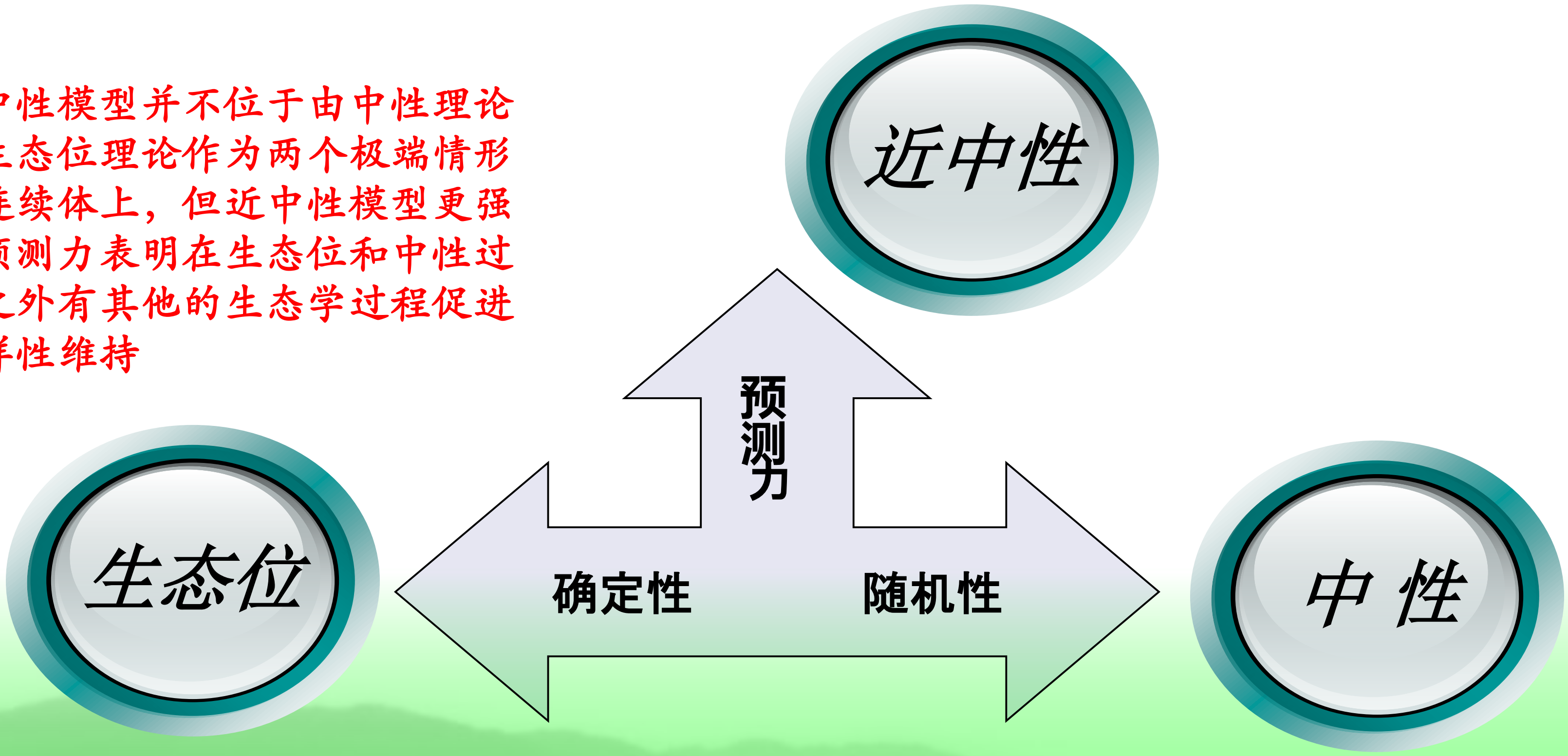
对数级数、对数正态和幂律分布的模型比较

植物群落倾向于服从幂律分布！

近中性取代中性？

- 近中性理论是在发展生物多样性维持机制的一般化框架过程中迈出的一大步

近中性模型并不位于由中性理论和生态位理论作为两个极端情形的连续体上，但近中性模型更强的预测力表明在生态位和中性过程之外有其他的生态学过程促进多样性维持

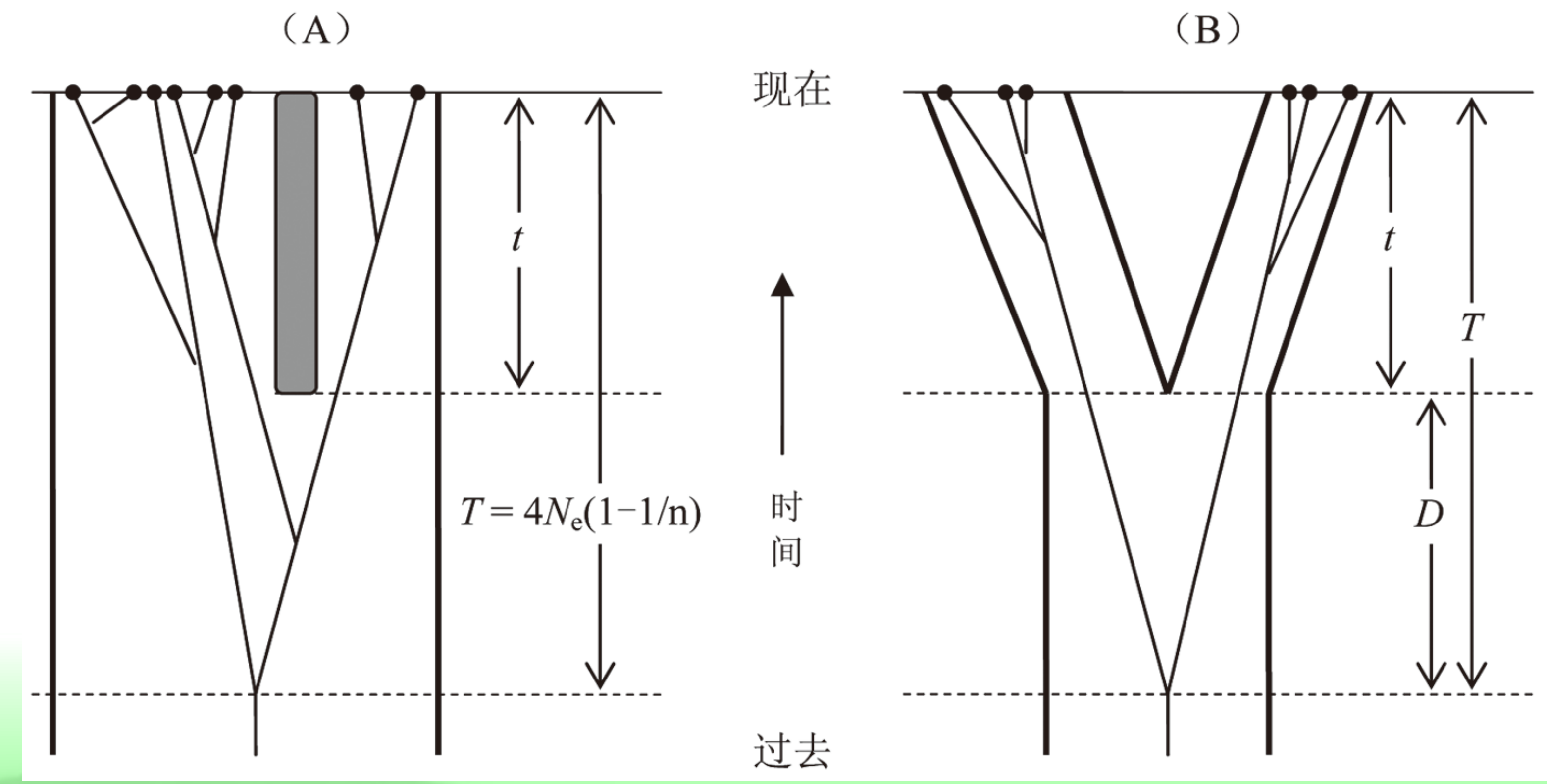


J-C效应是一个生态位过程！

- 竞争与似然竞争的关系
- 稳定维持物种多样性（稀有种在群落中的存在）需要稀有优势！
- J-C效应的重要性?

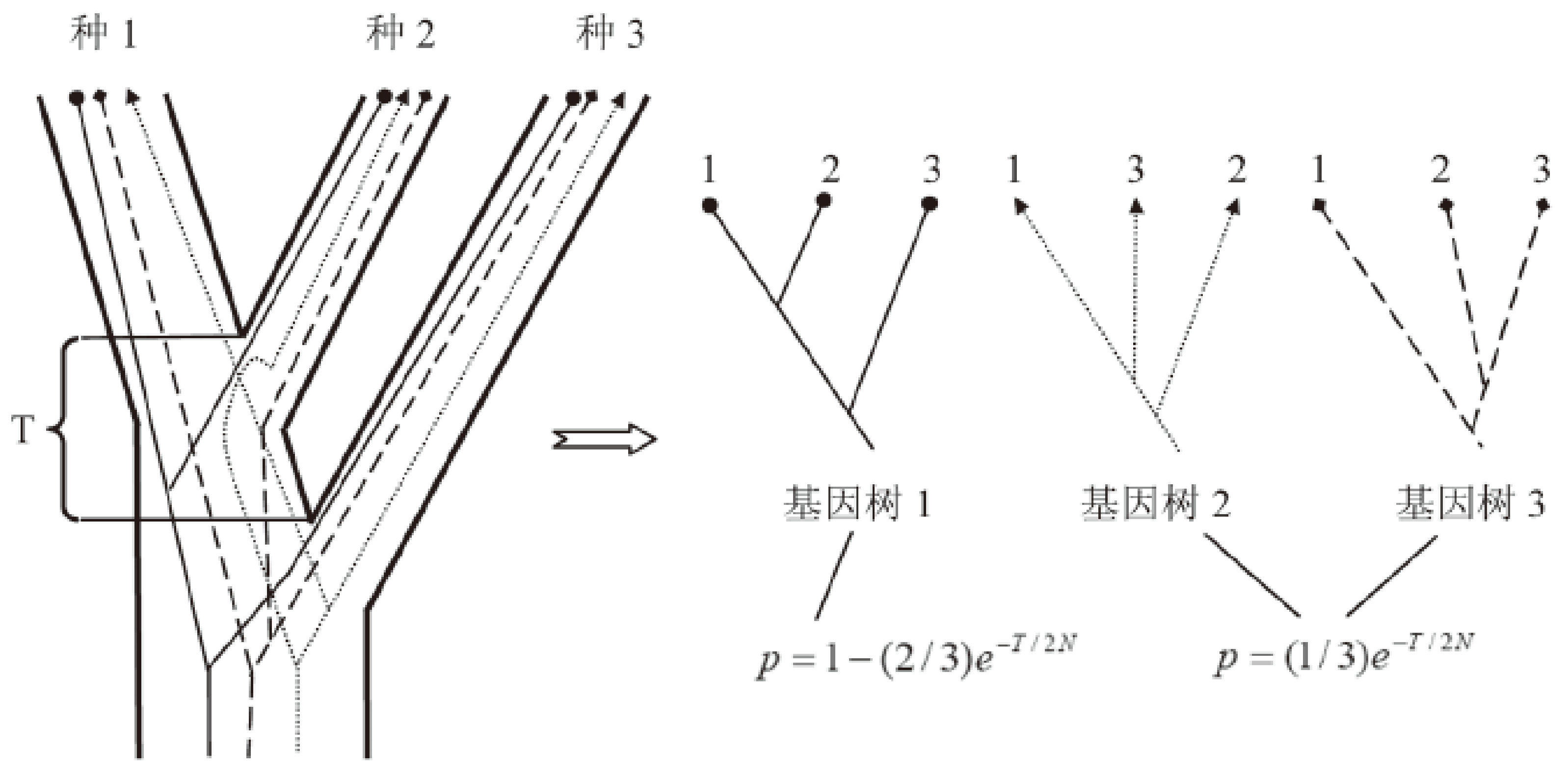
群落系统发育关系的不确定性

- 基因树不等于物种树



群落系统发育关系的不确定性

- 基因树不等于物种树



群落系统发育关系的不确定性

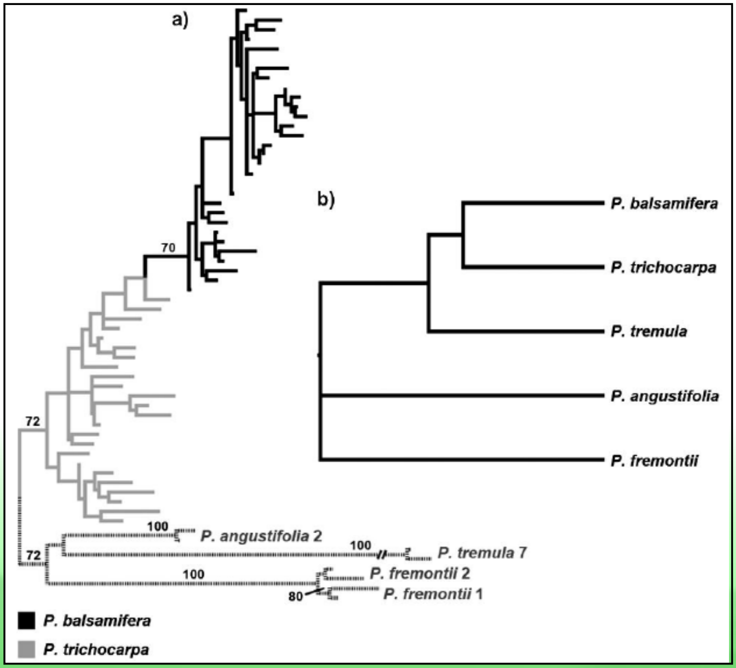
北美钻天杨与毛果杨

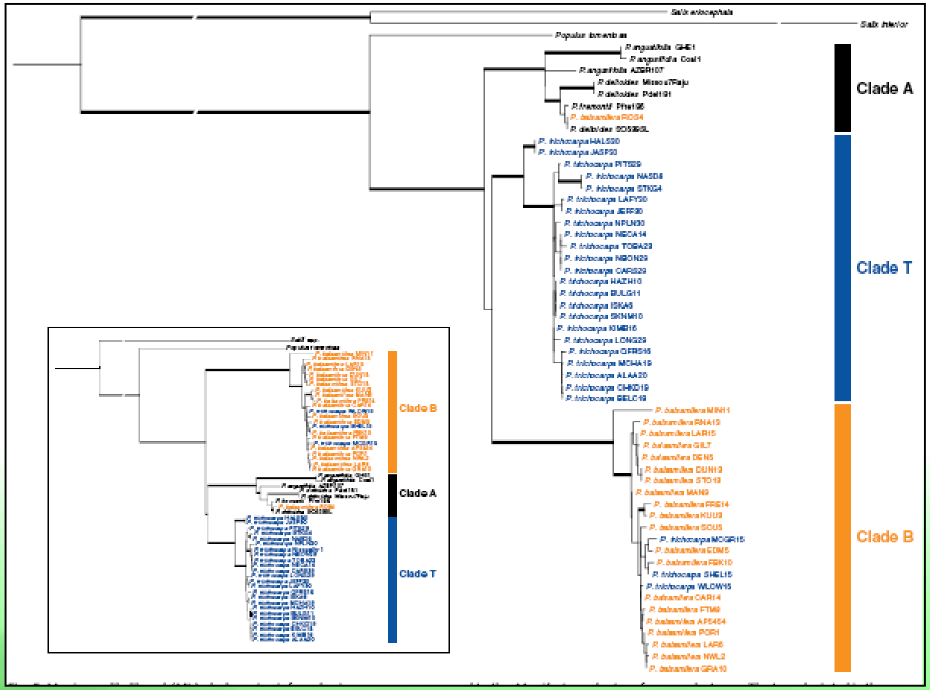
叶绿体组：6-700万年；而
32个核基因：7.5万年！

New Phytologist
Research

Whole plastome sequencing reveals deep plastid divergence and cytonuclear discordance between closely related balsam poplars, *Populus balsamifera* and *P. trichocarpa* (Salicaceae)

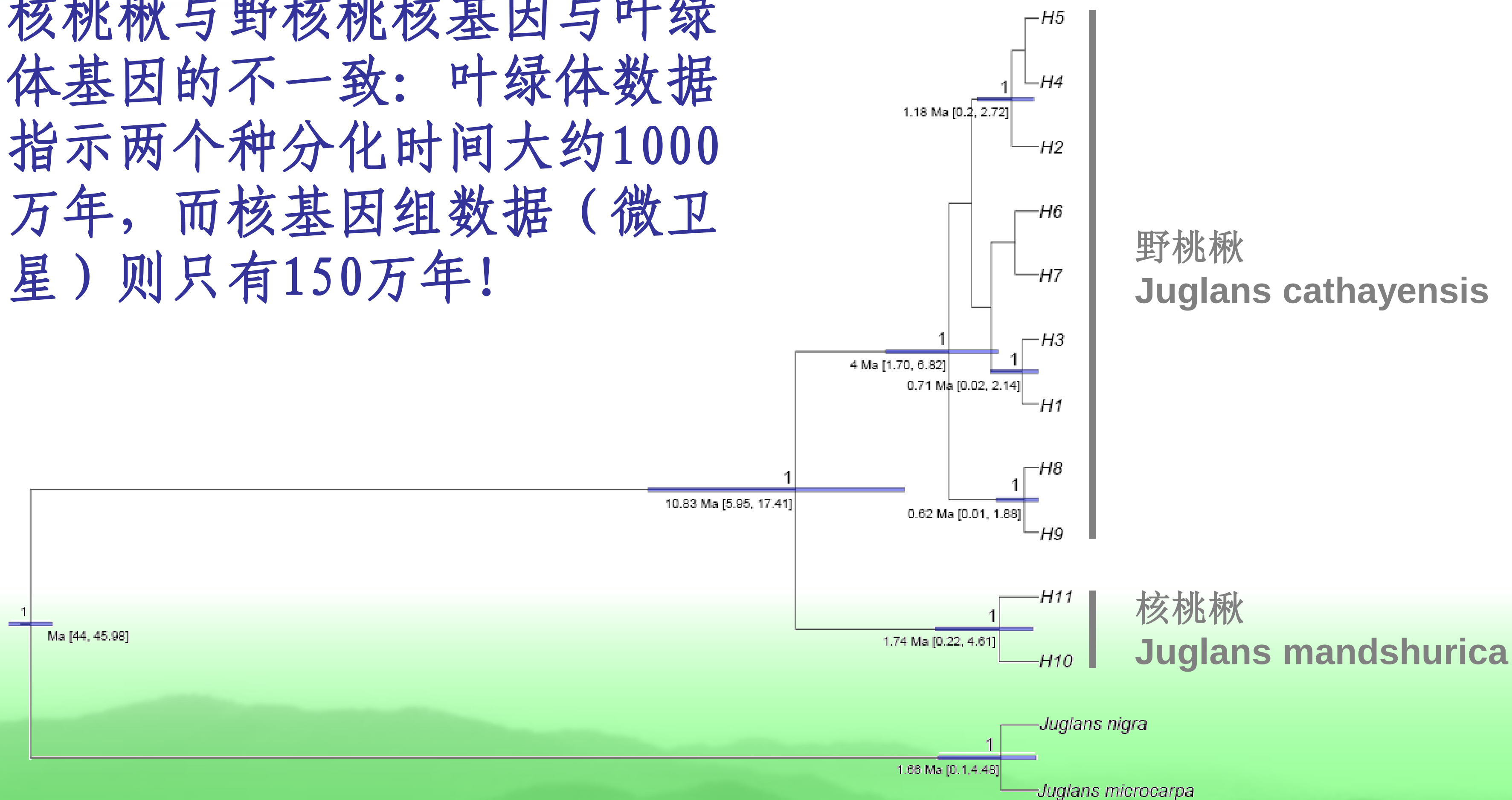
Daisie I. Huang[1,2], Charles A. Hefer[1,2], Natalia Kolosova[1], Carl J. Douglas[1] and Quentin C. B. Cronk[1,2]

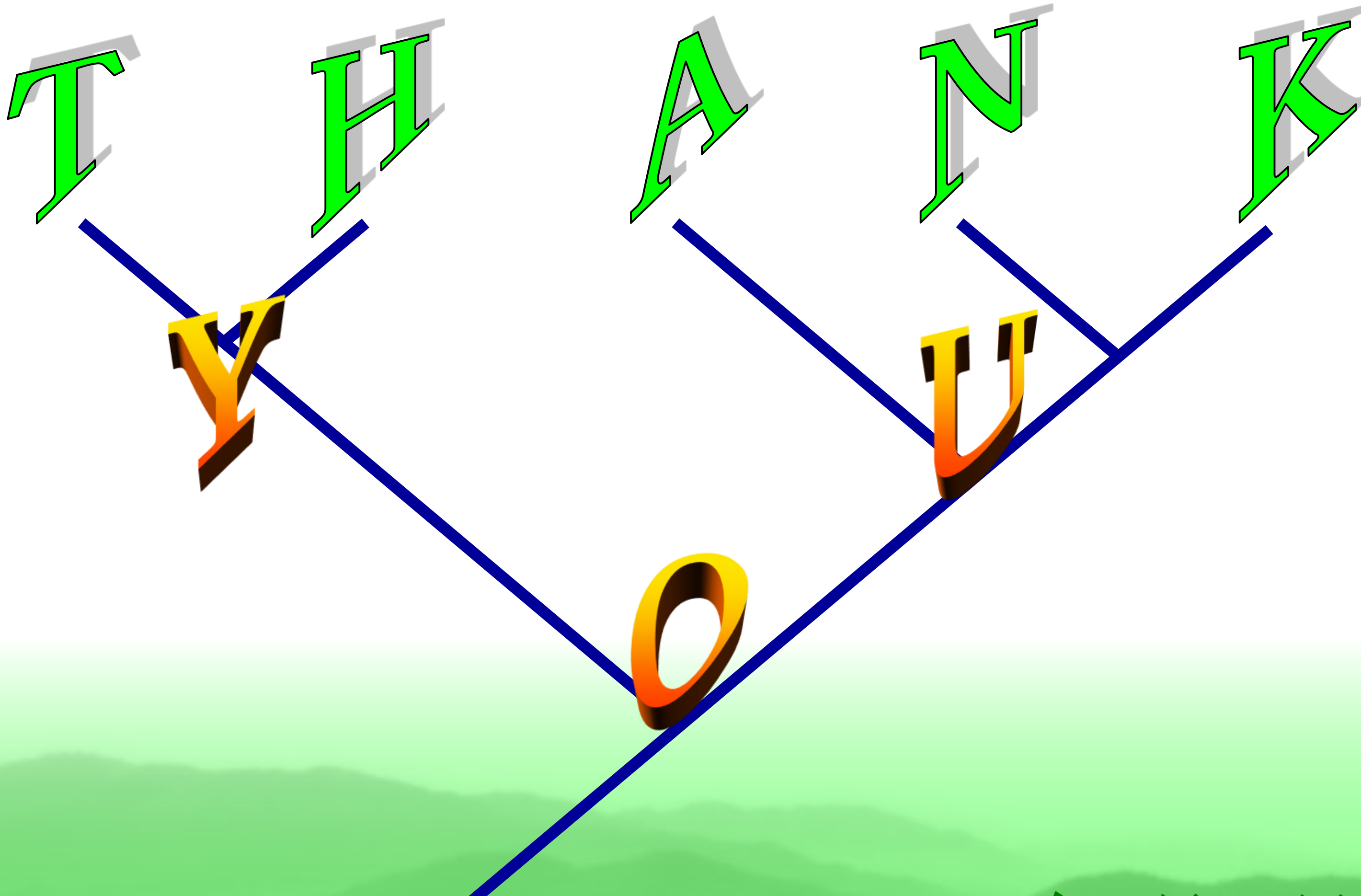




群落系统发育关系的不确定性

核桃楸与野核桃核基因与叶绿体基因的不一致：叶绿体数据指示两个种分化时间大约1000万年，而核基因组数据（微卫星）则只有150万年！





2014年8月18日，沈阳

群落组建的统一理论框架

1. 选择
2. 漂变
3. 扩散
4. 种化

物种形成

区域物种库

迁入

环境筛选
(方向选择)

局域群落
（生态位分化）

竞争淘汰
(方向选择)

随机灭绝
(漂变)

Vellend M (2010) Conceptual synthesis in community ecology. *Quarterly Review of Biology*, 85, 183-206.

群落组建的统一理论框架

物种形成

区域物种库

迁入

环境筛选
(方向选择)

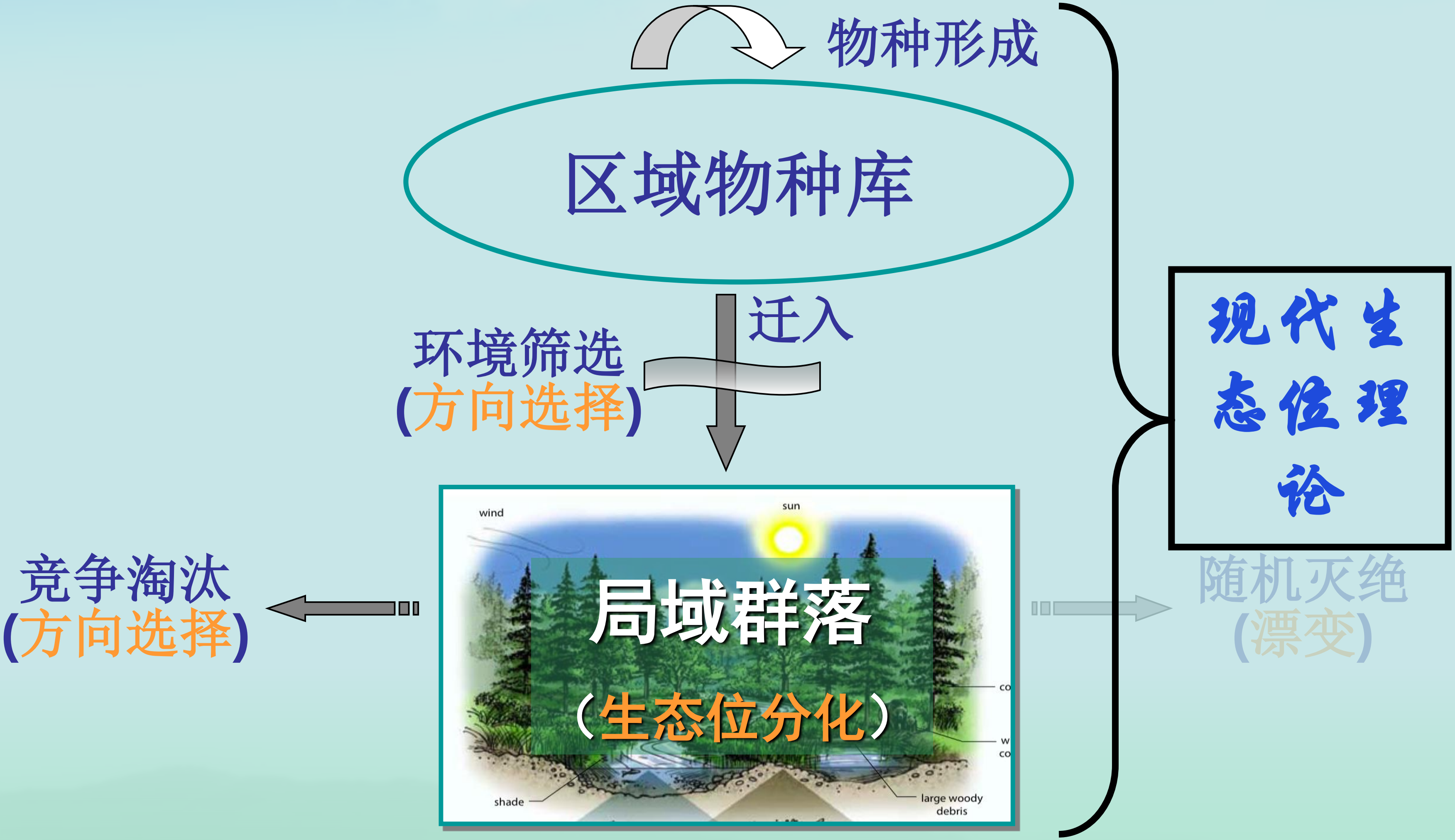
经典生态位理论

竞争淘汰
(方向选择)

随机灭绝
(漂变)

局域群落
（生态位分化）

群落组建的统一理论框架



群落组建的统一理论框架

物种形成

区域物种库

迁入

环境筛选
(方向选择)

中性
理论

竞争淘汰
(方向选择)

随机灭绝
(漂变)

群落组建的统一理论框架

区域群落理论

物种形成

区域物种库

迁入

环境筛选
(方向选择)

局域群落
（生态位分化）

竞争淘汰
(方向选择)

随机灭绝
(漂变)

群落组建的统一理论框架

1. 选择
2. 漂变
3. 扩散
4. 种化

物种形成

区域物种库

迁入

环境筛选
(方向选择)

竞争淘汰
(方向选择)

随机灭绝
(漂变)