

Time for a paradigm shift in biodiversity?

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What is a paradigm?

The view point and set of background assumptions of the discipline (Margolis 1993).

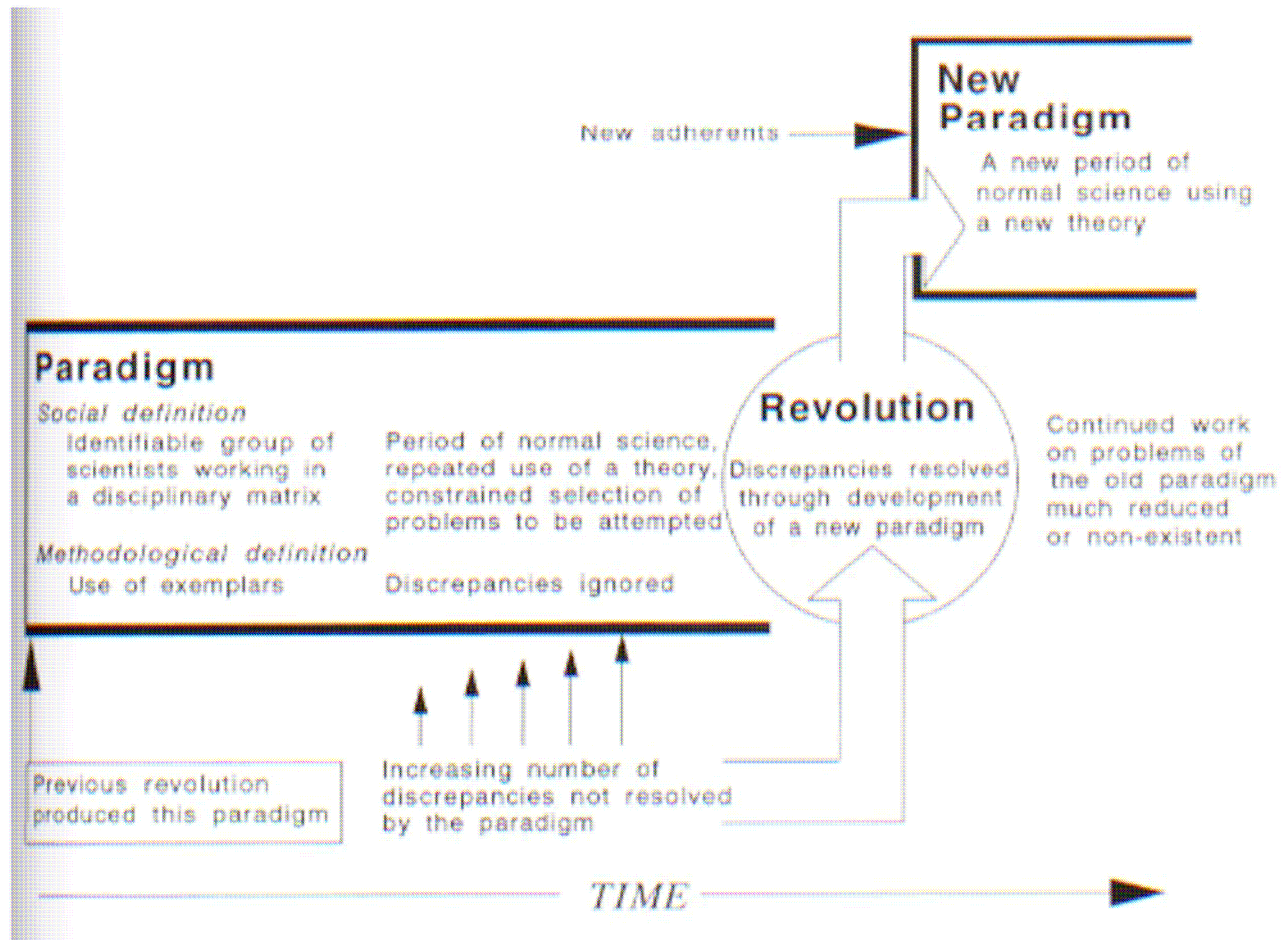
The general principles that structure the science as well as the judgements about what areas and questions are of interest, how to approach those questions, and what constitutes a valid answer (Parker and Pickett 1997).

A paradigm is a particular way of doing science in a given subdiscipline. (Cuddington and Beisner 2005)

What is a Kuhnian paradigm?

- What is to be observed and scrutinized
- The kind of questions that are supposed to be asked and probed for answers in relation to this subject.
- How these questions are to be structured
- How the results of scientific investigations should be interpreted

Theory changes through crises or revolutions leading to a paradigm shifts



How does theory change in ecology?

Paradigm shifts are rare

Clement's superorganism



Phillips concept of succession
Gleason's individualistic hypothesis

Anomaly: The "climatic climax" did not fit European Vegetation



Tansley's ecosystem concept



Lindeman's trophic dynamics approach

Paradigms bounce back, linger and are usually reborn in disguise to coexist.

Clement's superorganism → Lovelock's GAIA

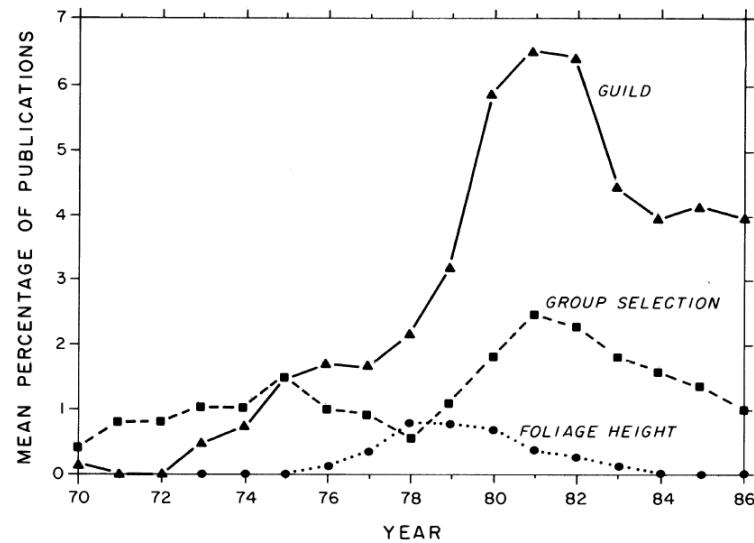
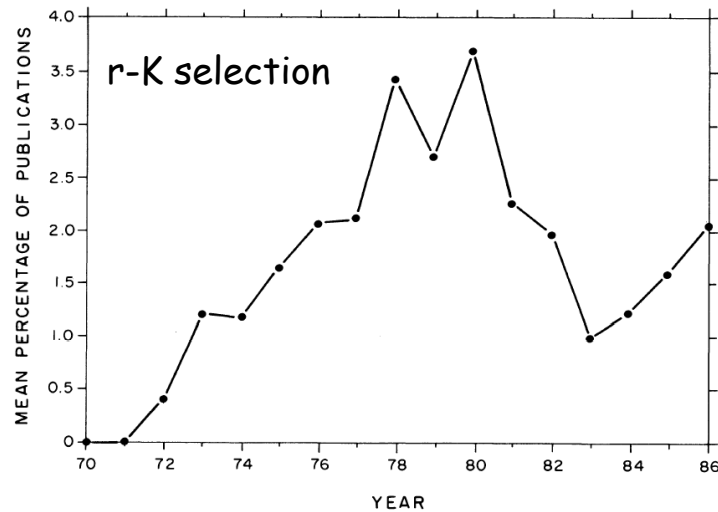
Phillips concept of succession
Gleason's individualistic hypothesis

Anomaly: The "climatic climax" did not fit European Vegetation

Tansley's ecosystem concept

Lindeman's trophic dynamics approach

Some theories or hypothesis are never proved wrong, they just become out of fashion



Theory development is best described as an evolutionary process (see Cuddington and Beisner 2005)

- Anagenetic transformations
(unstructured → structured population models)
- Speciation
(e.g. Evolutionary ecology, Ecophysiology, Ecological stoichiometry, Ecological genomics)
- Adaptive radiations (e.g. Neutral models)

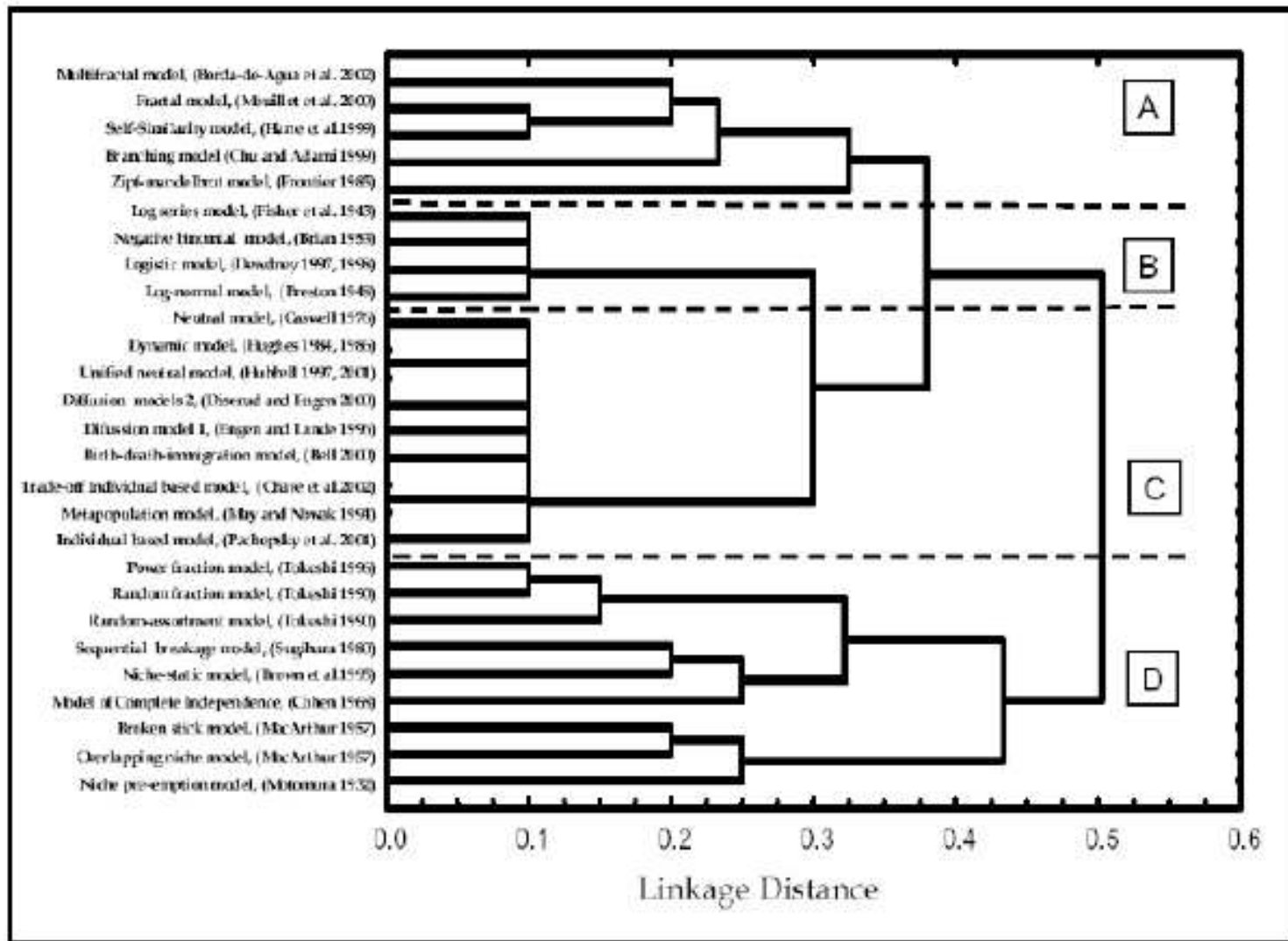
Is it time for a paradigm shift in biodiversity?

Yes, it is a good time for a paradigm change in Biodiversity.

Innovation and change is an essential part of science.

But...we should avoid doing a random walk in theory space!!!!

Species relative abundance distribution



from Marquet et al. (2003)

A paradigm changes in ecology will ensue only if it leads to substantial progress in the discipline.



A testable, prediction rich, assumption poor,
quantitative theory of biodiversity,
based on first principles.

Are we at the verge of a theory change in ecology
akin to a paradigm shift?

or are we as Pinochet said referring to his coming
into power...?

We were at the edge of the abyss and now we
have taken a step forward!!

There is a tension between reductionistic and holistic approaches, between world views emphasizing the existence of general principles and others their impossibility.

Imagine if Galileo, noting that different objects fell at differing speeds, were to have wrote 42 volume treatise on the diversity of falling bodies.

(Geoffrey West, pers.comm.)



"Ecology is a science of contingent generalizations, where future trends depend (much more than in the physical sciences) on past history and on the environmental and biological setting" (**May 1986**)

" The answers to general ecological questions are rarely universal laws, like those of physics. Instead, the answers are conditional statements such as: for a community of species with properties A1 and A2 in habitat B and latitude C, limiting factors X2 and X5 are likely to predominate." (**Diamond & Case 1986**)

"..our own recent research is based on the premise that the general statistical patterns of macroecology ,..., are emergent phenomena of complex ecological systems that do indeed reflect the operation of Universal law-like mechanisms." **Brown et al. (2004)**

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; 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. **Simberloff (2004)**

But are there first principles or general laws in ecology?

First principles:

Law-like statements about processes and mechanisms underlying the structure and functioning of systems.

PRIMORDIAL SOUP ECOLOGY



But why is this quest for first principles is relevant for ecology?

We could better solve the environmental problems facing humanity if we could discover the laws of nature that underlie the complexity of ecological systems.

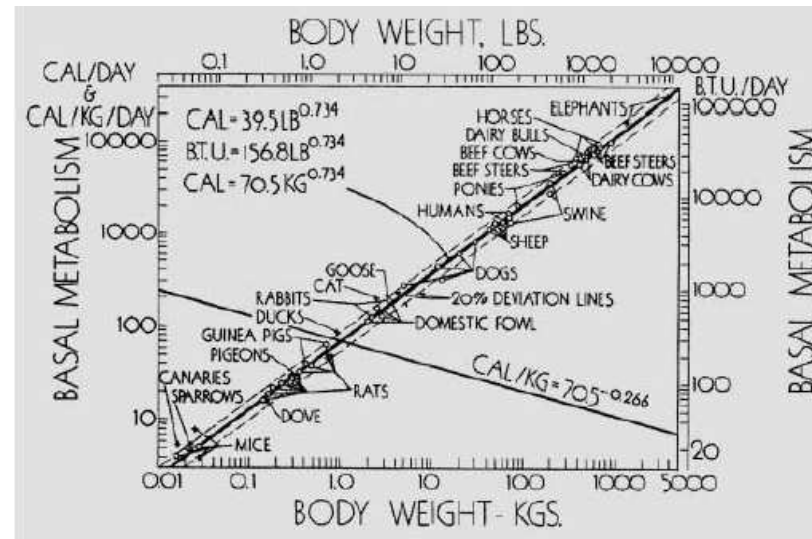
- Improve our ability to detect relevant changes
- Improve our understanding of their consequences
- Improve our ability to mitigate them

AND

Provide the basis for synthesis and unification...

Some general principles in ecology

- The principle of geometric growth (Malthus' law)
- The principle of self-limitation, density dependence
- Malthusian-darwinian dynamics
- **Metabolic scaling**



Brody S. (1945) Bioenergetics and Growth, Reinhold, New York

Individual energy requirements

$$B = B_0 M^{3/4}$$

The maximum number of individuals that can be supported in an environment with an amount R of resources per unit area is predicted to be:

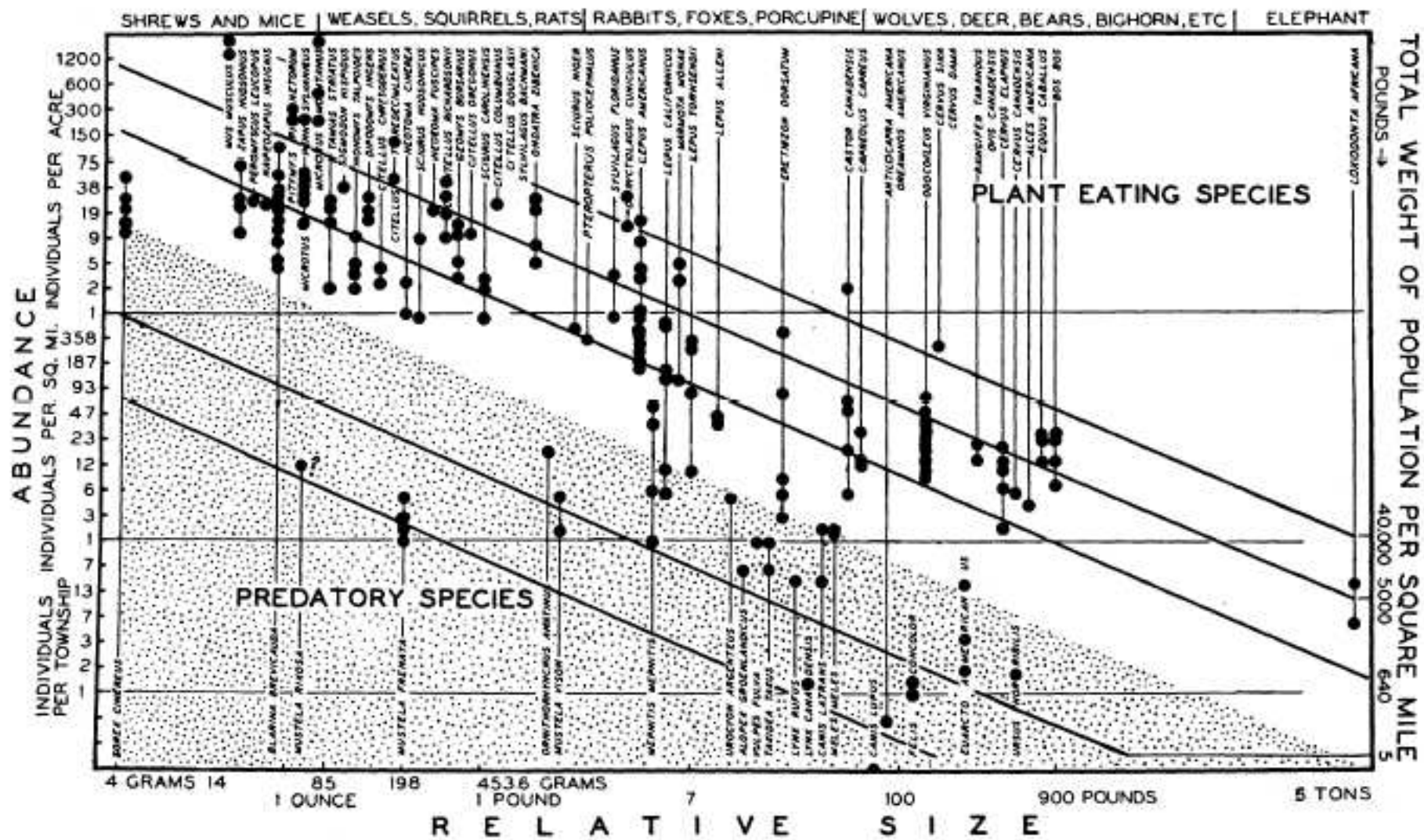
$$N \propto R/B$$

which is equivalent to:

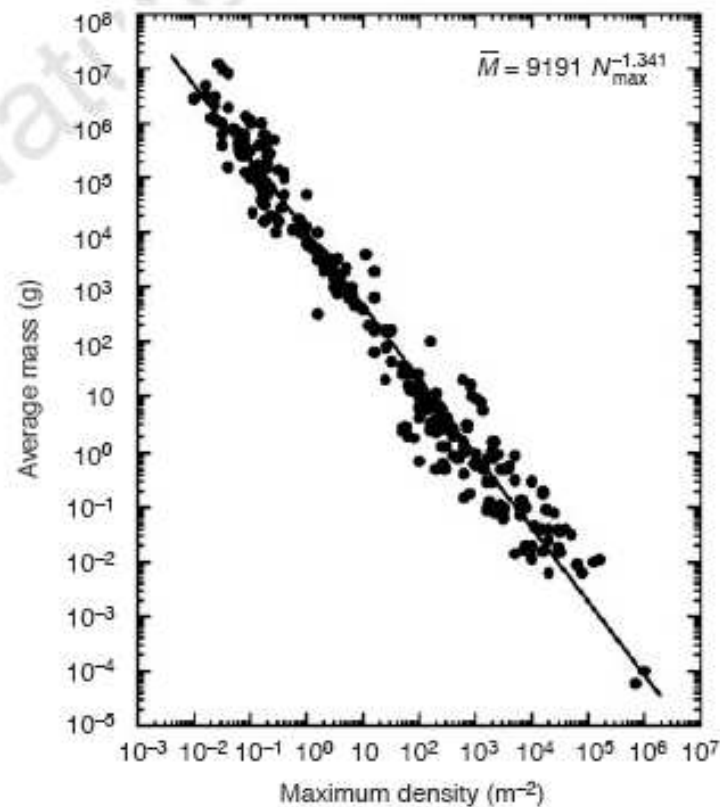
$$N = C_1 M^{-3/4}$$

Thus implying that, on average, species tend to use a similar amount of energy within trophic groups in ecosystems !!!!

This relationship was first identified by Van Valen (1976,1977) as a consequence of zero sum dynamics.



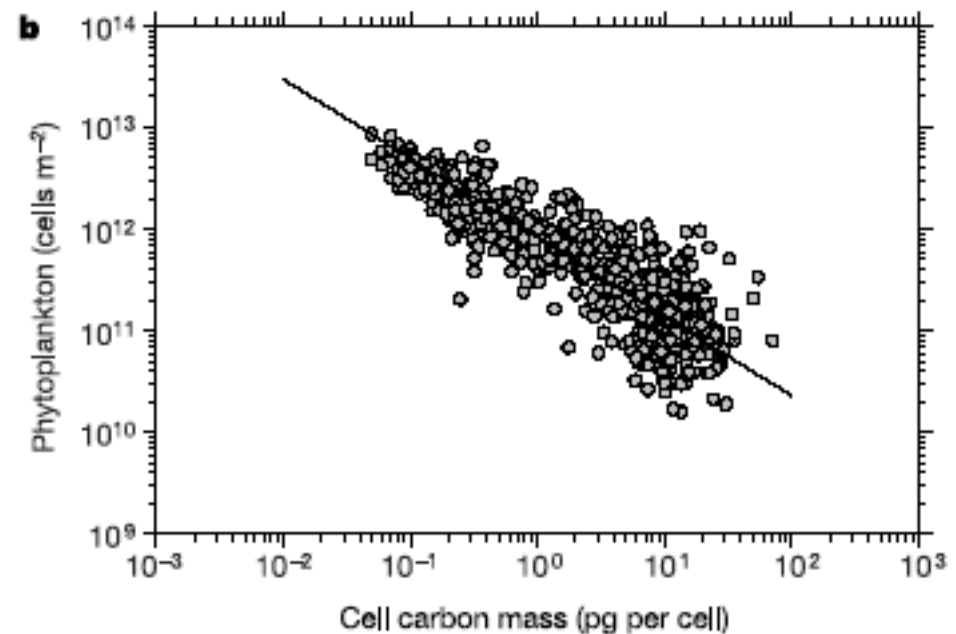
Carl O. Mohr (1940) Comparative Populations of Game, Fur and Other Mammals. *American Midland Naturalist*, 24: 581-584.



Allometric scaling of plant energetics and population density

Brian J. Enquist*, James H. Brown* & Geoffrey B. West†

NATURE | VOL 395 | 10 SEPTEMBER 1998

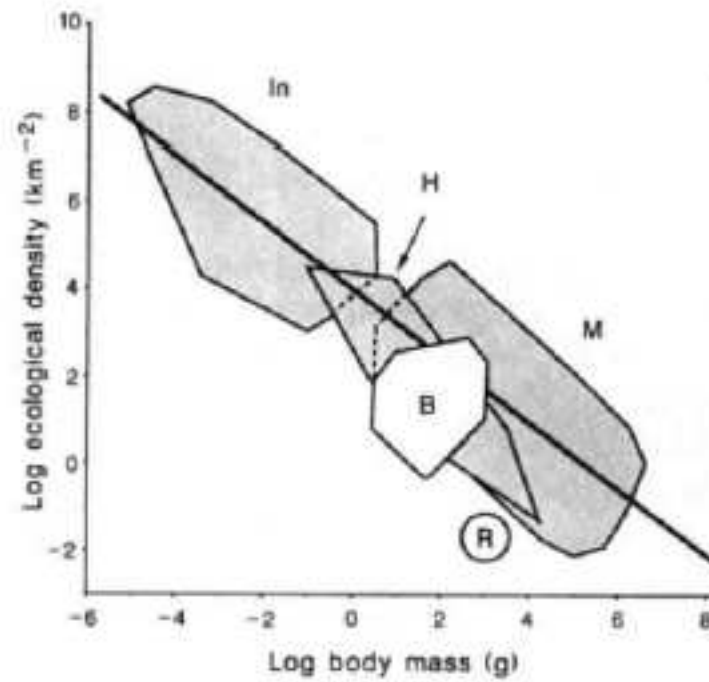


Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean

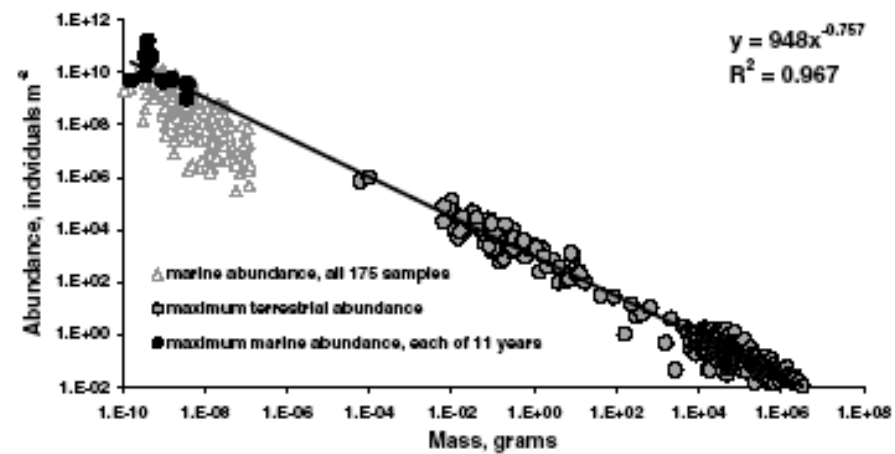
W. K. W. Li

NATURE | VOL 419 | 12 SEPTEMBER 2002

Damuth (1991)



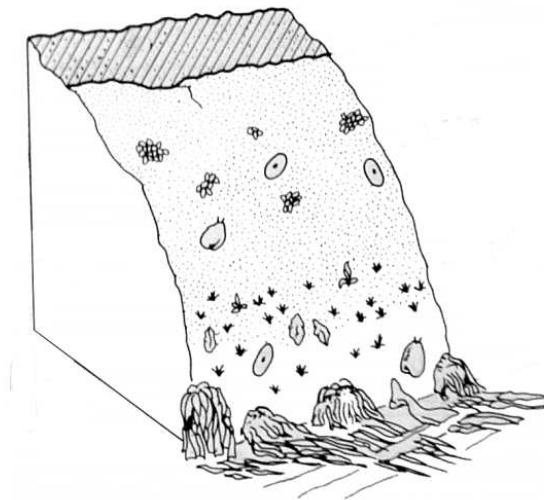
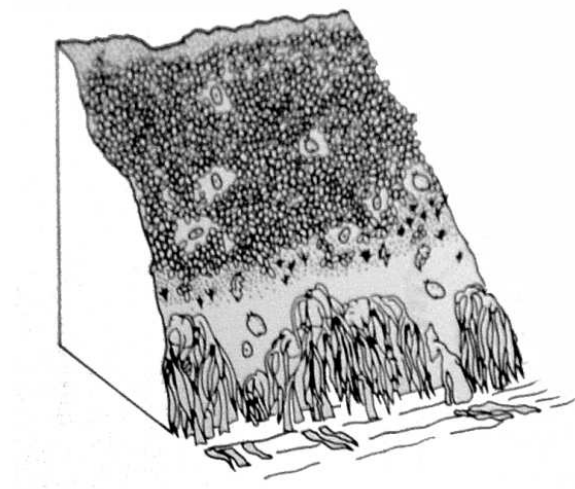
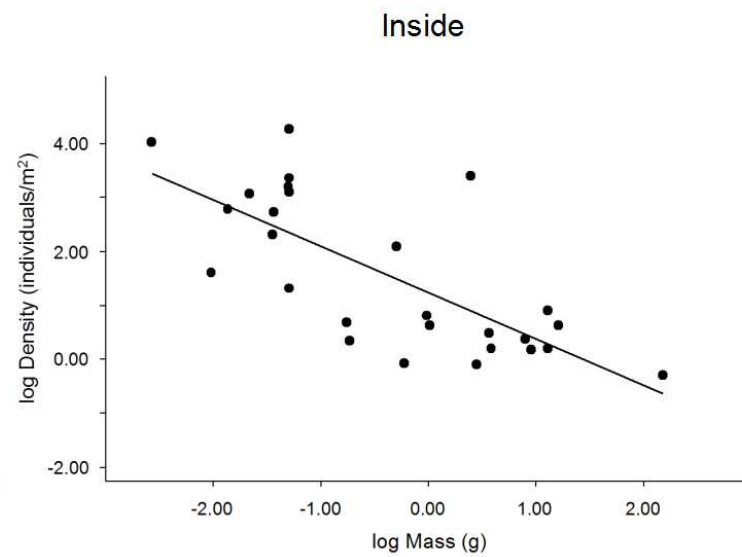
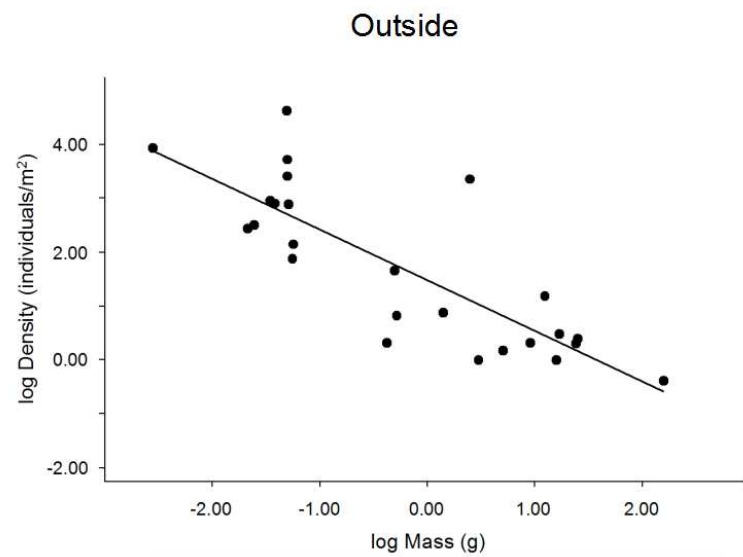
Belgrano et al (2002)



There are several remarkable aspects to this scaling relationship:

- It is invariant across time and space.





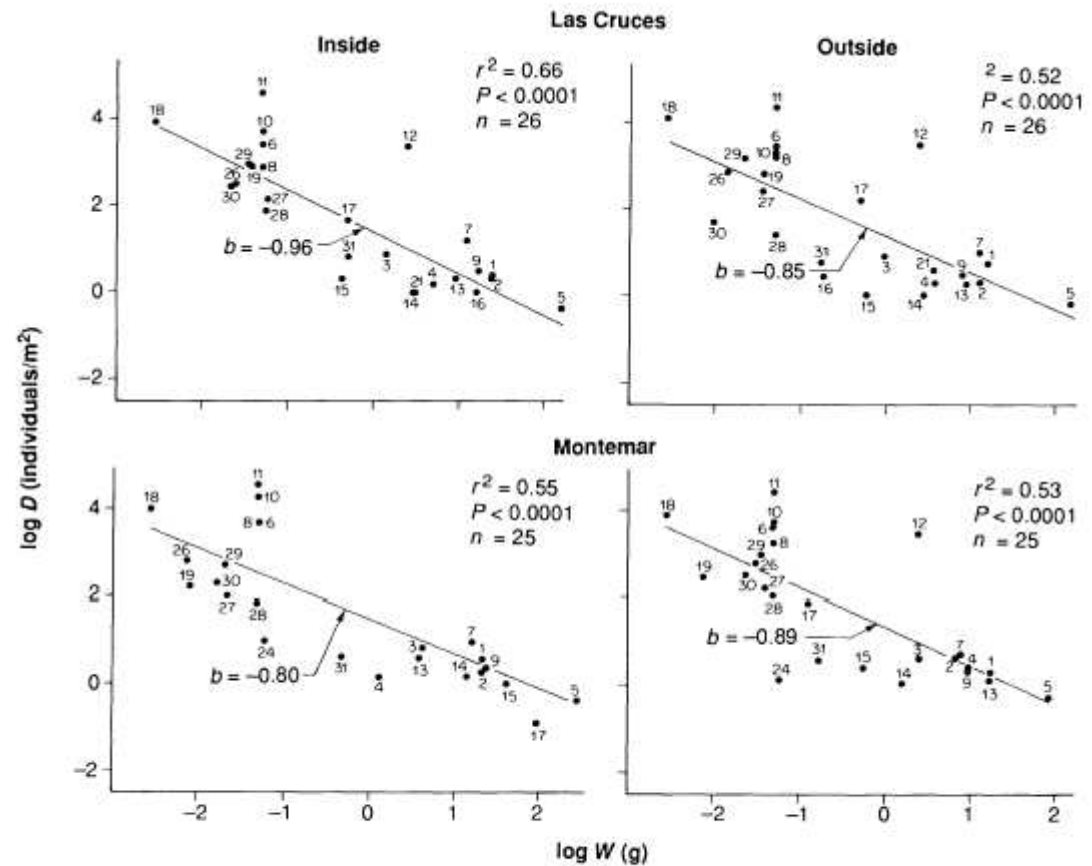
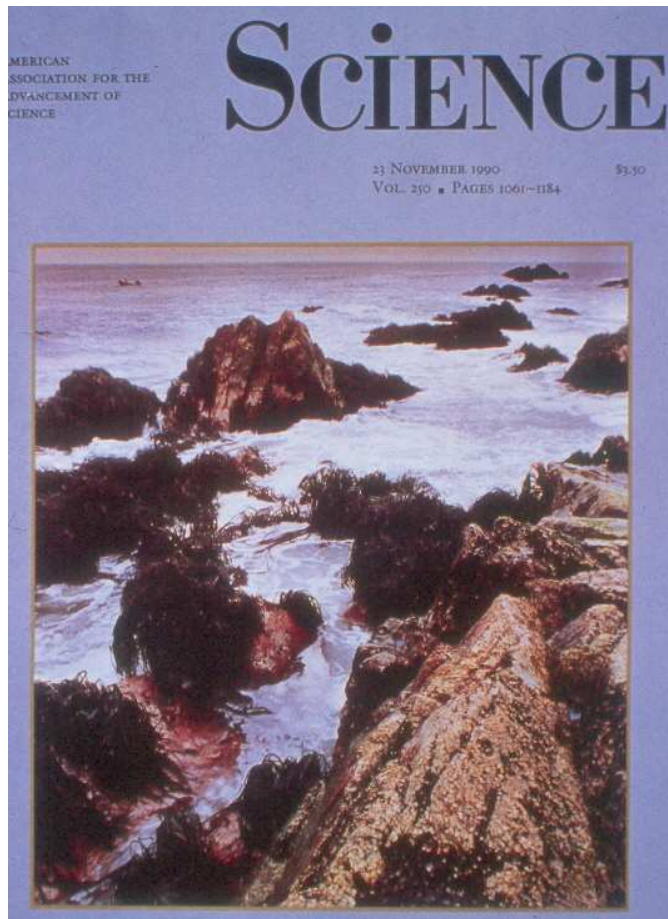
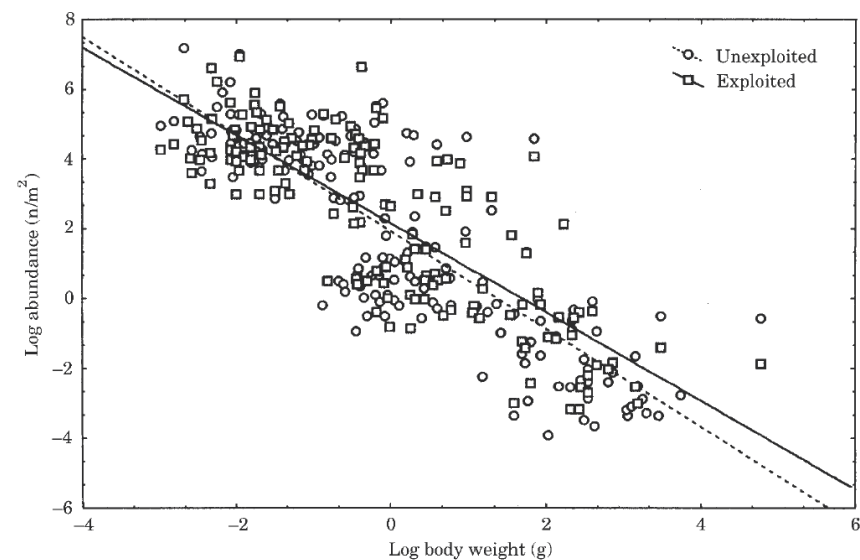
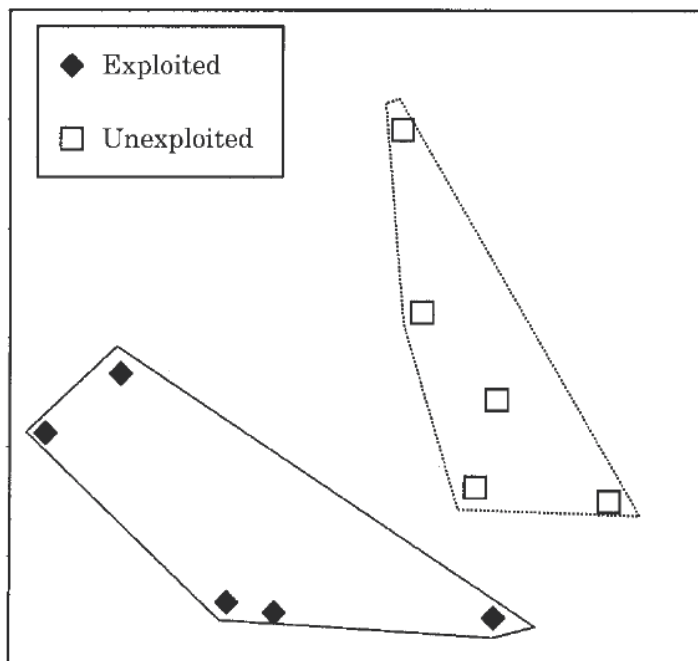


Fig. 2. Population density scaling, inside and outside two marine preserves (Las Cruces and Montemar). The regression equations were: Las Cruces inside, $\log D = 1.44 + (-0.96) \log W$; Las Cruces outside, $\log D = 1.38 + (-0.85) \log W$; Montemar inside, $\log D = 1.49 + (-0.80) \log W$; Montemar outside, $\log D = 1.35 + (-0.89) \log W$. Species identity and symbols as in Fig. 1.

Marquet, Navarrete & Castilla (1990)



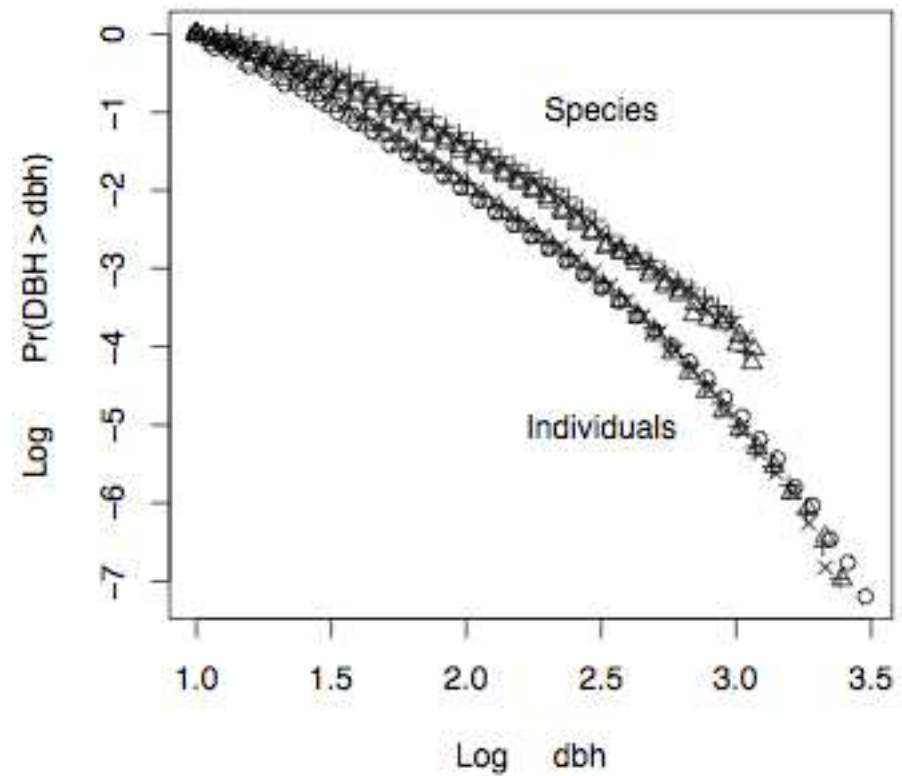
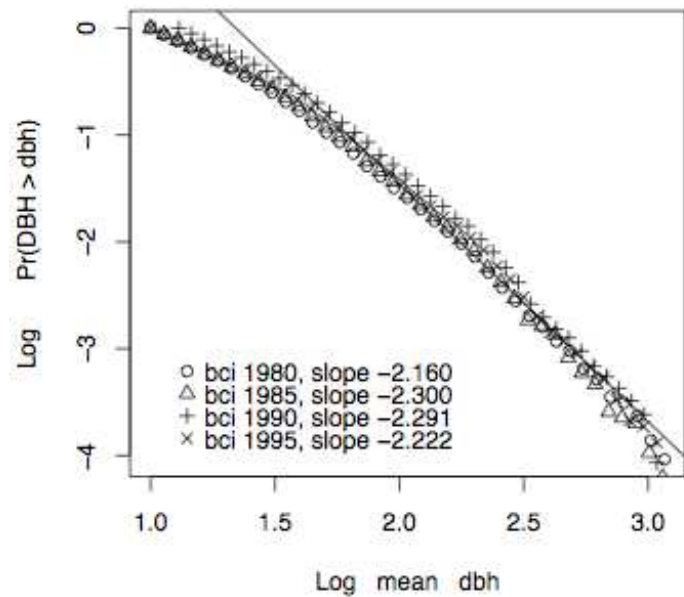
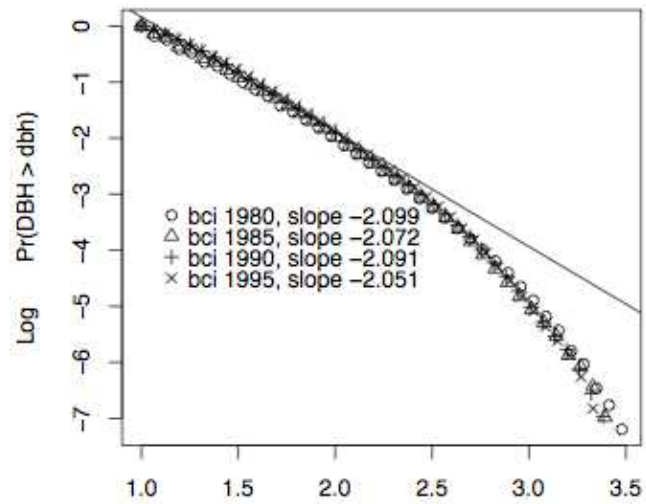
ICES Journal of Marine Science, 59: 1237–1247. 2002

doi:10.1006/jmsc.2002.1287, available online at <http://www.idealibrary.com> on IDEAL[®]

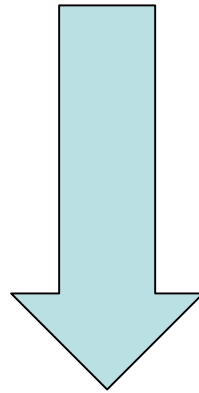
The community structure of a tropical intertidal mudflat under human exploitation

W. F. de Boer and H. H. T. Prins

BCI PLOTS (tree species)



The scaling of energy acquisition and transformation from individual to ecosystems



METABOLIC THEORY OF ECOLOGY

Ecology, 85(7), 2004, pp. 1771–1789
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TOWARD A METABOLIC THEORY OF ECOLOGY

JAMES H. BROWN,^{1,2,4}

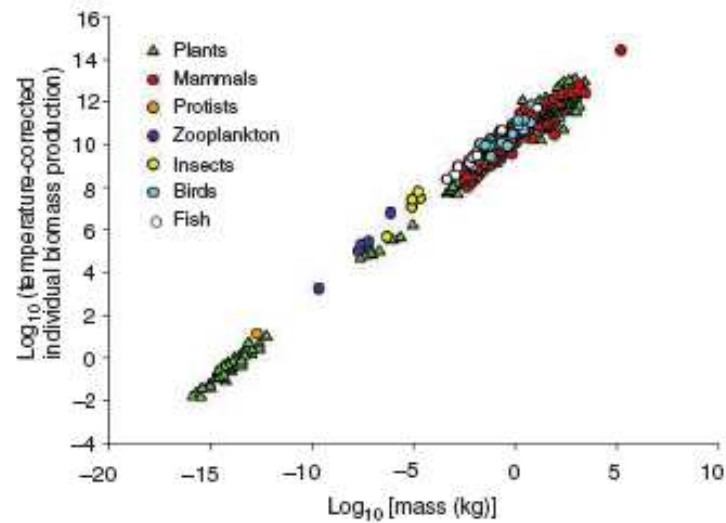
with JAMES F. GILLOOLY,¹ ANDREW P. ALLEN,¹ VAN M. SAVAGE,^{2,3} AND GEOFFREY B. WEST^{2,3}

$$B = f(M, T)$$

$$B \propto M^{3/4} \times e^{-E/kT}$$

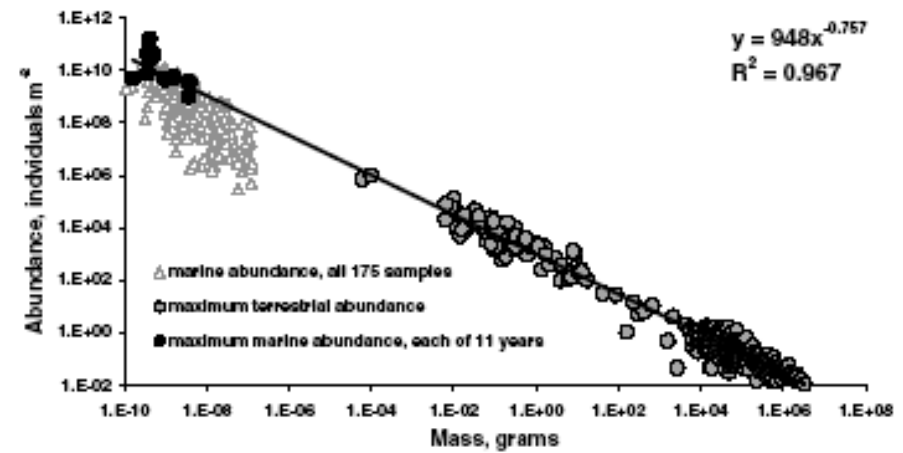
- Ontogenetic growth and individual biomass production
- Population growth rate and r_{\max}
- Population density
- The pace of interspecific interactions
- Species diversity
- Standing stock of biomass
- Energy flux, biomass production, and turnover
- Trophic dynamics

Individual production



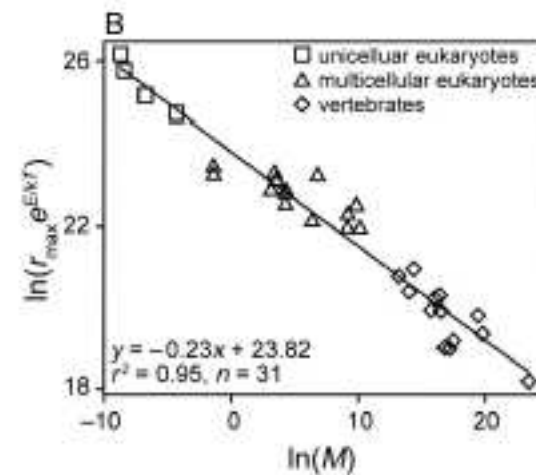
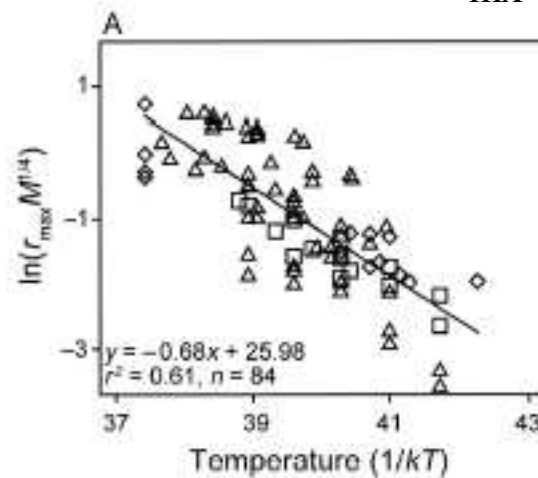
Ernest et al (2003)

Population density



Belgrano et al (2002)

r_{mx}



Savage et al. 2004

In addition of theories grounded in first principles we also need a strategy for theory development.

I submit that this strategy is to start simple (i.e., build understanding from symmetric/neutral theories whose aim should be to produce the theoretical foundations and general laws valid for a great variety of systems, while making as few hypotheses as possible about the nature of the components of the system under analysis.

Example: The analysis of fluctuations

The zero-sum Red queen hypothesis entails the existence of interacting assemblages wherein the amount of energy captured by one species is balanced by equal losses of some other members of the assemblage.



Compensatory changes within assemblages

McArthur (1960)

communities are biotically saturated such that total community abundance is constant. That is...

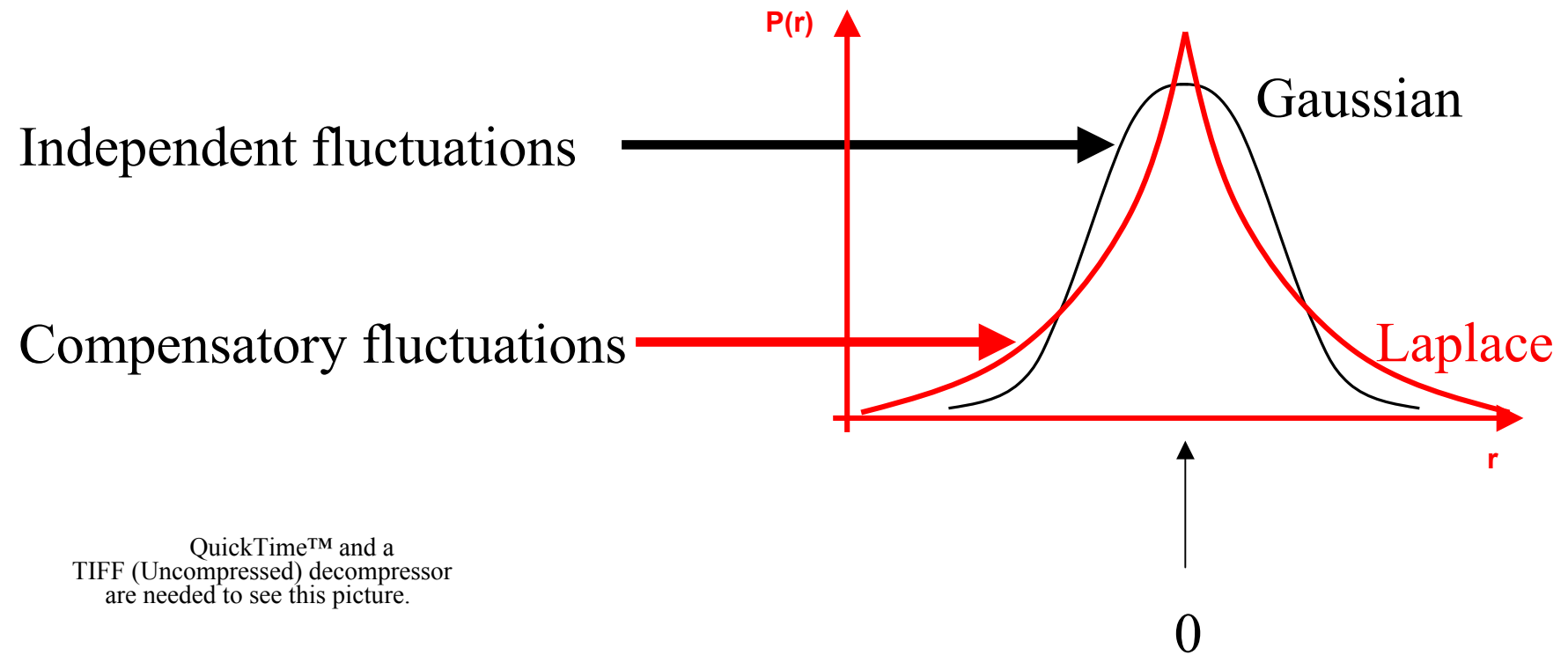
" an increase in one species population results in a roughly equal decrease in the populations of other species."

Hubbell (2001)

"...any increase in one species must be accompanied by a matching decrease in the collective number of all other species in the community . The sum of all changes in abundance is always zero."

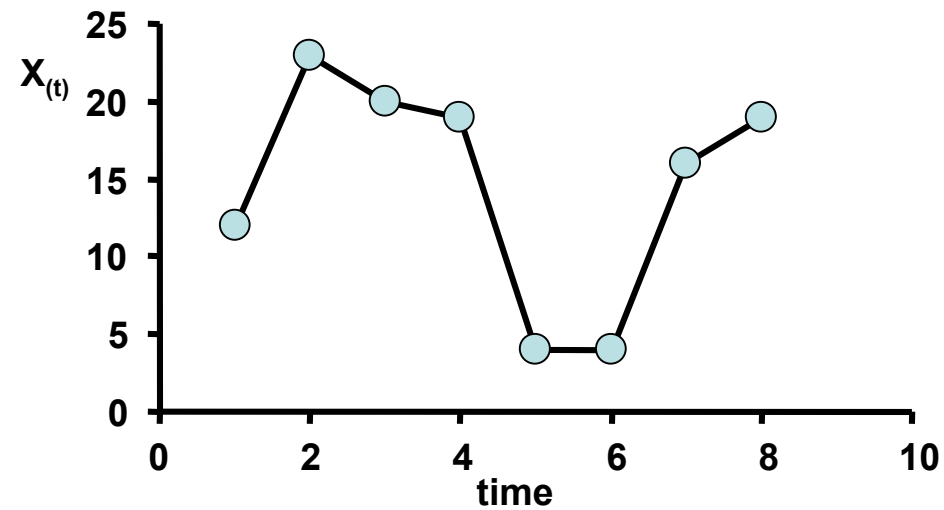
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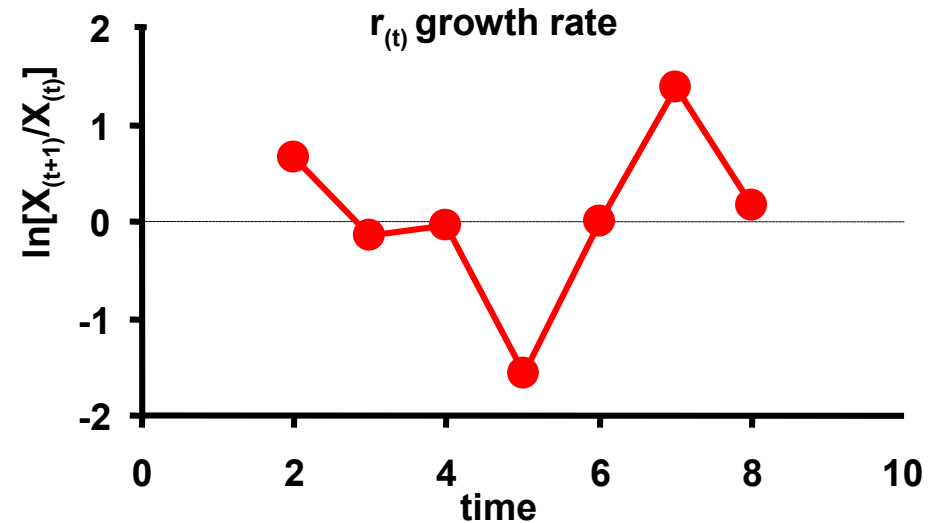
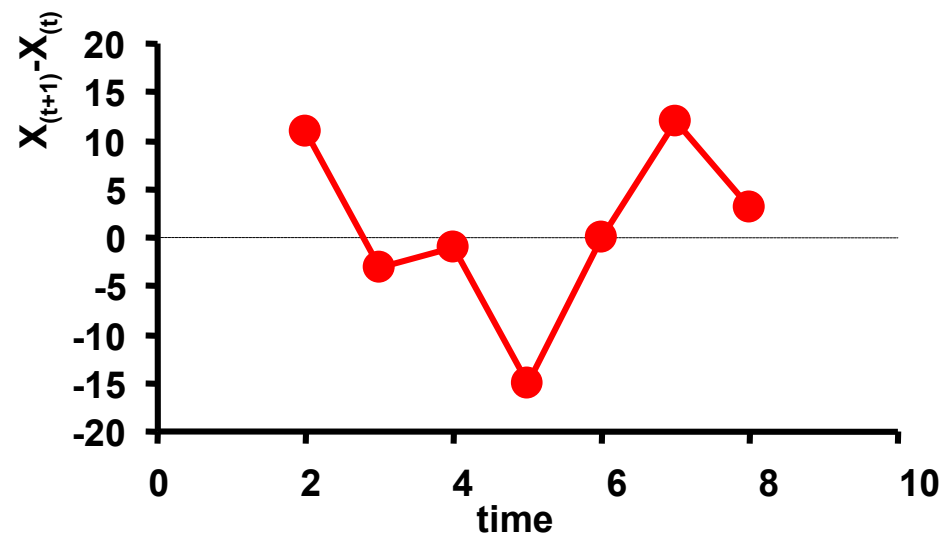
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¿How to measure fluctuations?



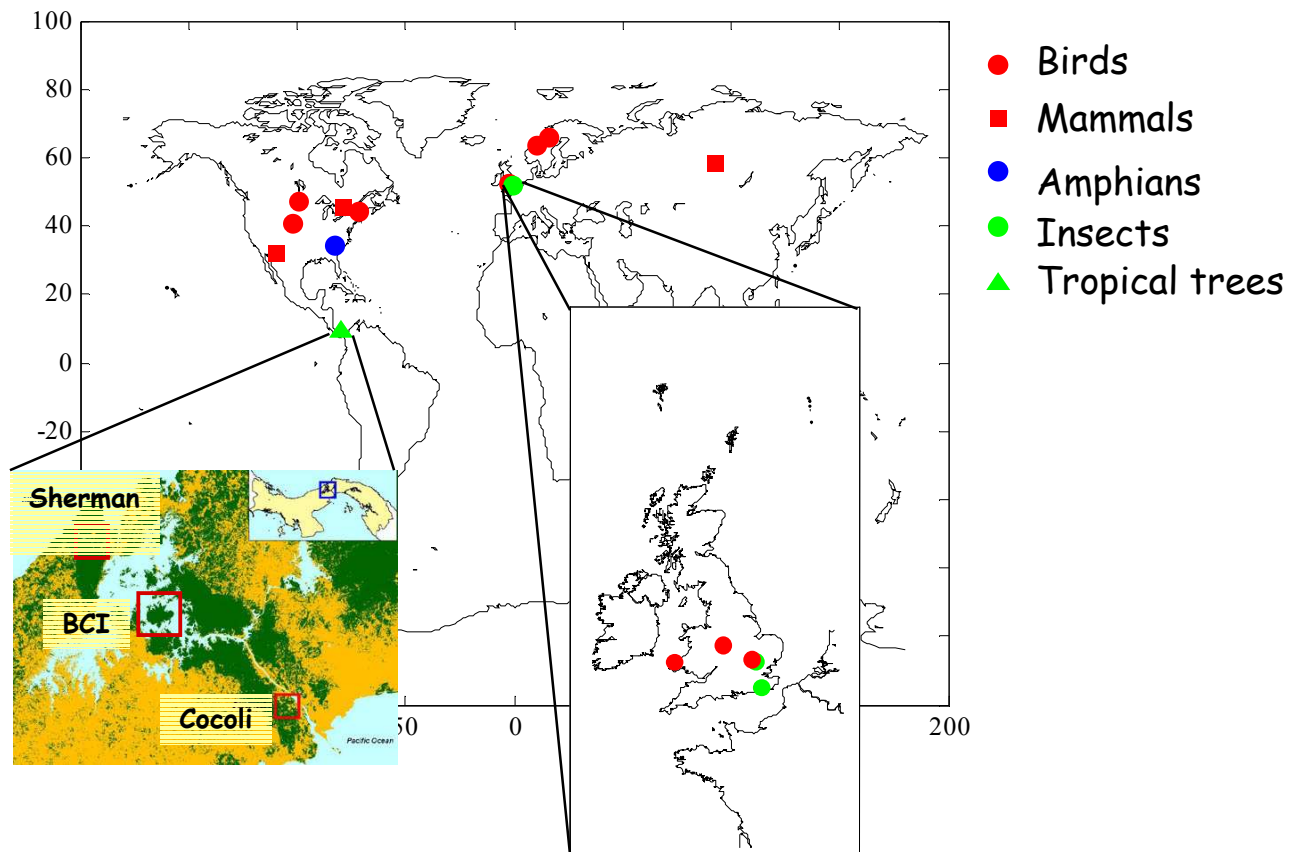
$$X_{(t+1)} - X_{(t)}$$

$$\ln(X_{(t+1)}) - \ln(X_{(t)}) = \ln[X_{(t+1)}/X_{(t)}]$$

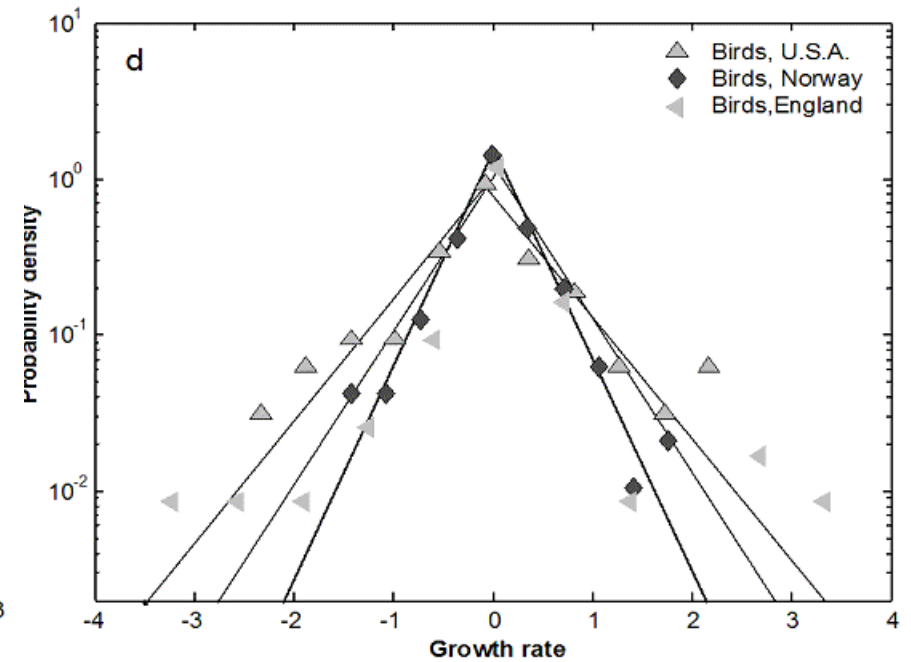
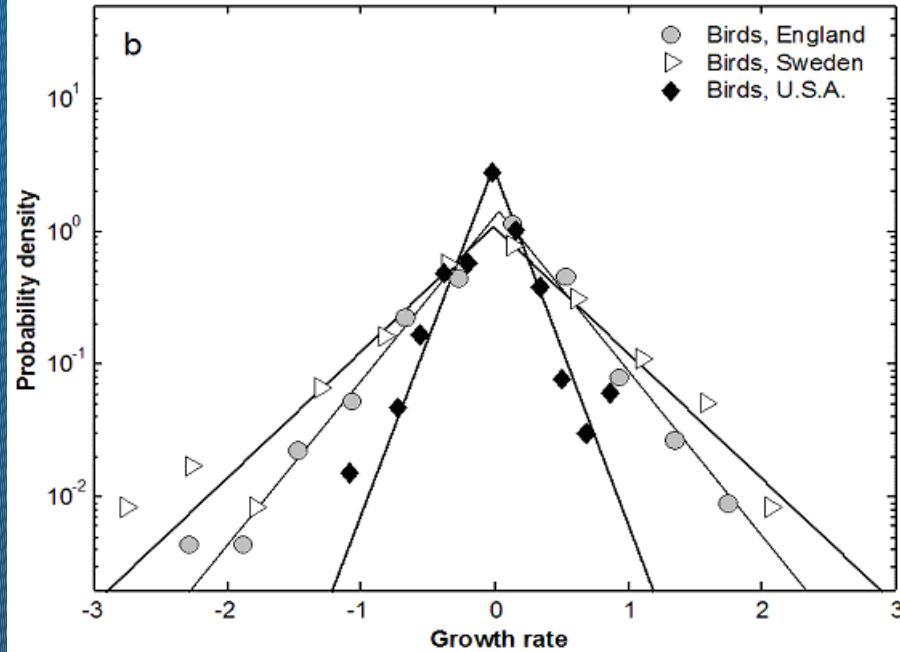
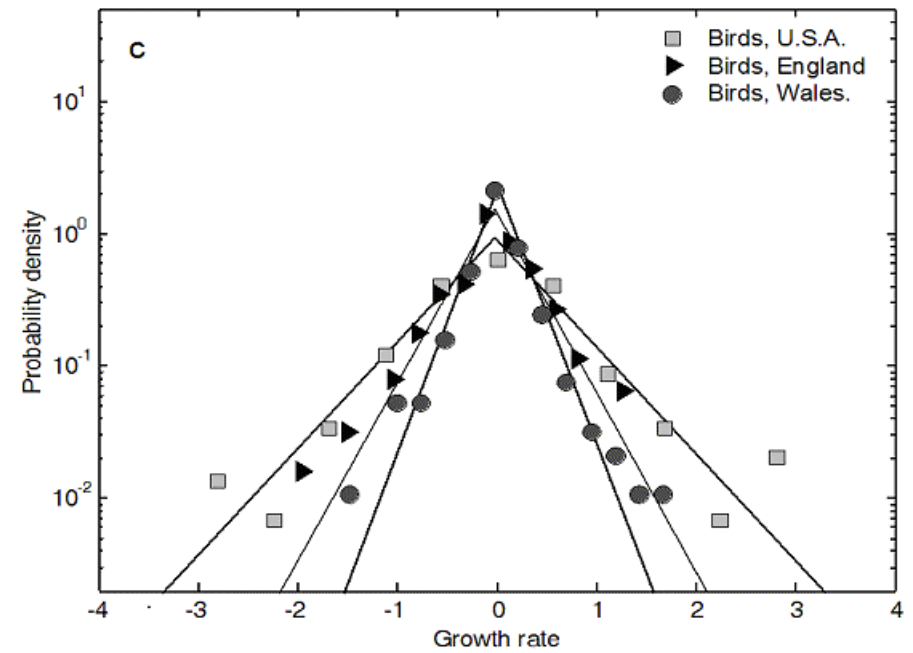


Data

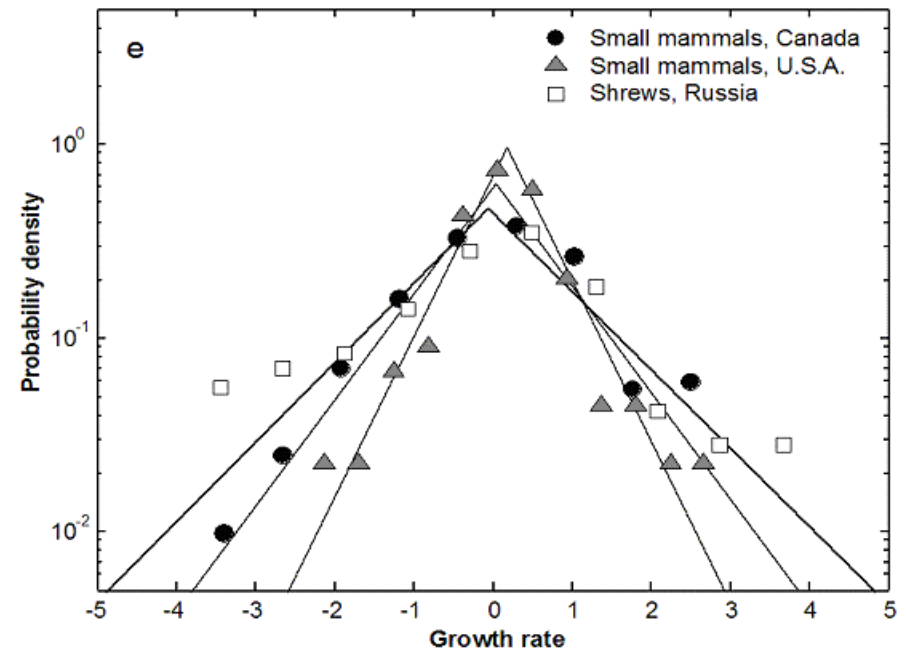
- Population dynamics for 18 species assemblages across the globe found in different biomes.



Birds

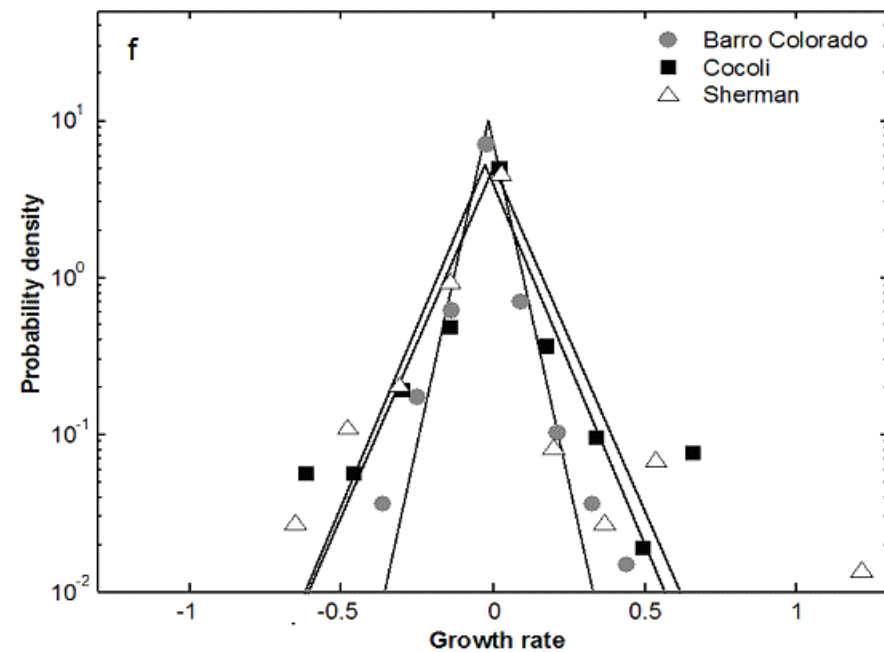


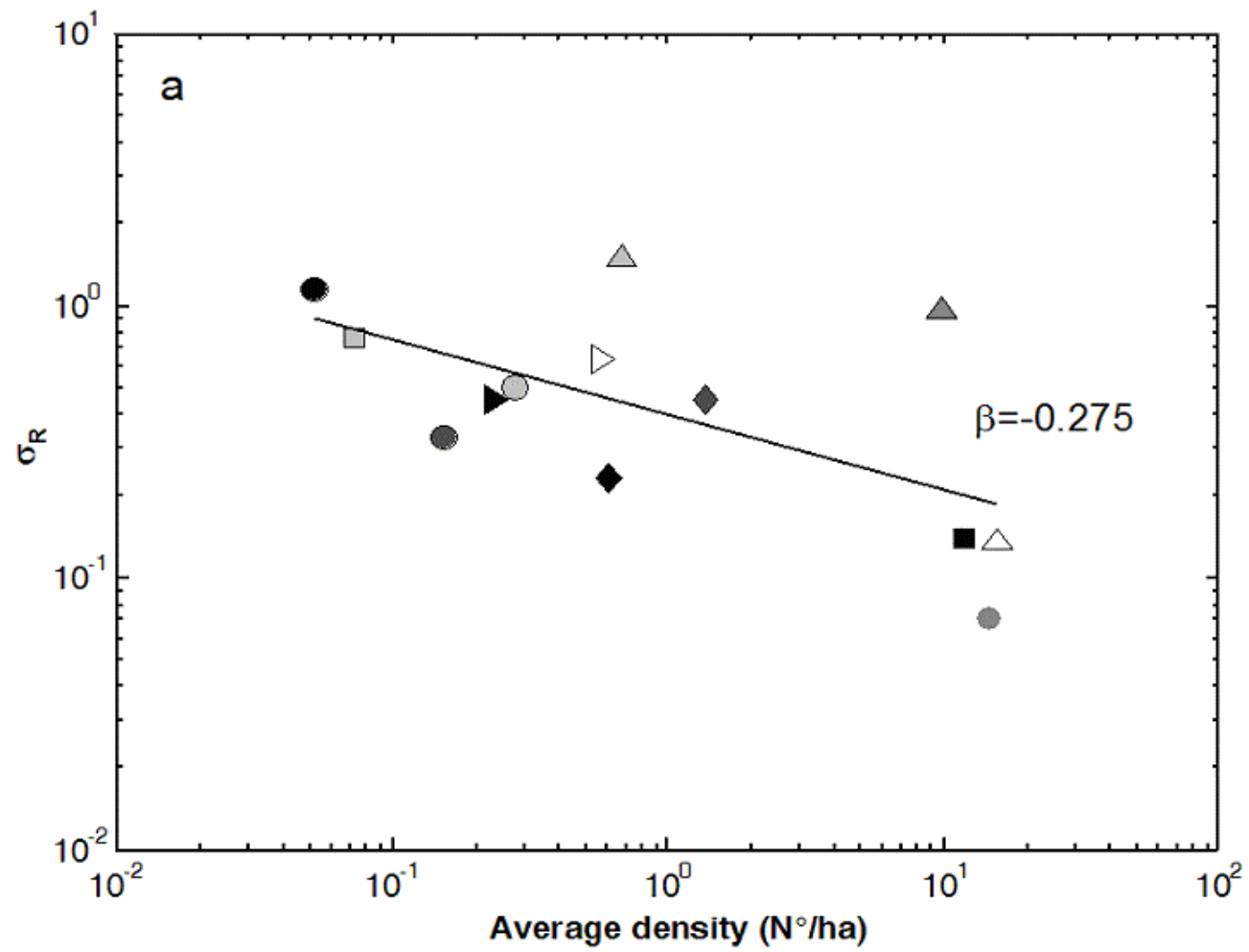
Small mammals



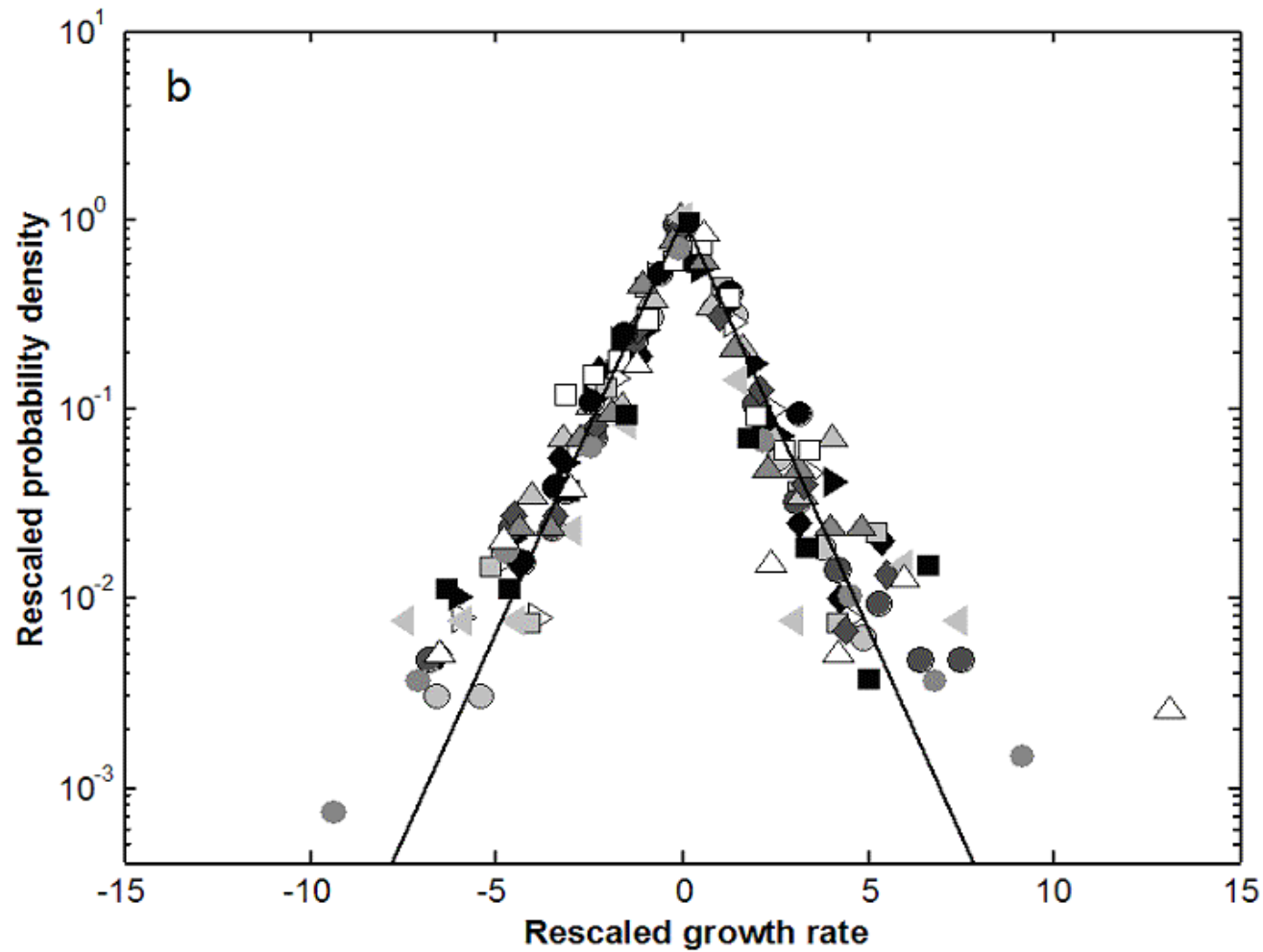
Tropical trees

- All these distributions show similar shape but different amplitudes





$$\sigma(N) \propto N^{-\beta}$$

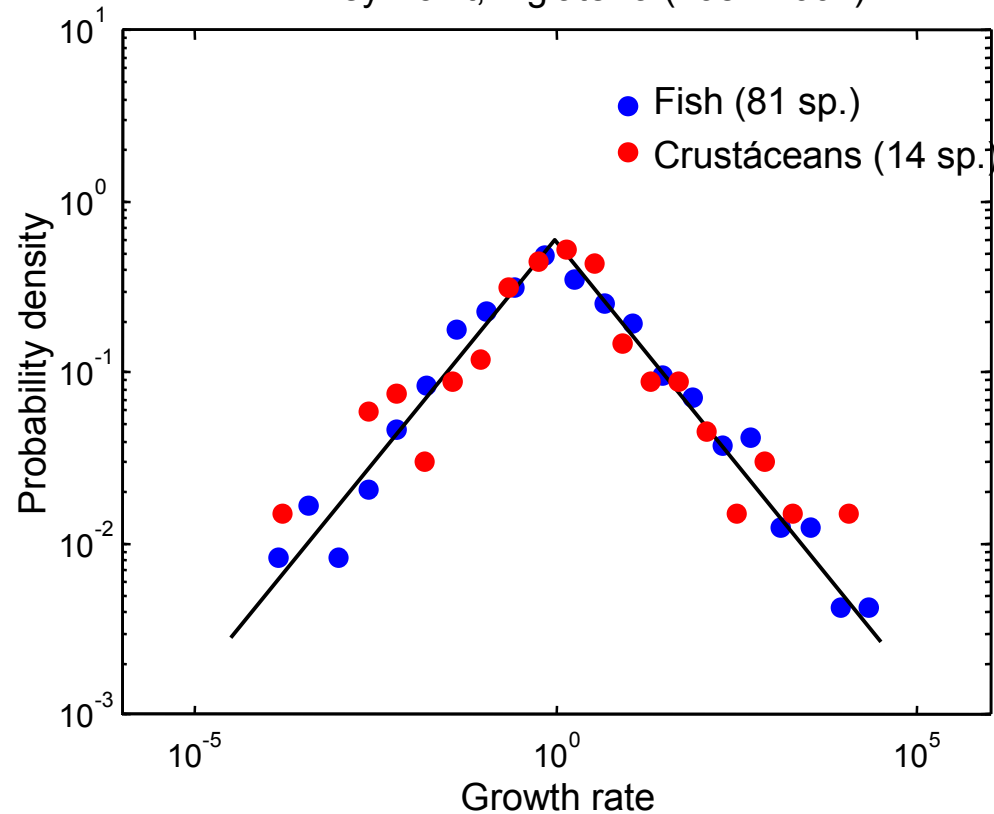


Re-scaling by $\sigma_r(n)$ and average density all distributions collapse to:

$$p_{\text{scal}} = e^{(-|r_{\text{scal}}|)}$$

Within food webs

•Hinkley Point, Inglaterra (1981-2002)



Magurran & Henderson (2003)

letters to nature

Explaining the excess of rare species in natural species abundance distributions

Anne E. Magurran¹ & Peter A. Henderson²

¹ Gatty Marine Laboratory, School of Biology, University of St Andrews, St Andrews, Fife KY16 9LB, UK
² Pinn Conservation Ltd, IRC House, The Square, Pennington, Lymington, Hampshire SO41 6RN, UK

³ The authors contributed equally to this work

The observation that a few species in ecological communities are exceptionally abundant, whereas most are rare, prompted the development of species abundance models^{1–5}. Nevertheless, despite the large literature on the commonness and rarity of species inspired by these pioneering studies, some widespread empirical patterns of species abundance resist easy explanation⁶. Notable among these is the observation⁷ that in large assemblages there are more rare species than the log-normal model predicts^{8,9}. Here we use a long-term (21-year) data set, from an estuarine fish community, to show how an ecological community can be separated into two components. Core species, which are persistent, abundant and biologically associated with estuarine habitats, are log-normally distributed. Occasional species occur infrequently in the record, are typically low in abundance and have different habitat requirements; they follow a log-series distribution. These distributions are overlaid, producing the negative skew that characterizes real data sets.

Concern about rapid biodiversity loss has intensified the need to understand community structure. It is generally accepted that most distributions of species abundance in large assemblages tend towards the log-normal^{10–12}. However, whereas the ‘canonical hypothesis’ was the focus of debate in the past half-century¹³, it is negative skew that now captures attention. Two neutral theories predict species abundance distributions that replicate the negative skew observed in empirical data sets. The unified theory of biodiversity and biogeography develops a new species abundance distribution, the zero-sum multinomial, in which the degree of negative skewness is a function of community size and immigration

rate. The self-similarity model¹⁴ predicts that the change in species richness with area is constant across all spatial scales. Both approaches assume the ecological equivalence of all species in the community. A process of multi-dimensional niche subdivision has been postulated¹⁵ that also leads to negative skew¹⁶. We argue that the observed patterns can be more parsimoniously explained by dividing an assemblage into two components—persistent and occasional species—and without invoking neutrality.

Here we examine the relative abundance of species in an exceptionally large data set—a 21-year investigation (with monthly sampling) of a fish community at Hinkley Point in the Bristol Channel, UK, in which $S = 80$ species and $N = 96,000$ individuals were recorded (see Methods). Our data clearly show that the maximum abundance of a species in the year in which it is most abundant is a function of the number of years for which it has been recorded (Fig. 1). The commonness and rarity of species in the assemblage is thus related to their persistence. Three species (sprat (*Sprattus sprattus*), sand goby (*Pomatoschistus minutus*) and whiting (*Merlangius merlangus*)) continuously dominate and together account for an average 70% of total abundance (by weight or by number). Adding the other 28 core species brings the total to 99%. The 49 infrequent species thus contribute only 1% of total abundance over the 21 years of the study. Importantly, the fish at Hinkley Point fall into two distinct groups: a core of persistent (more than 10 years in the record) and usually—but not invariably—abundant species and a set of occasional (less than 10 years in the record) and typically non-abundant species (Fig. 1). This allows us to decompose the empirical species abundance distribution (Fig. 1b) into two groups of species. The distribution of the occasional species, which are not continuously present in an assemblage but may sometimes breed there, follows a log-series distribution (Fig. 1d)¹⁷, whereas the persistent species are log-normally distributed (Fig. 1c)¹⁸. We employ three different methods to demonstrate that the division of species into two groups is not arbitrary.

First, we use a diversity statistic to reveal the shift from the log-series to the log-normal model as we work through the data set. The average value of Simpson’s diversity index, D , will remain approximately constant, once $S > 10$, if species are distributed according to the log-series model¹⁹. However, if a log-normal distribution persists, D will increase with S . We therefore expect Simpson’s index to track the transition from log-series to log-normal as persistent species are progressively included in the analysis. Figure 2 confirms this. The switch to the right of the natural break in our empirical data set

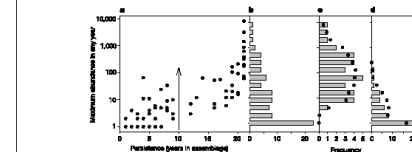
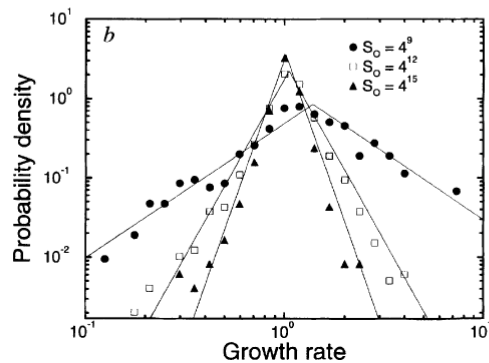
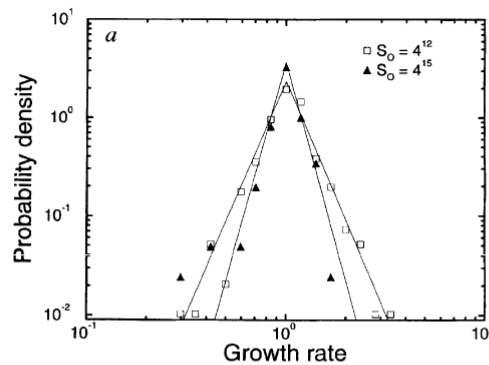


Figure 1 The pattern of abundance and persistence in the fish community of Hinkley Point, Bristol Channel. This data set is for a 21-year time series of monthly samples. **a**, The number of years for which each fish was observed, plotted against the maximum abundance in any one year. A discontinuity indicated by the vertical arrow shows the core and occasional species to be defined as those present for >10 and <10 years, respectively. **b**, The abundance distribution for all species. **c**, The abundance distribution of the core species; the frequency of each abundance class predicted with a log-normal model is shown as a solid line ($\chi^2 = 5.08$, $P = 0.208$). **d**, The abundance of the occasional species; the frequency of each abundance class predicted with a log-series model is shown as a solid line ($\chi^2 = 4.24$, $P = 0.536$).

Other complex systems:

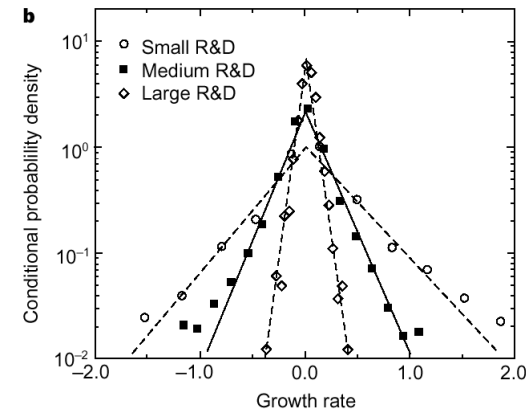
•Companies

$$p(r | s_0) = \frac{1}{\sqrt{2}\sigma(s_0)} \exp\left(-\frac{\sqrt{2}|r - \bar{r}(s_0)|}{\sigma(s_0)}\right) \quad (1)$$



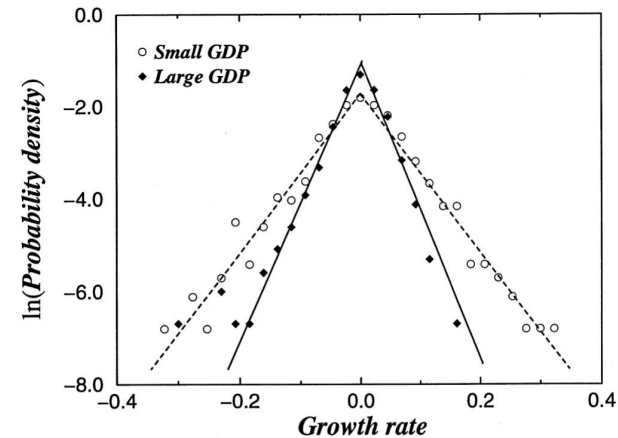
Stanley *et al.* 1996

•Universities



Plerou *et al.* 1999

•Country GDPs

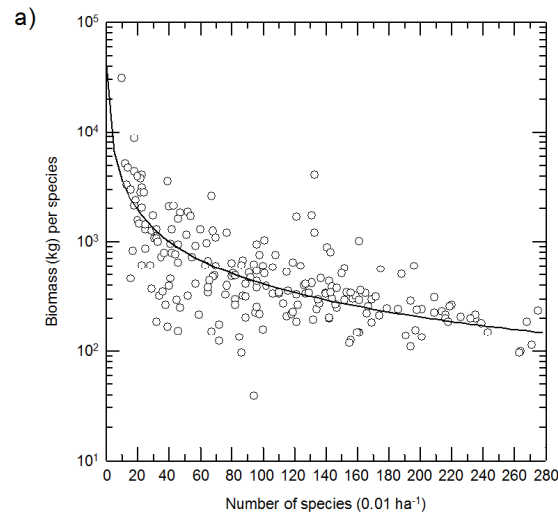


Canning *et al.* 1998

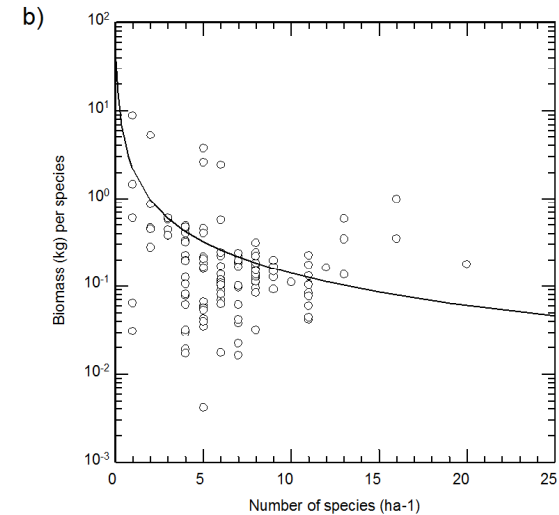
The analysis of biomass patterns

$$M_{\text{tot}} \propto S^0$$

$$M_{\text{tot}}/S \propto S^{-1}$$



TREES
(Enquist et.al. 2002)



SMALL MAMMALS
(Labra & Marquet)

Total biomass is independent of the number of species!!!

my predecessor Amyan Macfadyen (1975) who cited K. E. F. Watt's (1971) vivid image 'if we do not develop a strong theoretical core that will bring all parts of ecology back together we shall all be washed out to sea in an immense tide of unrelated information'.

T.R.E. Southwood's Presidential address to the BES.
Habitat the template for ecological strategies?
J.A.E. (1977)

Acknowledgements

- Fabio Labra, Sebastian Abades, Matias Arim, Tony Barnosky, CASEB, IEB