



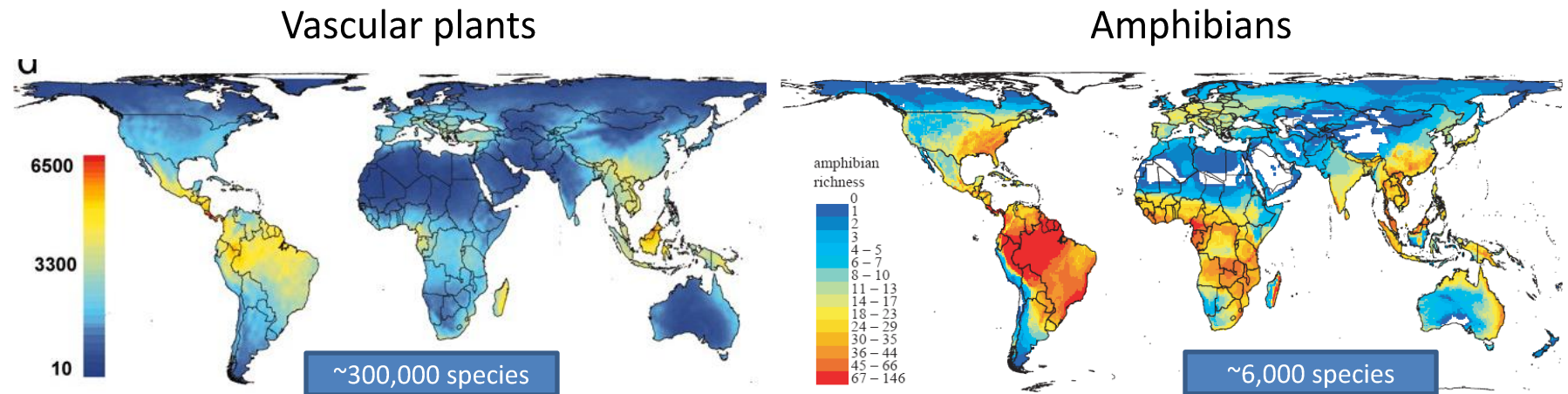
Local Diversity

Quiz

- Which of the following are measures by which ecologists quantify diversity?
 - a) Species richness
 - b) Simpson's Index
 - c) Paine's index
 - d) Shannon's index
 - e) Darwin's number
- Bonus points for describing how the previous slide relates to the problem of maintaining diversity

The worldwide distribution of species

- The question “What determines patterns of species diversity?” was among the 25 key research themes for the future identified in 125th Anniversary issue of *Science* (July 2005)



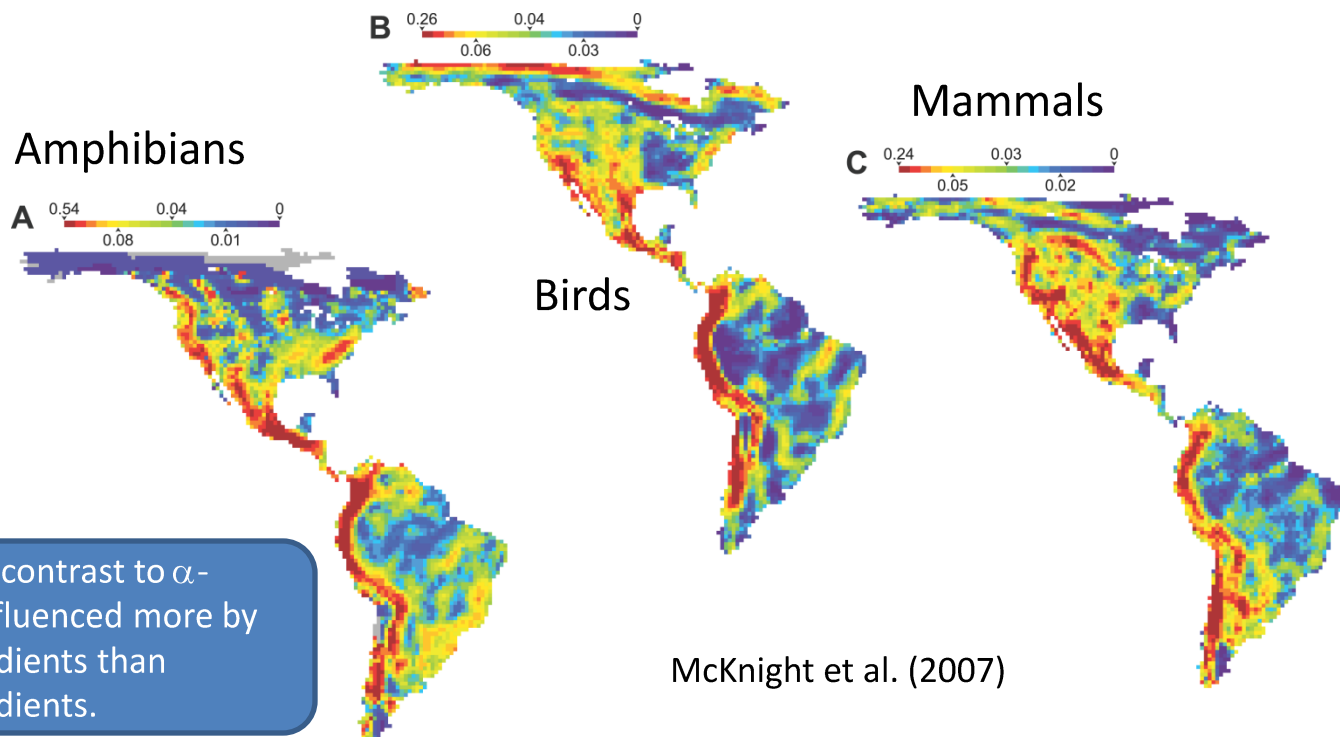
From Kreft & Jetz 2007

From Buckley & Jetz 2007

Quantifying biodiversity

Species richness

Species richness – the number of species present in a region. (When the region is small (“local diversity”), this is sometimes referred to as α -diversity; when the region is large (“regional diversity”, this is sometimes referred to as γ -diversity. The turnover in species composition along a gradient is called β -diversity.

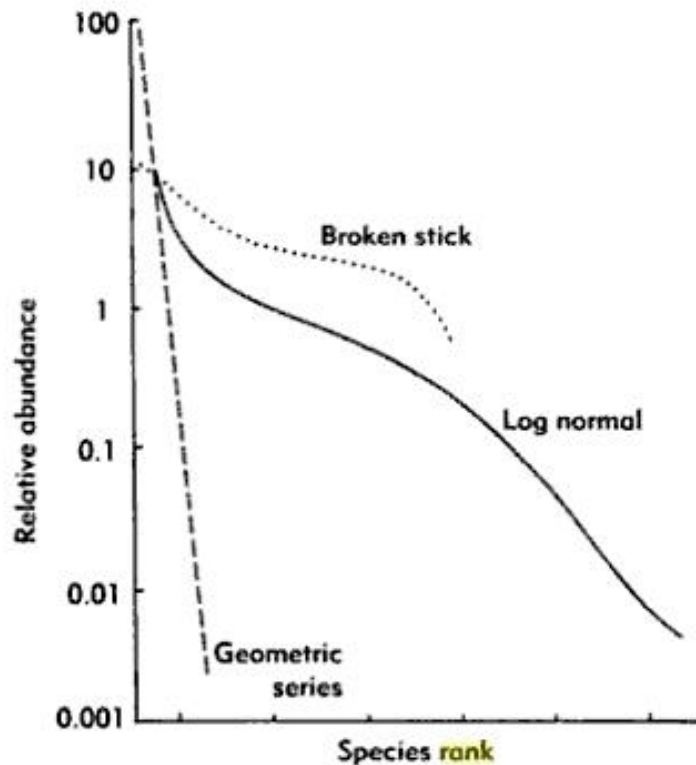


β -diversity (in contrast to α -diversity) is influenced more by altitudinal gradients than latitudinal gradients.

Quantifying biodiversity

Species evenness

Species evenness – the average relative abundance of species in a community

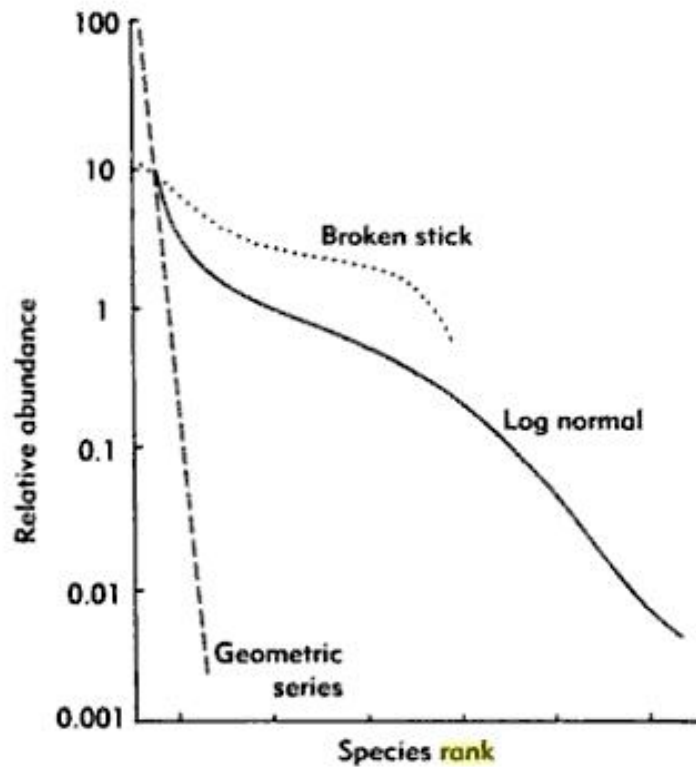


Whittaker (1970)

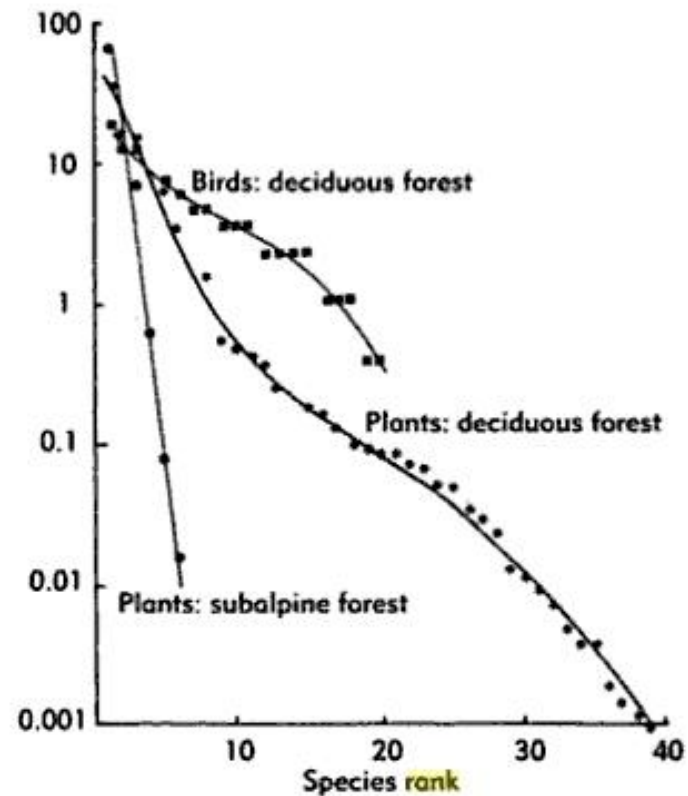
Quantifying biodiversity

Species evenness

Species evenness – the average relative abundance of species in a community

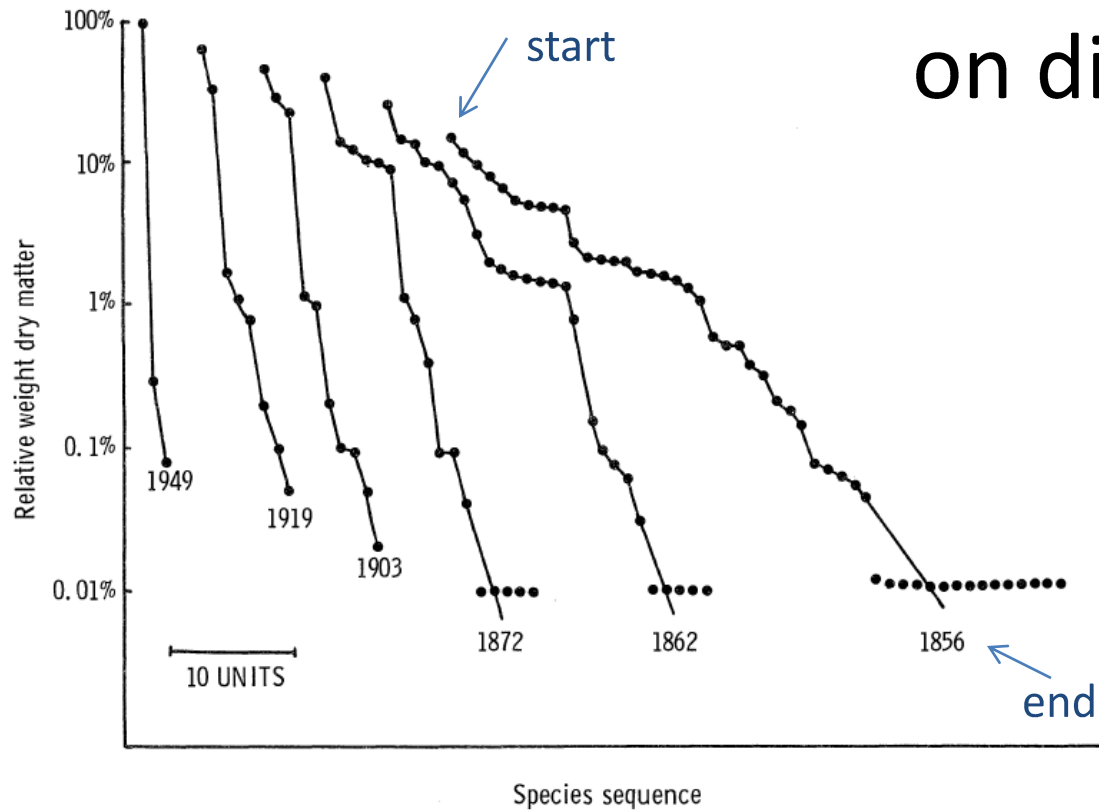


Whittaker (1970)



Magurran (1988)

Effect of fertilization on diversity



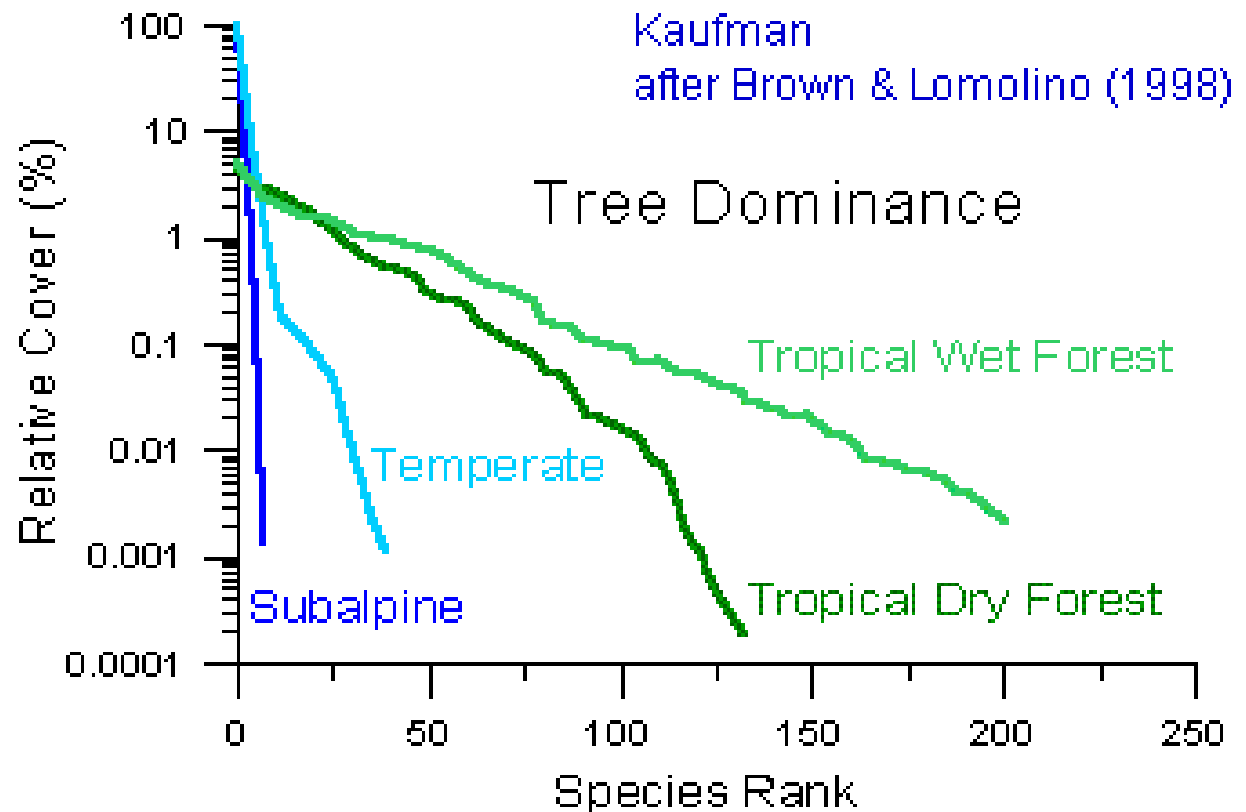
Fertilization led to a decrease in *species richness* (end points of each line) and *increasing dominance* (start points of each line). Thus, the effect of fertilization on biodiversity was through both the richness and evenness components.

This figure, originally reported in Kempton (1979), was used by May et al. (2007) as an example of the effect of overapplication of fertilizer on diversity. Specifically, it shows how the relative abundance of grass species changed over a century and a half of intense fertilization. **Fertilization led to decreased diversity.**

Effect of climate on diversity

Both richness and evenness change along a gradient from Subalpine (high latitude) to Tropical (low latitude) environments

Tropical Wet Forests show higher diversity than Tropical Dry Forests

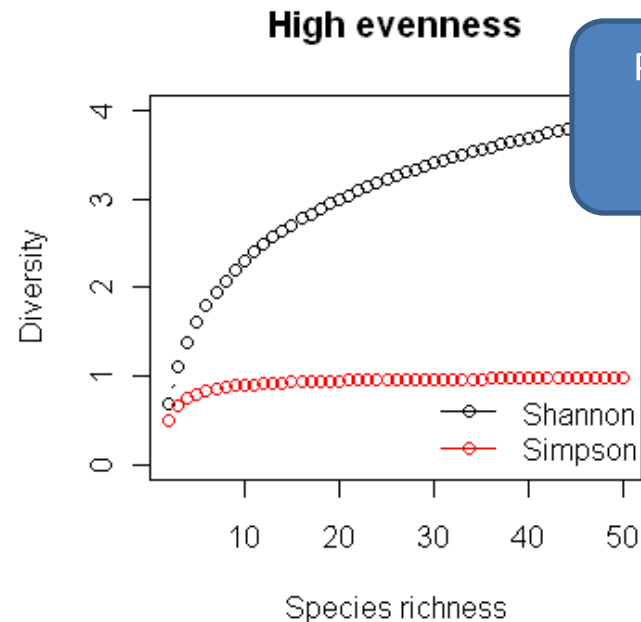
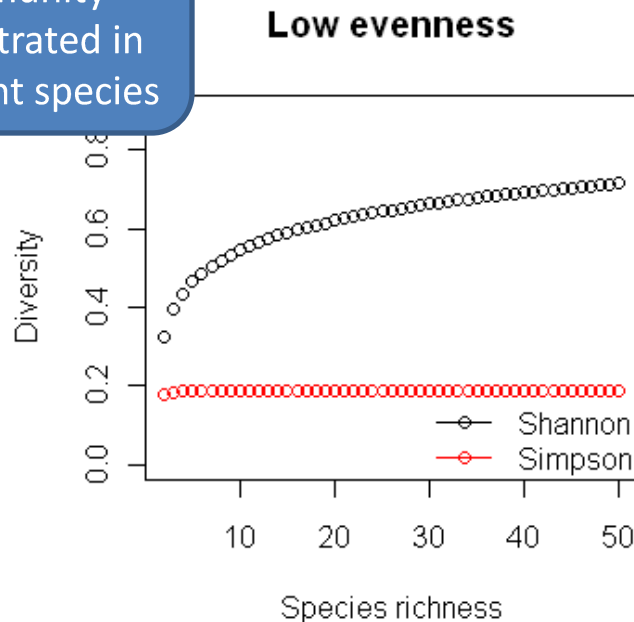


Quantifying biodiversity

Compound diversity measures

- Simpson's Index $\Delta_1 = 1 - \sum_{i=1}^S \pi_i^2$
- Shannon's Index $\Delta_2 = - \sum_{i=1}^S \pi_i \ln \pi_i$

90% of community concentrated in dominant species

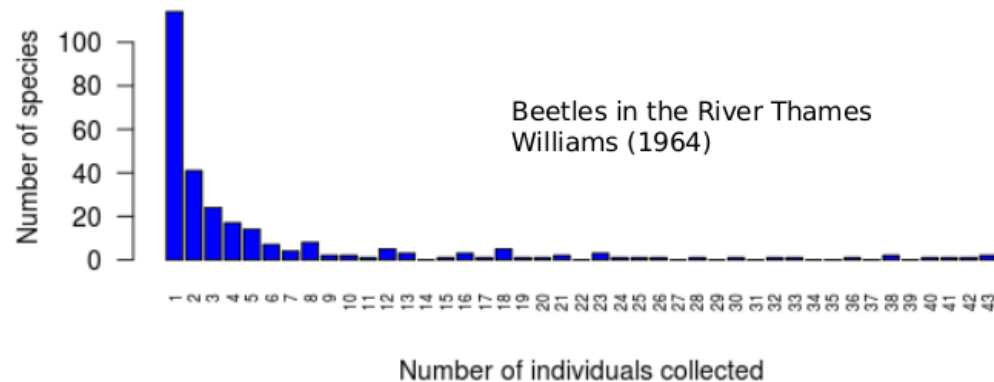


Perfectly even allocation of abundance

Measurement of diversity

- Indices: Species richness, Simpson's Index, Shannon's index
- Species abundance distribution
- Preston plots

Frequency histogram



“Frequency-of-frequencies”

Species richness estimators

Nonparametric estimators are based exclusively on sampling and do not assume any underlying model

Variables

S : total number of species in community (unknown)

X_i : number of times the i^{th} species is observed (observed frequency)

f_k : number of species represented k times

n : sample size

D : number of distinct species discovered in a sample

Jackknife Estimator

$$S_1 = D + (n-1)f_1/n$$

Jackknife techniques aim to *reduce bias*. A correction factor is derived to estimate the number of *unseen species*. In the case of the first-order jackknife, the number of unseen species is related only to the number of *singletons*.

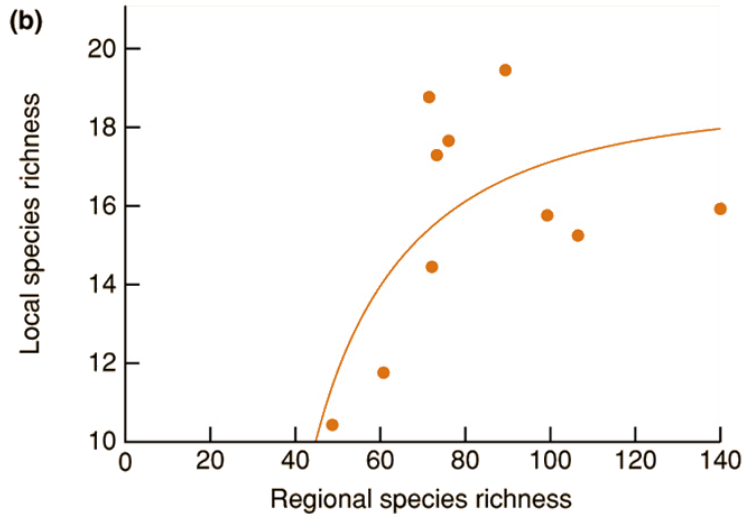
Bias-corrected Chao's Estimator

$$S_C = D + f_1(f_1 - 1) / [2(f_2 + 1)]$$

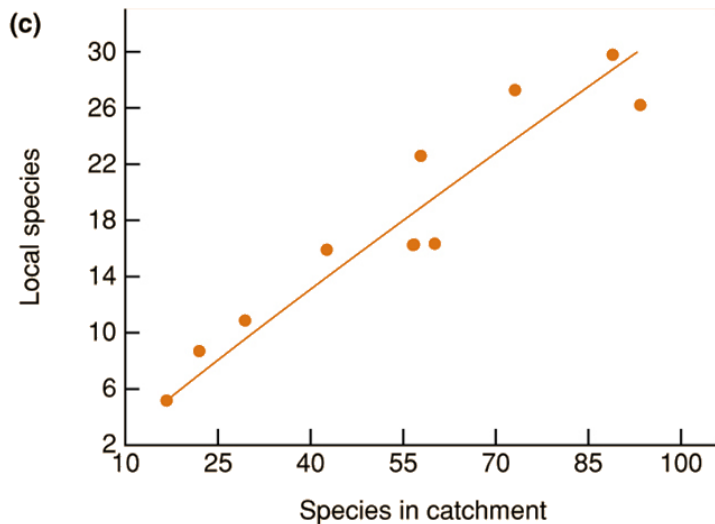
Chao derived a family of estimators based on the fact that all rare species contain information about the total number of species. This version is often used as a *lower bound* on the true number of species.

What determines biodiversity

Richness of the regional species pool



In a *saturated community* local species richness reaches an upper limit (litter-dwelling ant communities in 1 m² quadrats in forest remnants in Brazil)

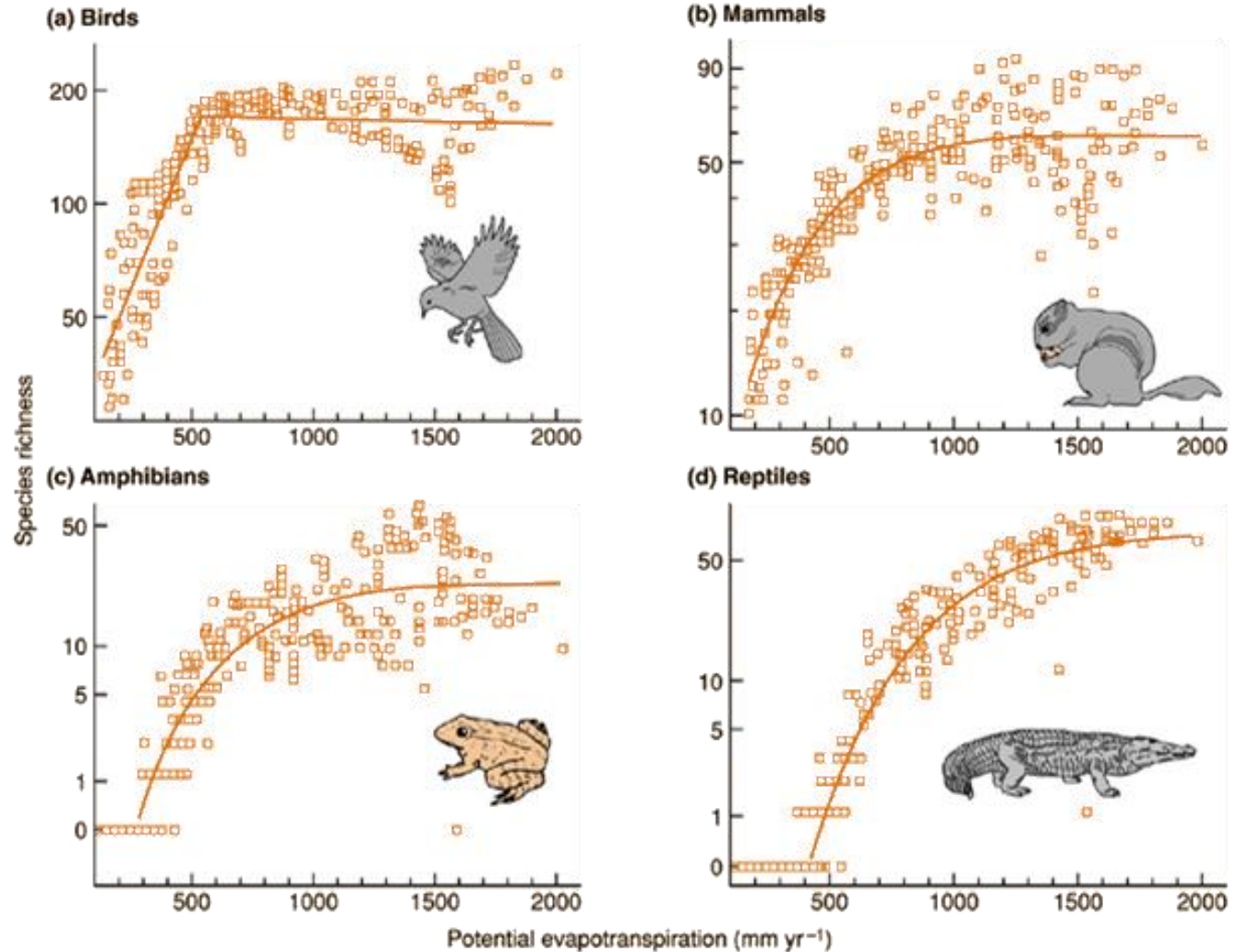


In an *unsaturated community* local species richness is proportional to regional species richness (Fish species in equal-sized pools of rivers in Côte d'Ivoire)

What determines biodiversity

Environmental variables: Energy

Potential evapotranspiration (PET) is the amount of water that evaporates or is transpired from a saturates surface (independent of water availability); PET is used as a crude, integrated measure of available energy reaching an ecosystem

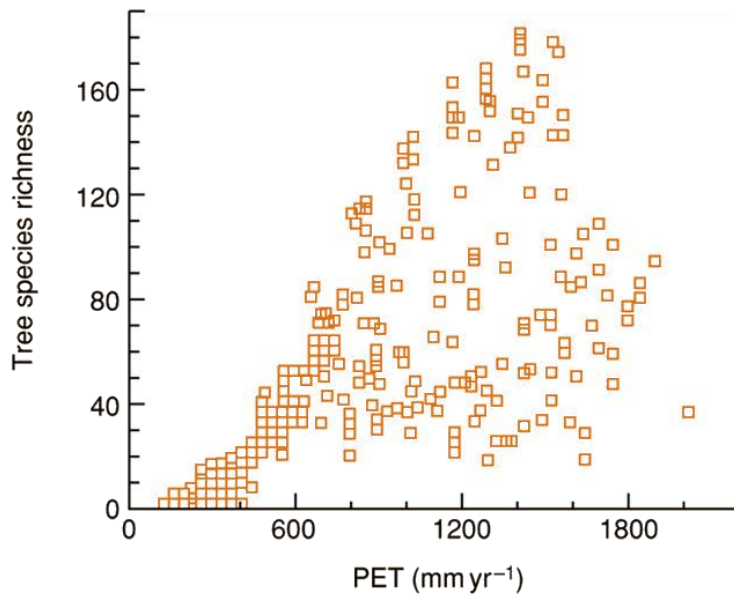


From Begon, Harper, Townsend (2005), after Currie (1991)

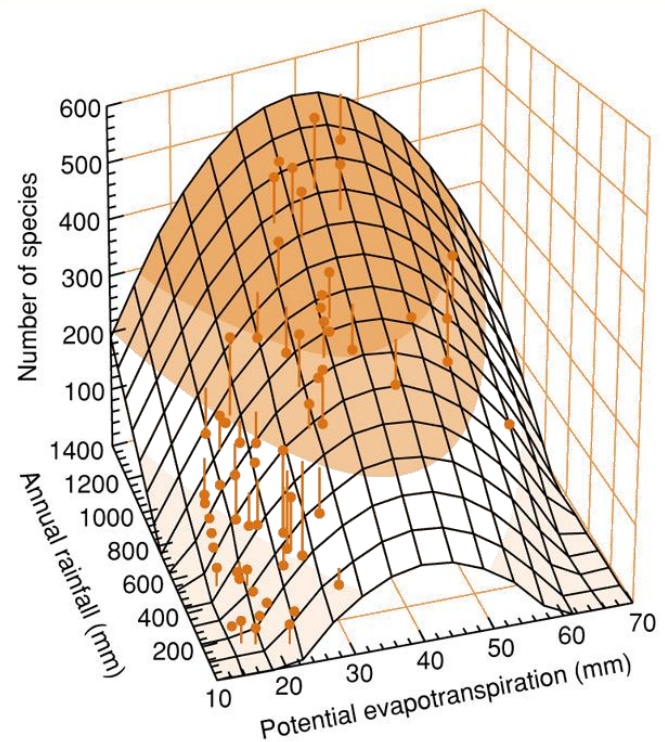
What determines biodiversity

Environmental variables: Precipitation

North American tree species north of Mexico

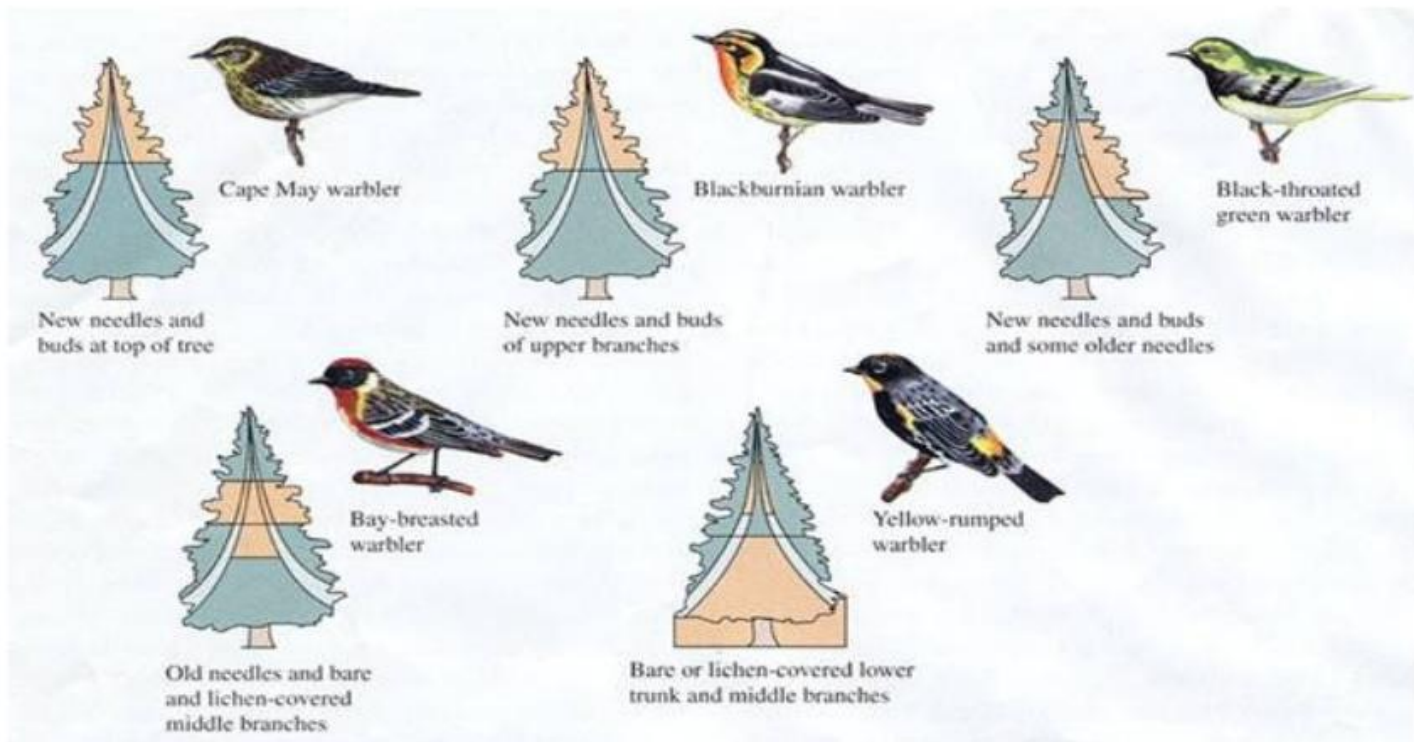


South African tree species



Habitat heterogeneity

- Niche differentiation promotes coexistence in more heterogeneous landscapes
- Subject to large-scale constraints such as overall energy inputs



Structural complexity



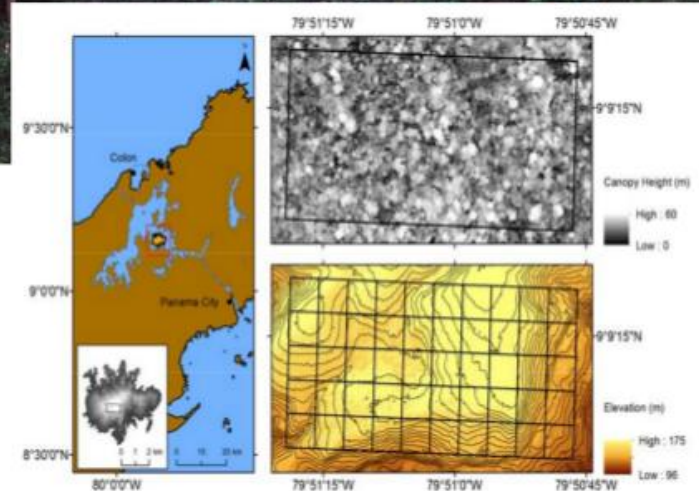
Image: [SmithsonianScience.org](https://www.smithsonian.org)

Structural complexity



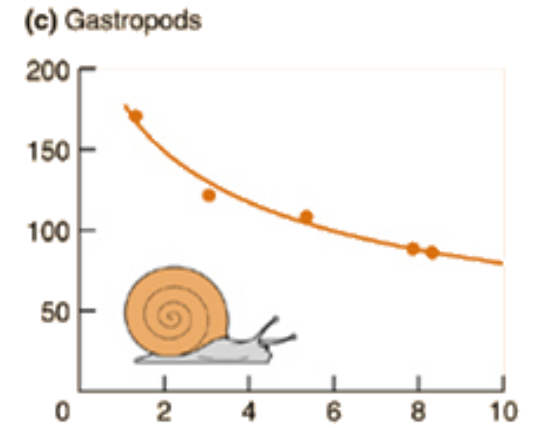
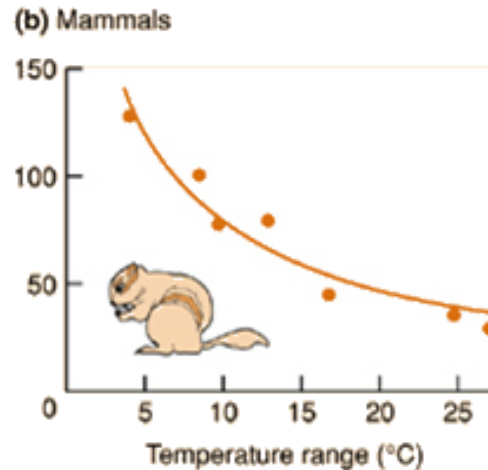
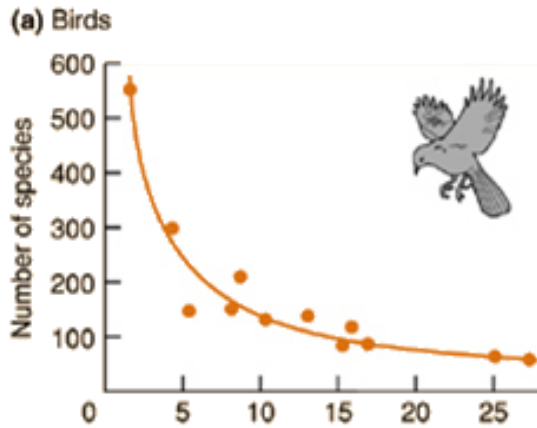
Effects of forest covariates on plant species richness

Parameter	Estimate	SE	95 % CI	
			Upper	Lower
Standard Deviation Canopy Height (SDCH)	2.87	1.10	5.03	0.70
Mean Canopy Height (MCH)	-0.97	0.38	-0.23	-1.71
Mean Elevation	-0.39	0.16	-0.07	-0.70
Mean Curvature	-31.7	10.7	-10.7	-52.6
Intercept	229.3	30.4	288.7	169.8



What determines biodiversity

Environmental variables: Temperature

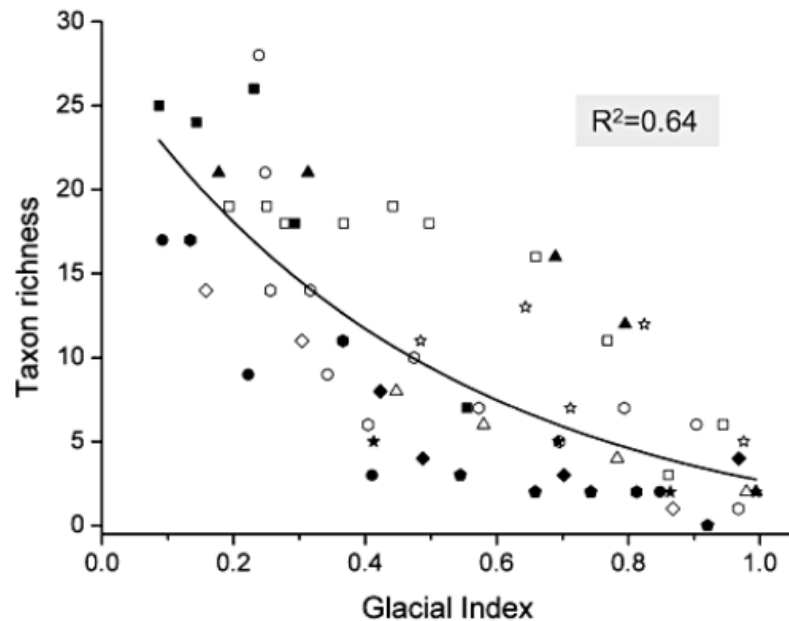


From Begon, Harper, Townsend (2005), after MacArthur (1975)

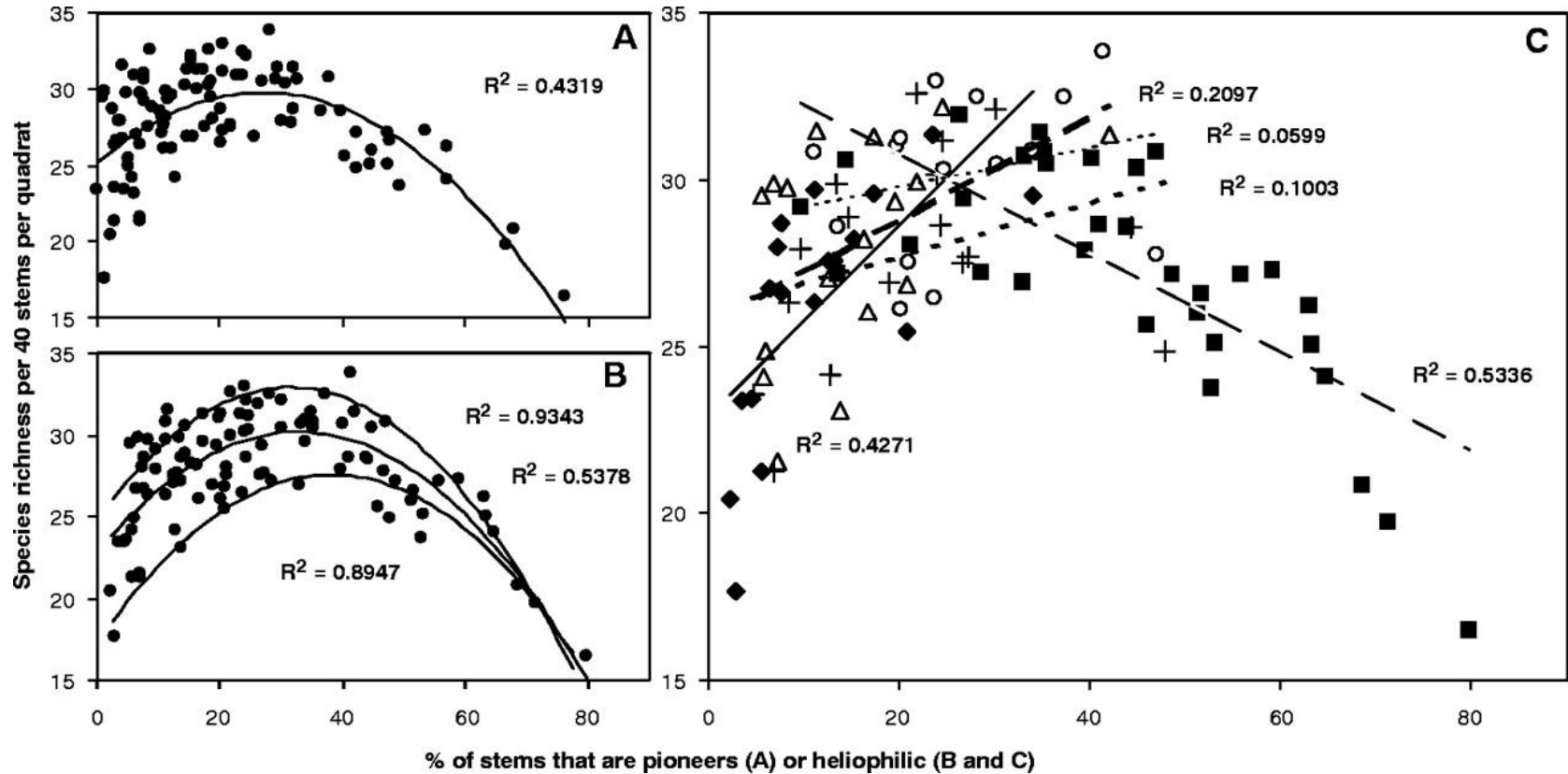
Environmental harshness

Glacial index is a measure of the proximity and size of glaciers (a kind of environmental harshness)

Stream macroinvertebrate density was found to decrease with environmental harshness



Intermediate Disturbance Hypothesis



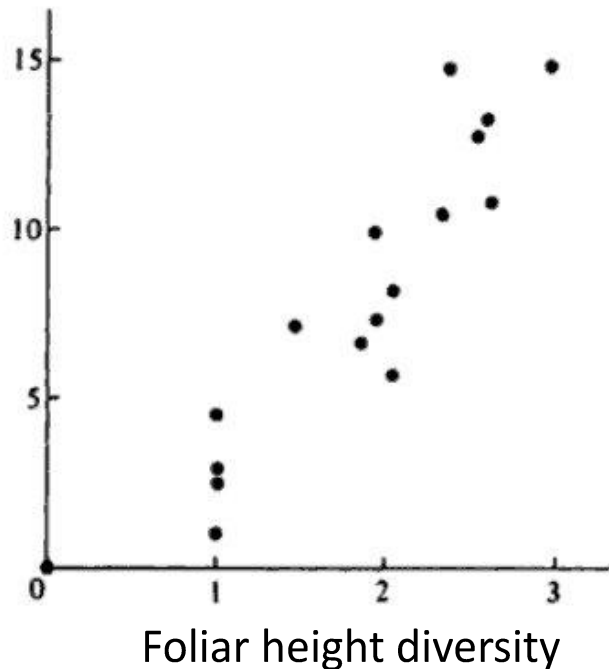
What determines biodiversity

Environmental complexity

- Habitat complexity within a landscape (Wright et al., ecosystem engineering by North American beaver)
- Structural complexity (Bird species diversity)

$$\Delta_3 = \frac{1}{\sum_{i=1}^S \pi_i^2}$$

A third diversity index
(closely related to
Simpson's index)



MacArthur (1964)

Foliar Height Diversity

π_1 = proportion of
vegetation in herbaceous
layer

π_2 = proportion of
vegetation in understory

π_3 = proportion of
vegetation in canopy

What determines biodiversity Ecological Community

Keystone species
concept

Vol. 100, No. 910

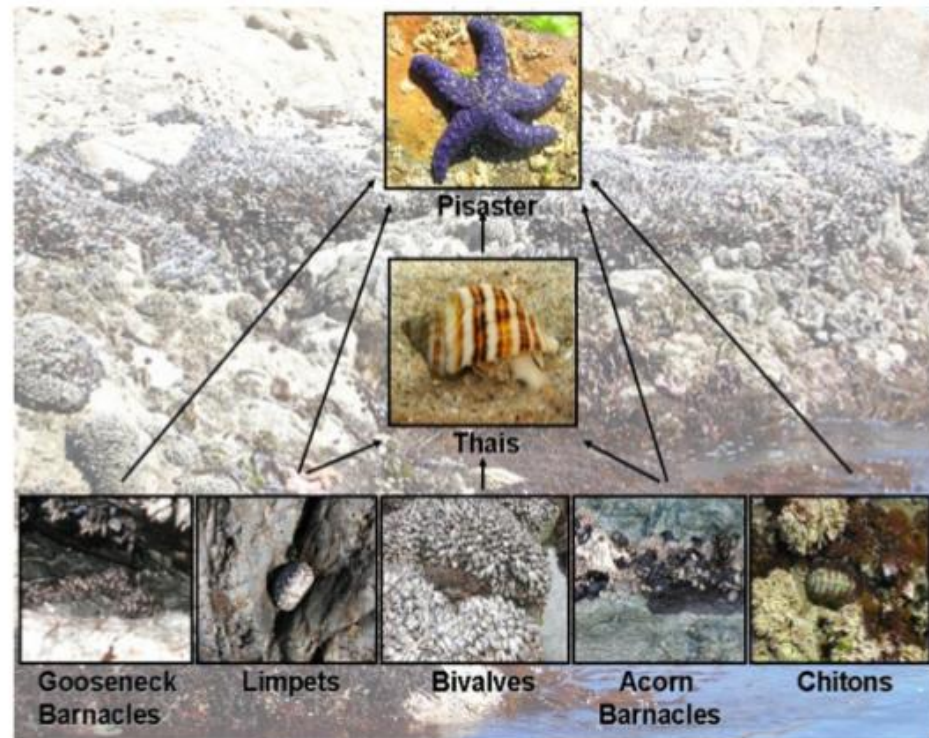
The American Naturalist

January-February, 1966

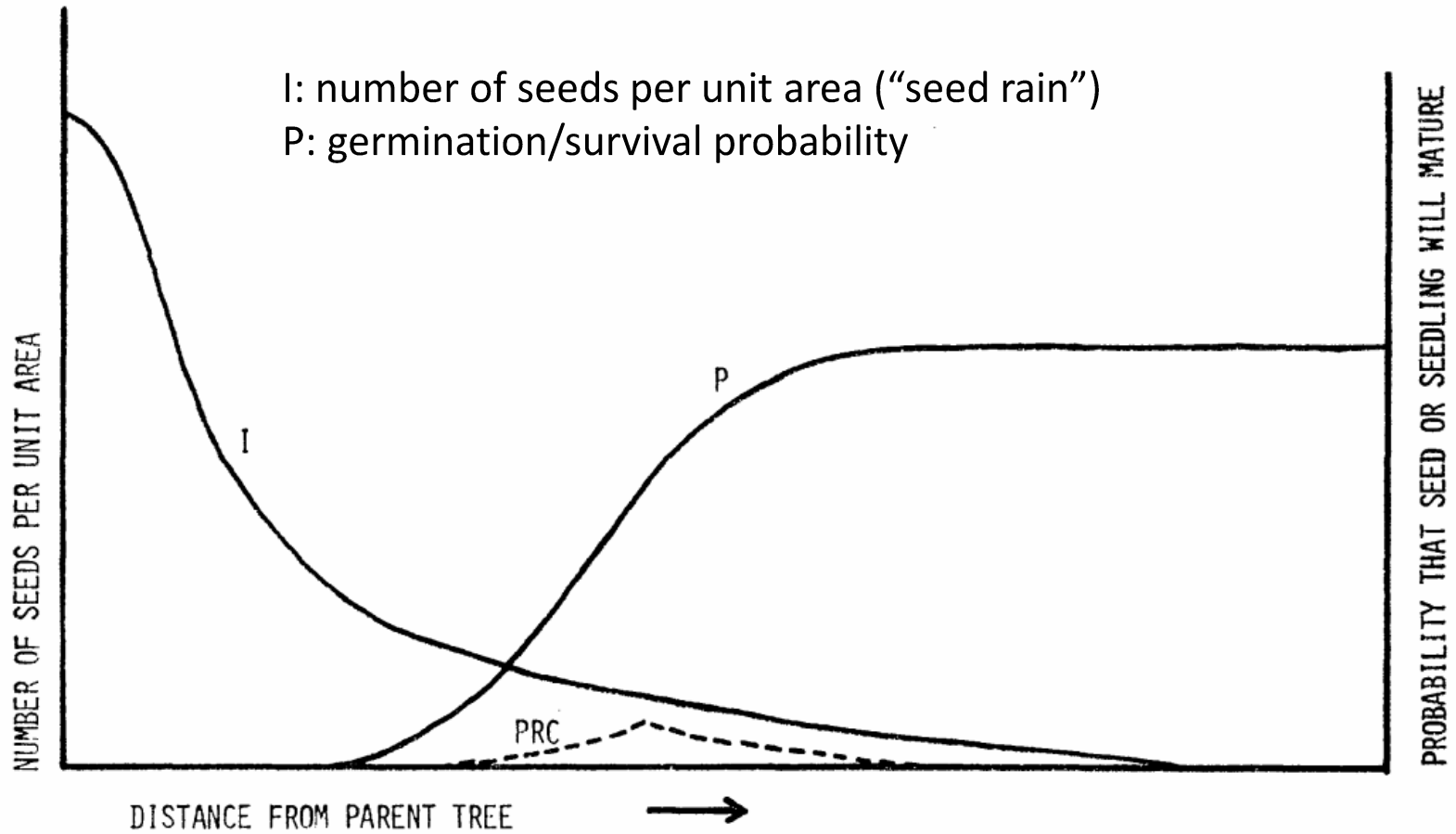
FOOD WEB COMPLEXITY AND SPECIES DIVERSITY

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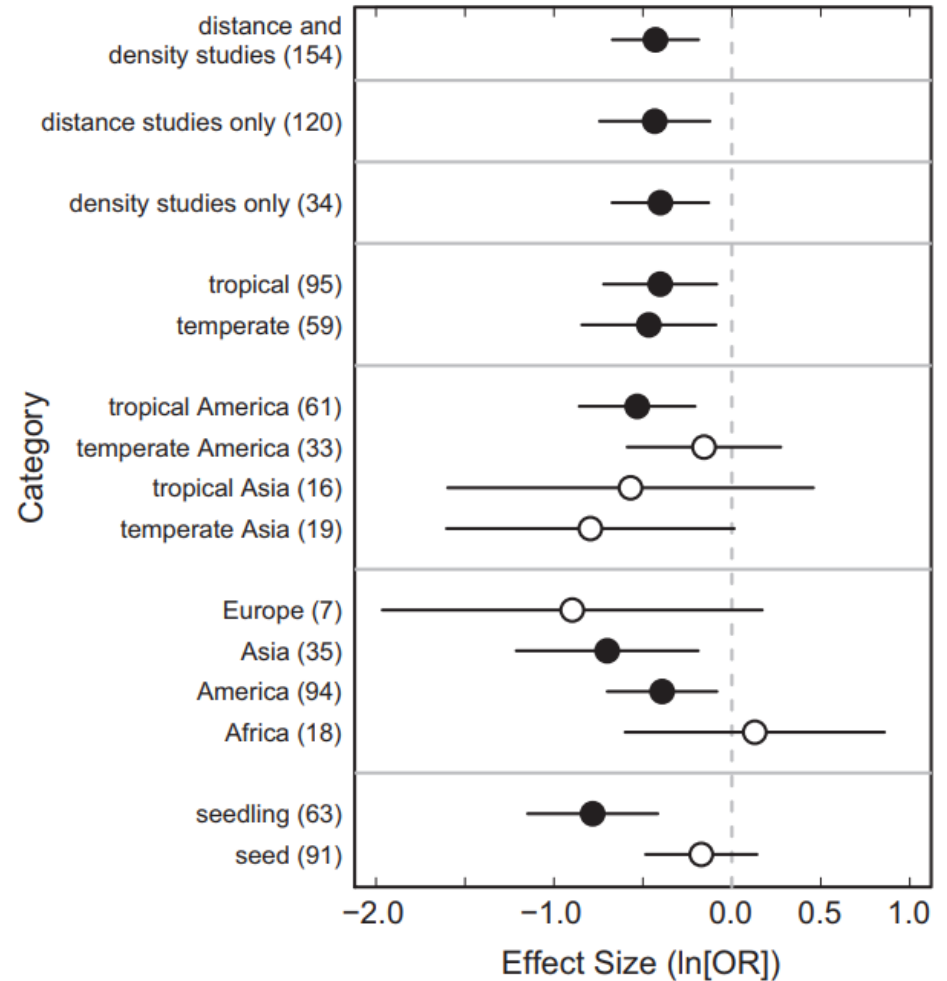
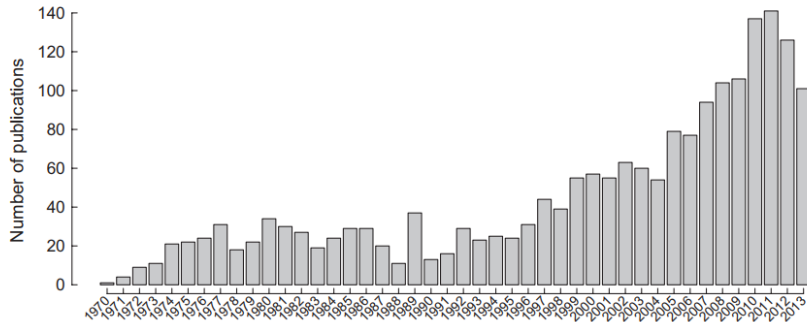


Janzen-Connell Effect



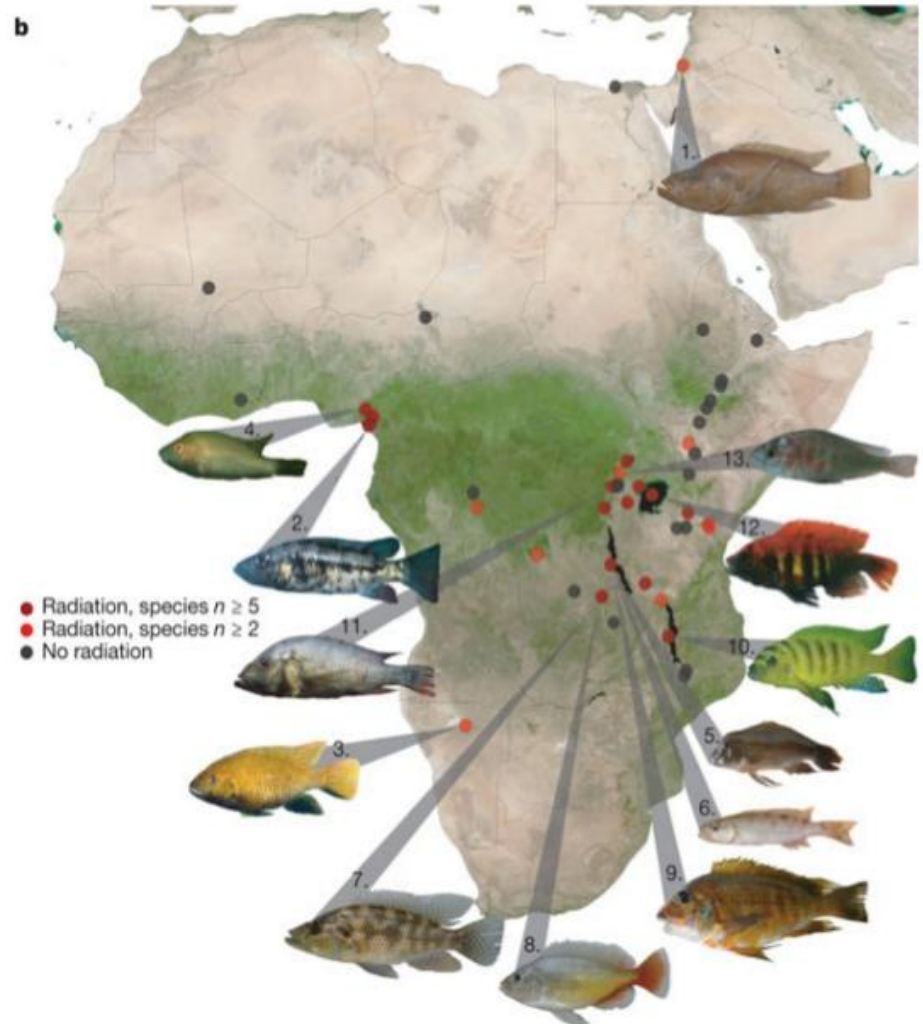
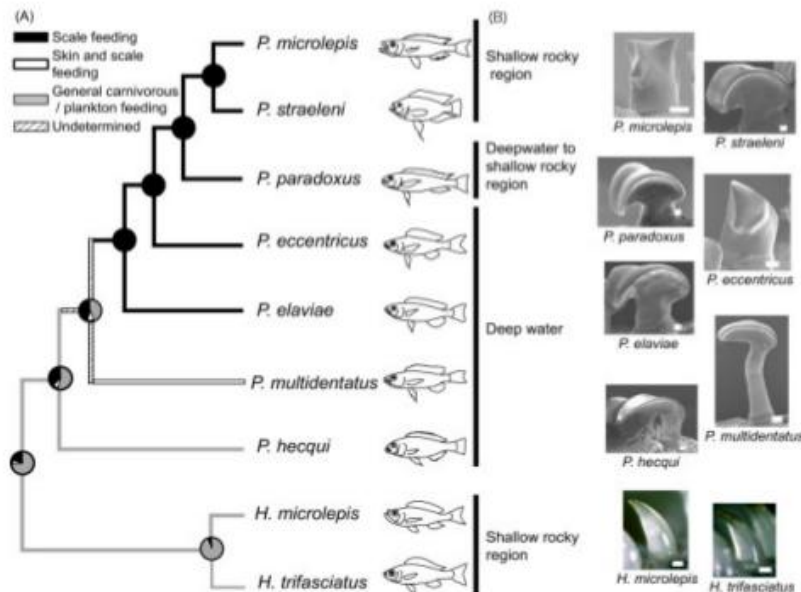
Meta-analysis

Number of papers citing Janzen (1970) or Connell (1971)



Diversification, colonization and ecological specialization

Evolution of feeding specialization in Tanganyikan scale-eating cichlids



Summary

- Diversity may be local (α) or non-local (β and γ)
- Diversity includes components of richness and evenness
- Maintenance of diversity may be physical (structural complexity, energy inputs, environmental variability, intermediate disturbance) or biological (Janzen-Connell effects, Keystone species)