Community assembly metrics

What characteristics of species would be useful to know to:

(i)   describe a community

(ii) to make comparisons among communities?

Species abundance patterns

Single most important index characterizing a community is the number of species present S_T or *species richness*.

Species diversity includes a measure of both species number and 'equitability' (or 'evenness') - a measure of how equally abundant those species are in a community.
e.g., Simpson Index, Fisher's alpha.

Exploring patterns of richness

Whittaker (1970) named the spatial measures of richness alpha, beta, gamma

Alpha diversity: is the number of species in a locality or habitat (not to be confused with the *Fisher's alpha* which is a diversity index…)

Beta diversity: *turnover* of species between habitats or localities. Several different methods of calculation. Can be (1/mean number of habitats or localities occupied by a species)

Gamma diversity: estimated number of species present within a large area (region) - not much used...

An example might help…

Cox and Ricklefs (1977) Bird species diversity on Trinidad and St Kitts (Lesser Antilles) examined in 9 habitat types

Trinidadian Gamma = 108 spp = alpha 28.2 x average beta 0.43 habitats x 9 habitats

Kittitian Gamma = 20 spp = alpha 11.9 x average beta 0.19 x 9 habitats

Spatial scale is also important in describing S

Larger areas contain more species. The relationship between species number and area *usually* fits the equation:
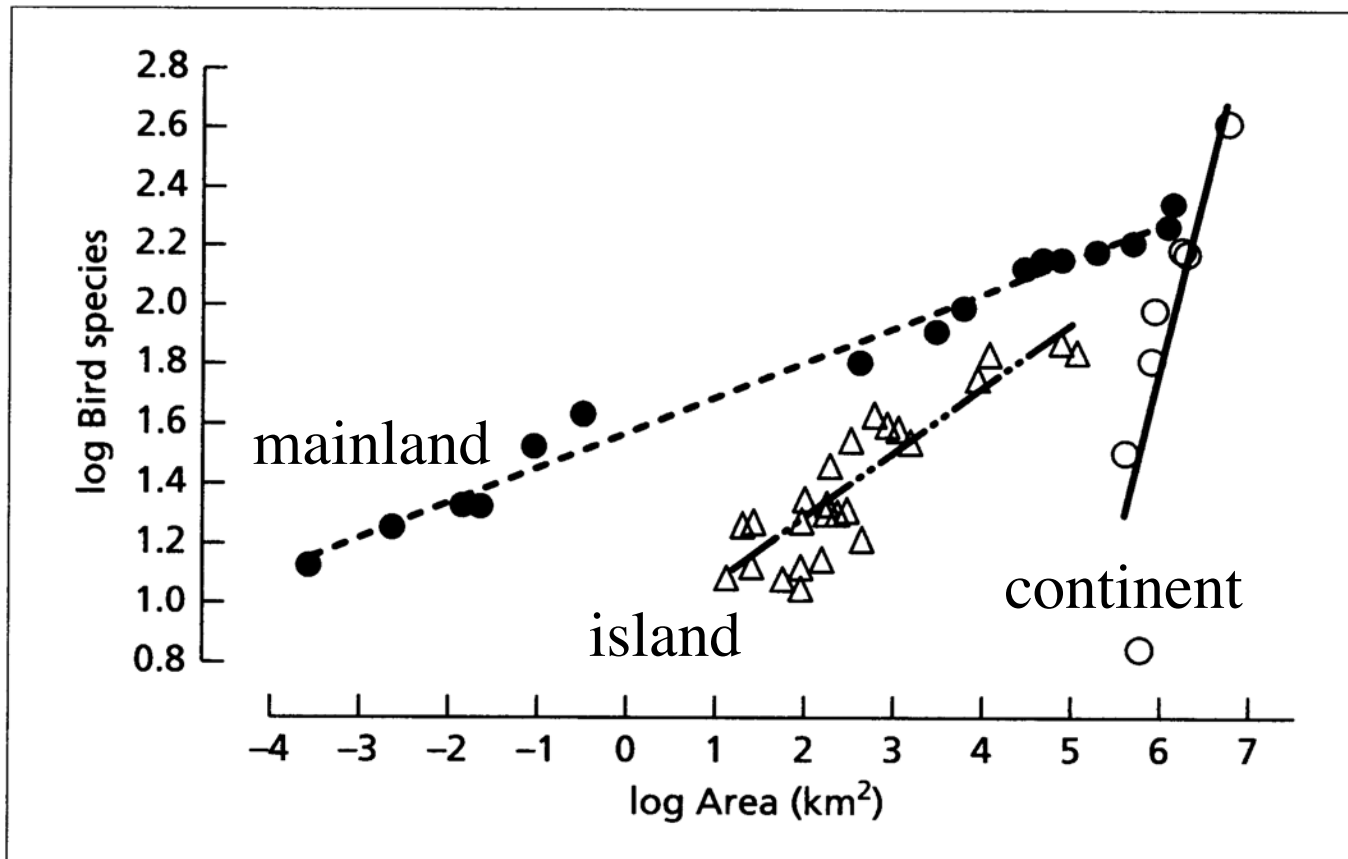
$S = cA^z$ where S = species, A = area

Log transformed:
$\log S = \log c + z \log A$ (z is the **slope** describing how log richness increases with log area)

Observations suggest that z is about 0.25 for many ecosystems, (higher at continental scales) (Rosenweig 1995)

Islands typically have higher z values compared to mainland areas.

Fig. D7 Three scales of species–area curve for birds. The shallow curve (filled circles) comes from increasingly larger areas within the Mediterranean scrub of Chile; $z = 0.12$. (Data from Cody 1975.) The intermediate curve (open triangles) comes from Caribbean islands; $z = 0.22$. (Data from Wright 1981.) The steep curve (open circles) comes from the tropical rain forests of separate biogeographical provinces ranging in size from the Australian to the Neotropical; $z = 1.23$. It includes only the frugivorous species. (Data from Fleming *et al.* (1987) and Rosenzweig (1995) which see for complete citations.)

z values represent how area influences species richness…

Compositional Beta Diversity (CBD) indicates turnover of species
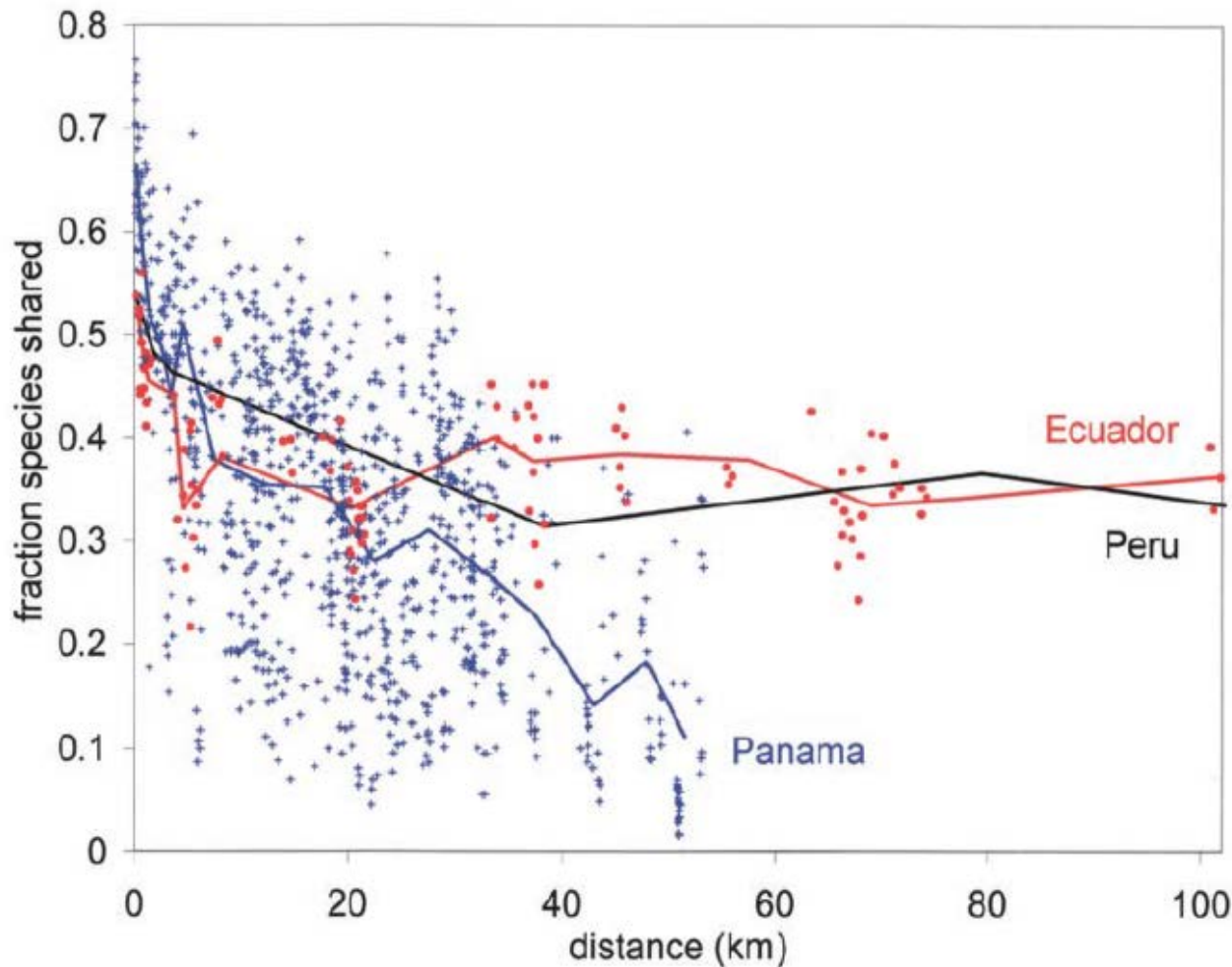
Turnover can also be measured as similarity in species composition or fraction of species in common

Quantifying local species richness

Accurate estimation of species richness is important (e.g., conservation strategies, habitat loss)

- But richness can usually only be *estimated*, many pitfalls (see Gotelli and Colwell (2001))

- Two common approaches: *individual-based estimation* and *sample-based estimation*. Add samples or individuals until an asymptote is reached (all species already encountered)

How many tree species are there in the forest??

Individual-based assessment: choose trees *at random* from the forest, record species sequentially for tree after tree (the best way)

Sample-based assessment: establish plots, record the number and identity of all the trees within each, and accumulate the total number of species as additional plots are added (the easy way)

Difference in unit of replication individual vs. sample of individuals can have important effects on richness estimates

e.g. rectangular plots have up to 25 % more species in them than square plots of the same area (Condit et al. 1996).
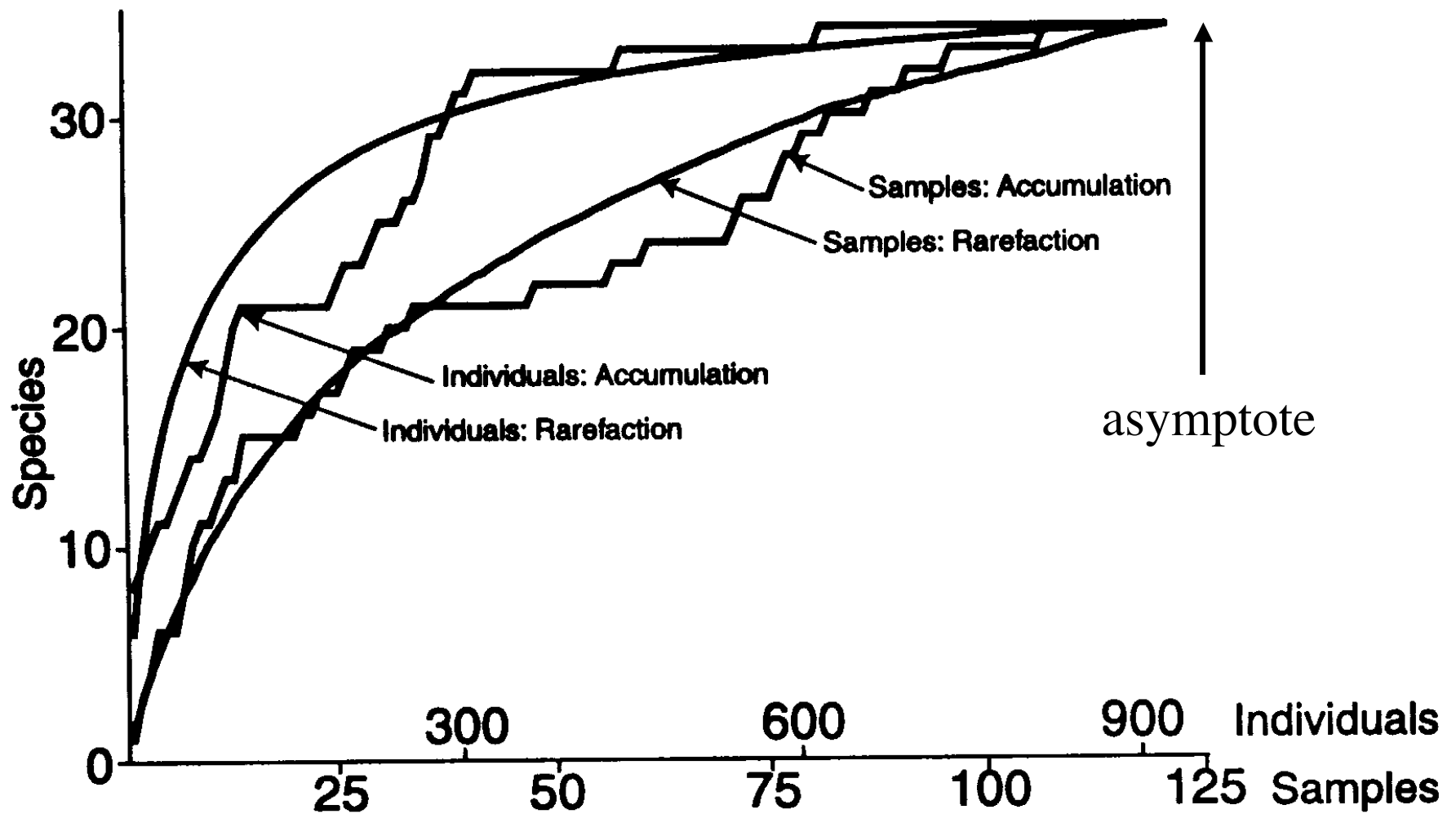
Why do species accumulate more slowly in the sample accumulation curve?

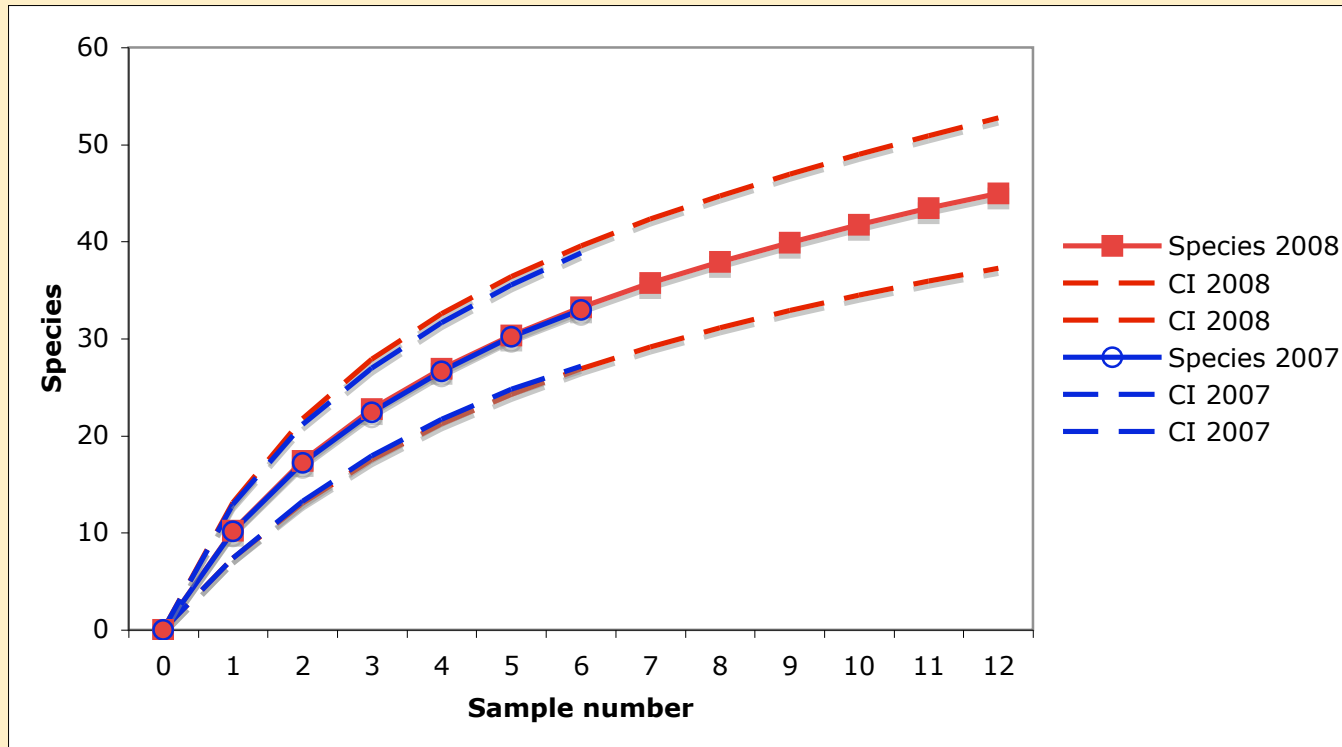# State Botanist John Taft working in Paxton Prairie, IL.

How many plant spp are there out here (*S*)??

Total spp richness is often difficult to measure
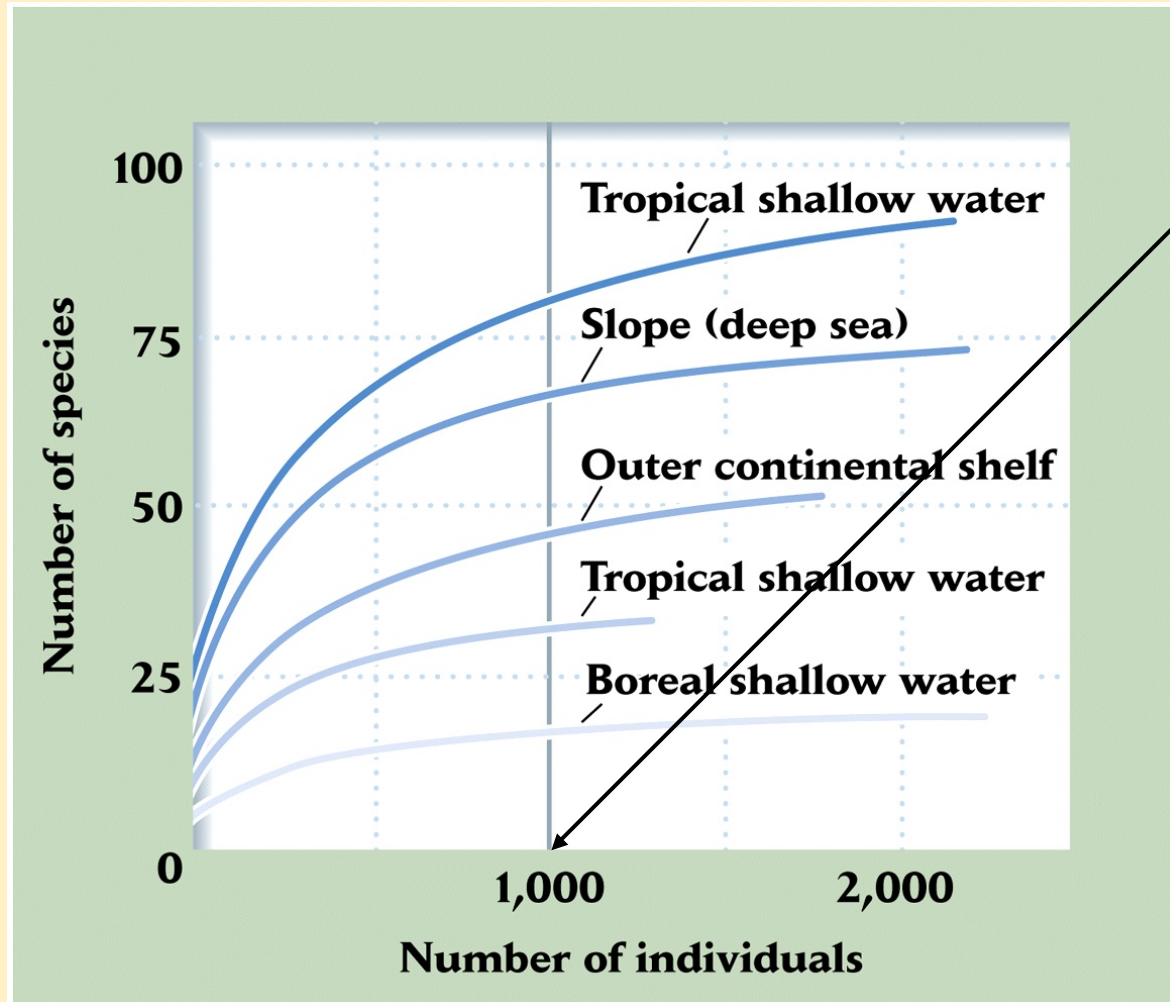
Species accumulation curve: Paxton prairie

Estimated (class data)
2007: 60 spp
2008: 67 spp

Observed (John Taft - professional botanist)
145 spp

How would you measure S_T?
How would you compare S among communities?

Rarefaction provides alternative means of comparing richness among communities

Compare species richness at a fixed number of individuals sampled

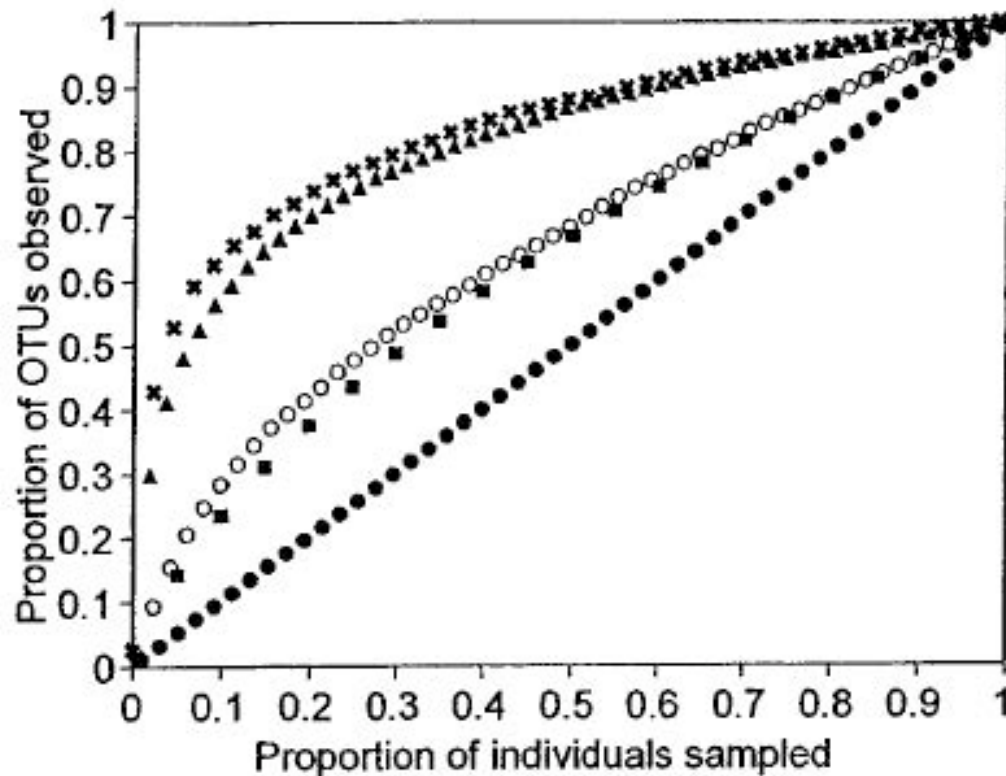*Why all the fuss on how species richness is estimated??*

FIG. 1. Accumulation curves for Michigan plants (✗; $n = 1,783$) (26), Costa Rican birds (▲; $n = 5,007$) (J. B. Hughes, unpublished data), human oral bacteria (○; $n = 264$) (33), Costa Rican moths (■; $n = 4,538$) (56), and East Amazonian soil bacteria (●; $n = 98$) (6). Curves are averaged over 100 simulations using the computer program EstimateS and are standardized for the number of individuals and species observed.

Diverse lineages (eg insects, microbes) *cannot be sampled sufficiently to reach the asymptote*

Microbes: species are often defined based on sequence information = "operational taxonomic units" OTUs

Exploring patterns of diversity

Fisher (1943) noticed that no community existed in which all species were equally common. *Instead only a few species tend to be abundant while most are represented by only a few individuals*

Differences in species abundance can be incorporated into species diversity measurements (e.g., Simpson, Fisher's alpha diversity), or they can be plotted in species relative abundance curves or species abundance distributions (SAD).

Simpson Index of species diversity

$$D = \frac{1}{\Sigma p_i^{\,2}}$$

Where p_i is the proportion of all individuals belonging to the ith species

D will be greatest if all species have the same relative abundance (p_i)

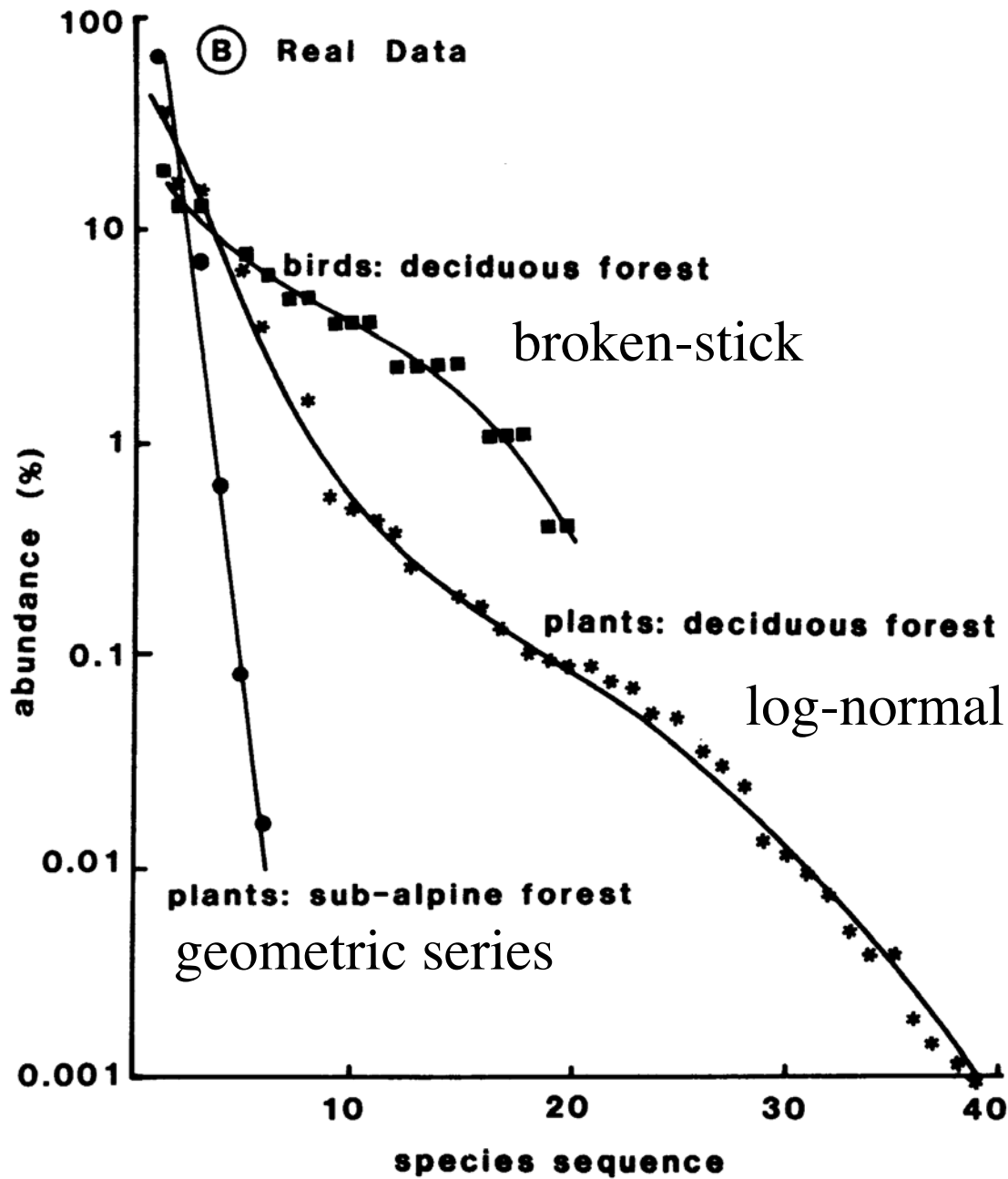| Proportion of sample represented by species					
A	B	C	D	E	D
0.20	0.20	0.20	0.20	0.20	5.00
0.25	0.25	0.25	0.25	0.00	4.00
0.24	0.24	0.24	0.24	0.04	4.30
0.25	0.25	0.25	0.25	0.001	4.02
0.50	0.30	0.10	0.07	0.03	2.81

Rank-abundance plots
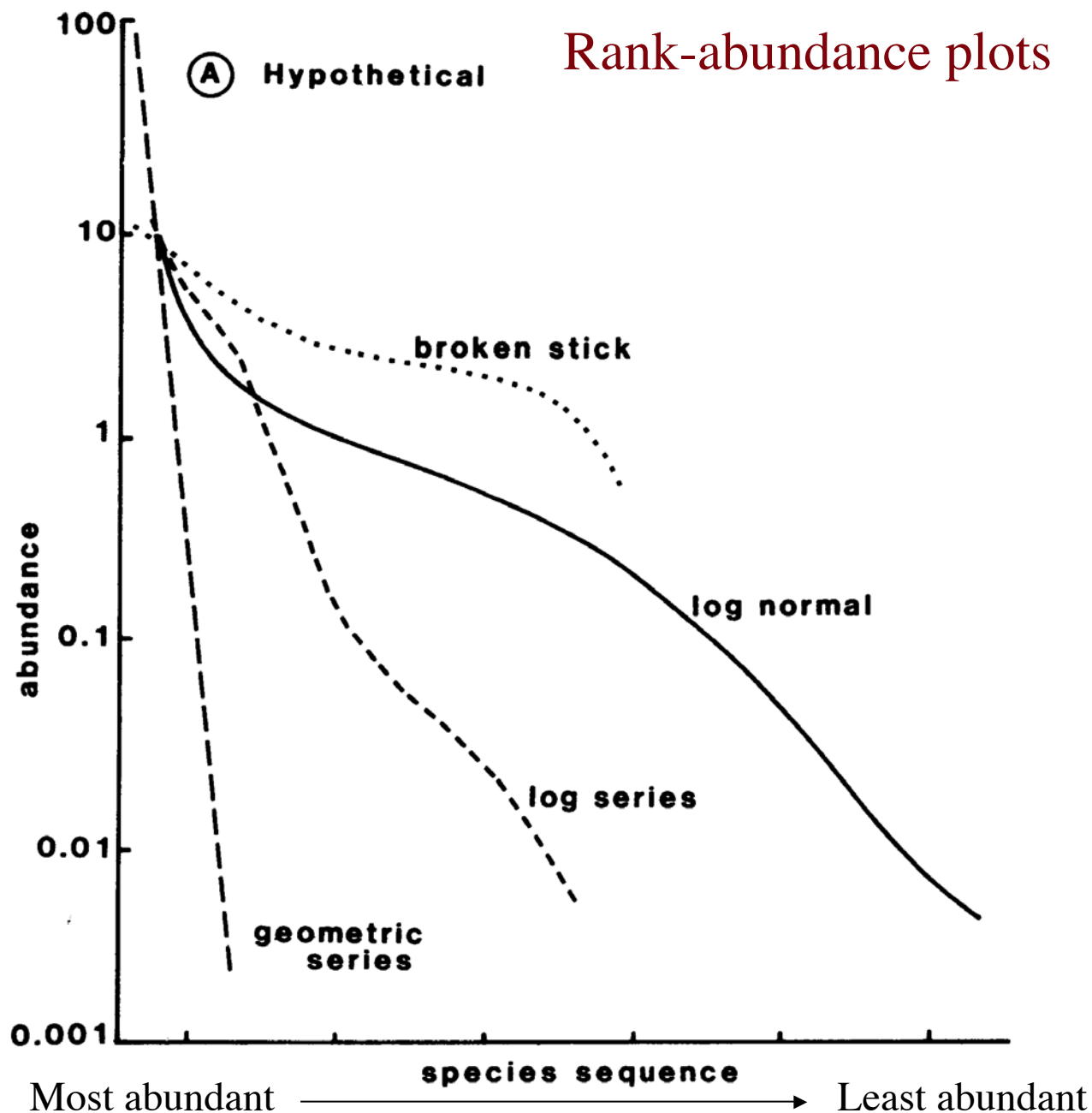
Rank abundance plots of four spp-abundance models

x axis = *rank* order of abundance (most abundant…least abundant)

y axis = log species abundance

Examples of abundance data that fit the four models

Geometric series:

This pattern of species abundance is found primarily in species-poor (harsh) environments or ??

The ratio of abundance of each species to the abundance next highest ranked is constant. Therefore rank abundance plot is linear

Indicates that species abundance is proportional to resource use?

The first species pre-empts proportion k of the limiting resource, second species proportion k of remaining resources, third species k of what's left and so on...

Rank-abundance plots
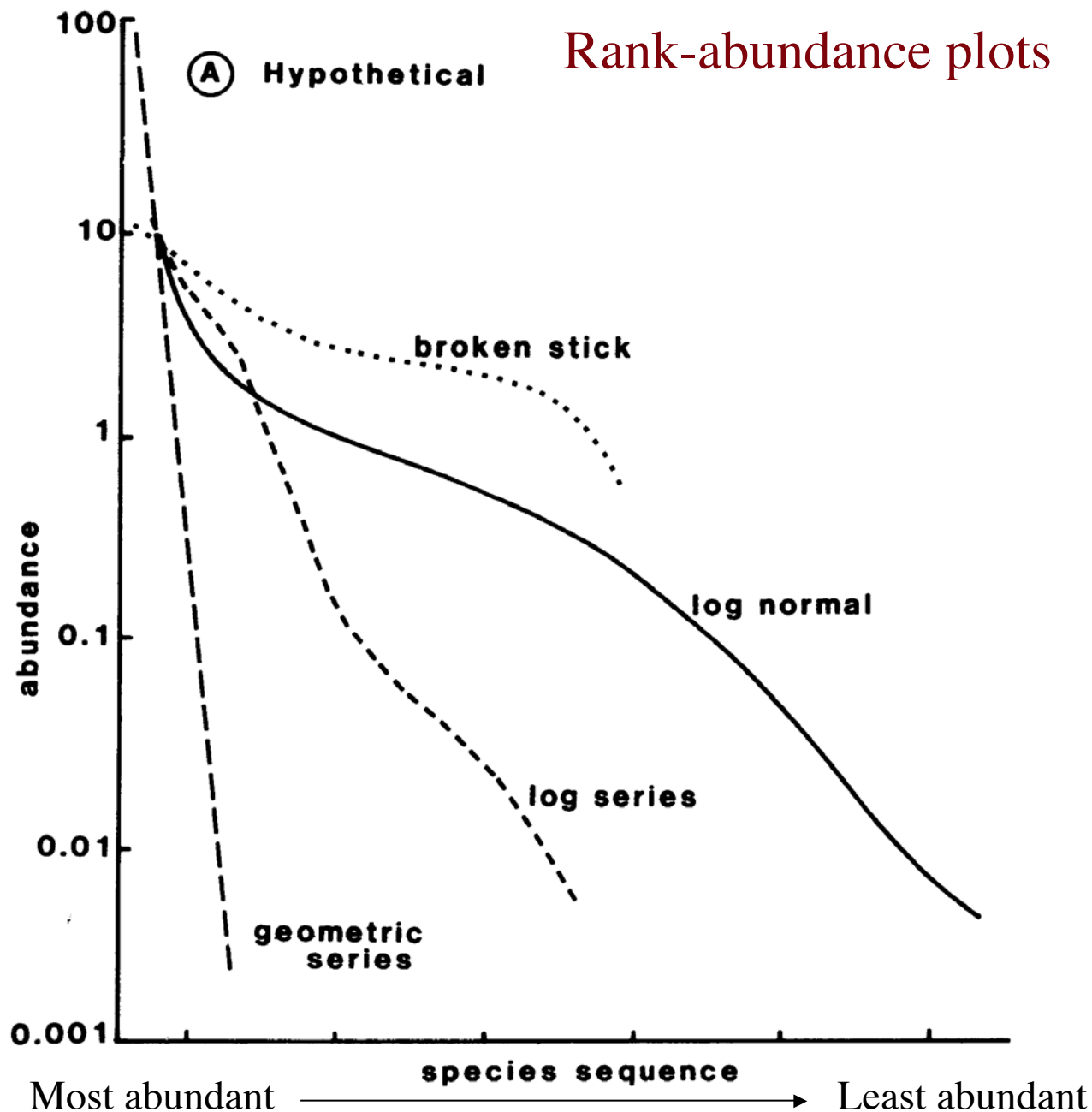
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Log series: (aka Fisher's alpha)

First described mathematically by Fisher et al. (1943)

Log series takes the form: αx, $\alpha x^2/2$, $\alpha x^3/3$,... $\alpha x^n/n$

Where αx is the number of species predicted to have one individual, αx^2 to have two individuals etc...

Estimate x from the iterative solution of:
$S/N = (1-x)/x(-\ln(1-x))$ where S=number of spp, N = total individuals

Once you know x, calculate α the diversity index
$\alpha = N(1-x)/x$
(*nice examples of calculations of this and other indices in Magurran* (1988))

Fisher's Alpha (α) widely used as a diversity index to compare among communities varying in number of individuals (N), because *theoretically independent of sample size*

Widely used in the literature because you can calculate the index knowing only species richness (S) and total number of individuals (N).

Fitting the logseries will always result in the *singleton category* having the most species
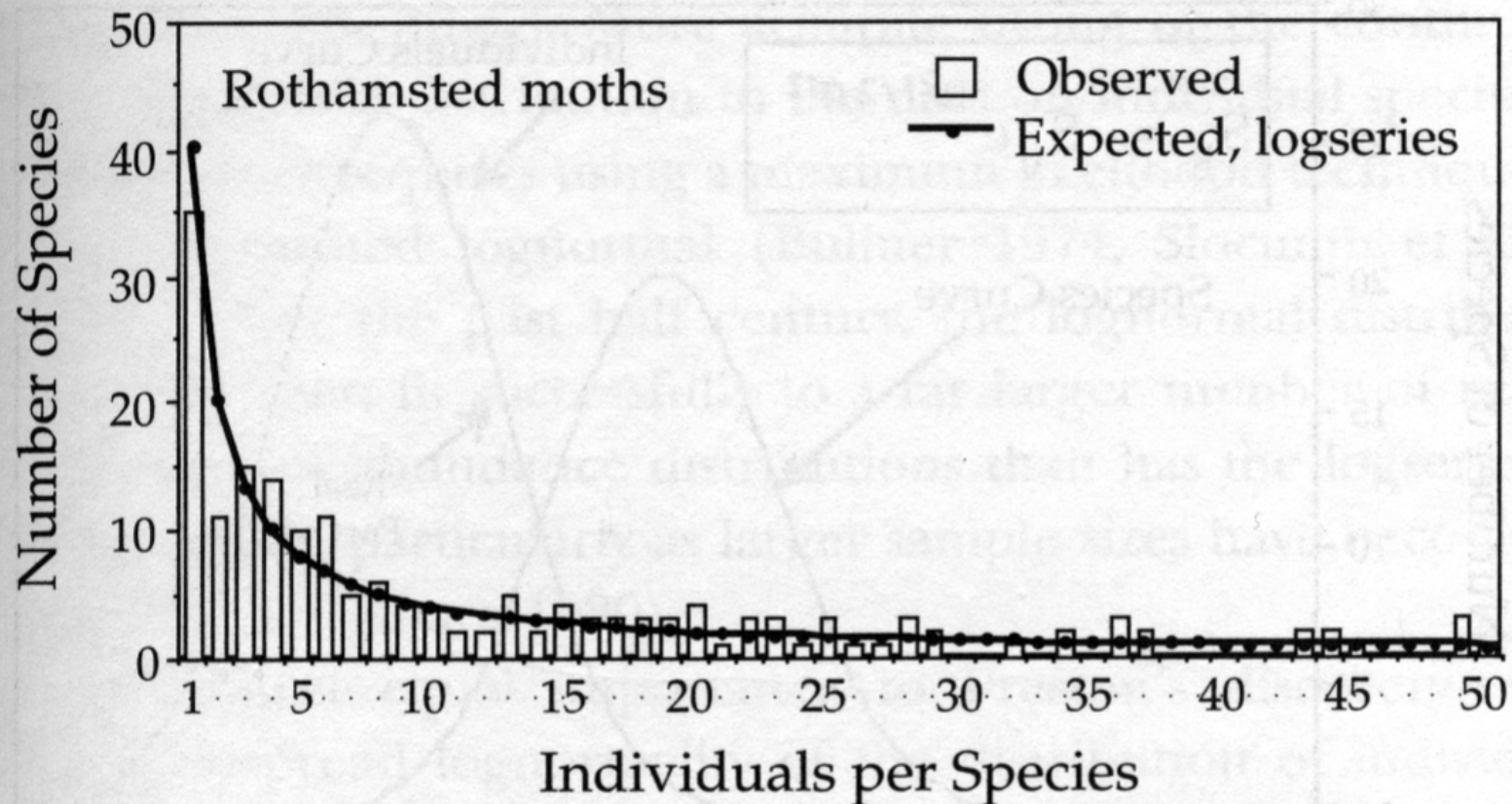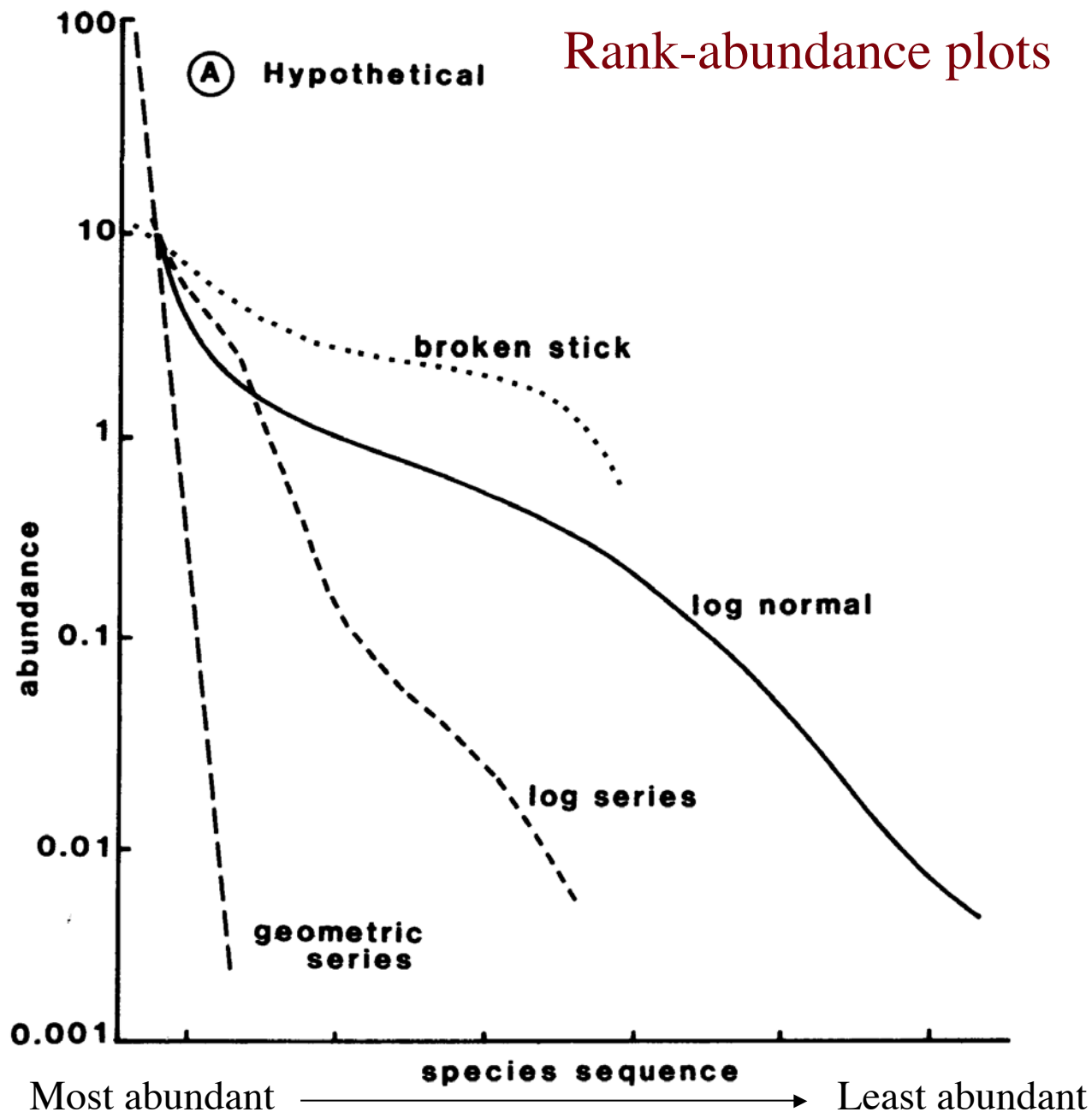
THEORIES OF RELATIVE SPECIES ABUNDANCE

FIG. 2.1. An example of the use of the logseries distribution to fit data on species abundance in collections of months at light trap over a 4-year period at Rothamsted Field Station, U.K. The logseries always predicts that the abundance class of singleton species will be the largest class.

Rank-abundance plots

Rank abundance plots of four spp-abundance models

x axis = *rank* order of abundance (most abundant…least abundant)

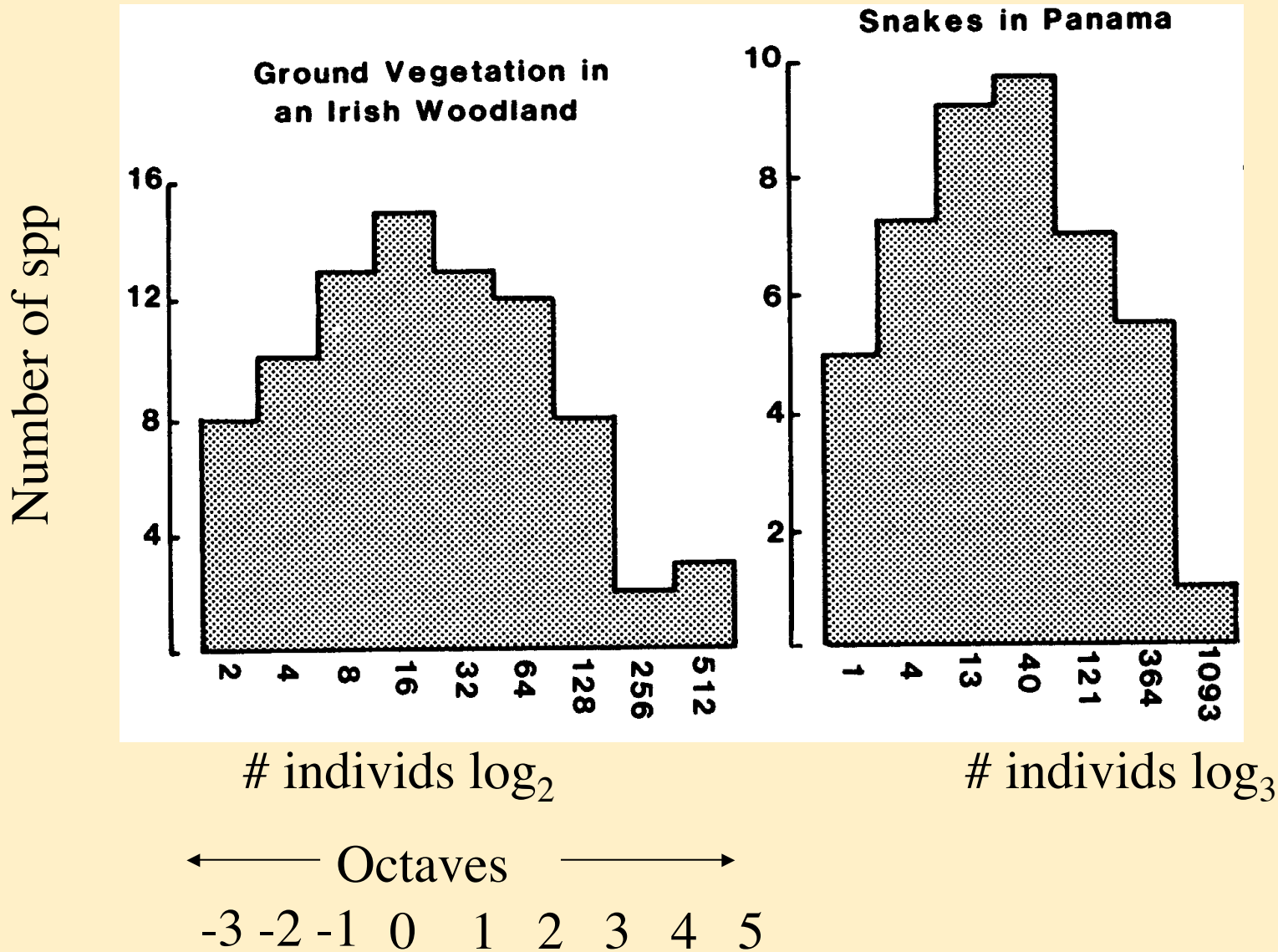y axis = log species abundance

Log-normal distribution:

Most taxa don't fit the log series if they are sampled intensively enough.

But… abundance distributions also not normal. Relative abundance could be normalized by log transformation.

Depicted abundance patterns by categorizing species in abundance classes in log base 2 (called these abundance classes 'octaves')

Log-normal fits many more species relative abundance distributions than does Fisher's log series distribution.

Species abundance distributions (SAD)

Number of spp

Ground Vegetation in an Irish Woodland

16
12
8
4

2 4 8 16 32 64 128 256 512

individs $\log_2$

Snakes in Panama

10
8
6
4
2

1 4 13 40 121 364 1093

individs $\log_3$

← Octaves →

-3 -2 -1 0 1 2 3 4 5

Back to the Rothamstead moths: Preston showed that fits to log series represented inadequate sampling.
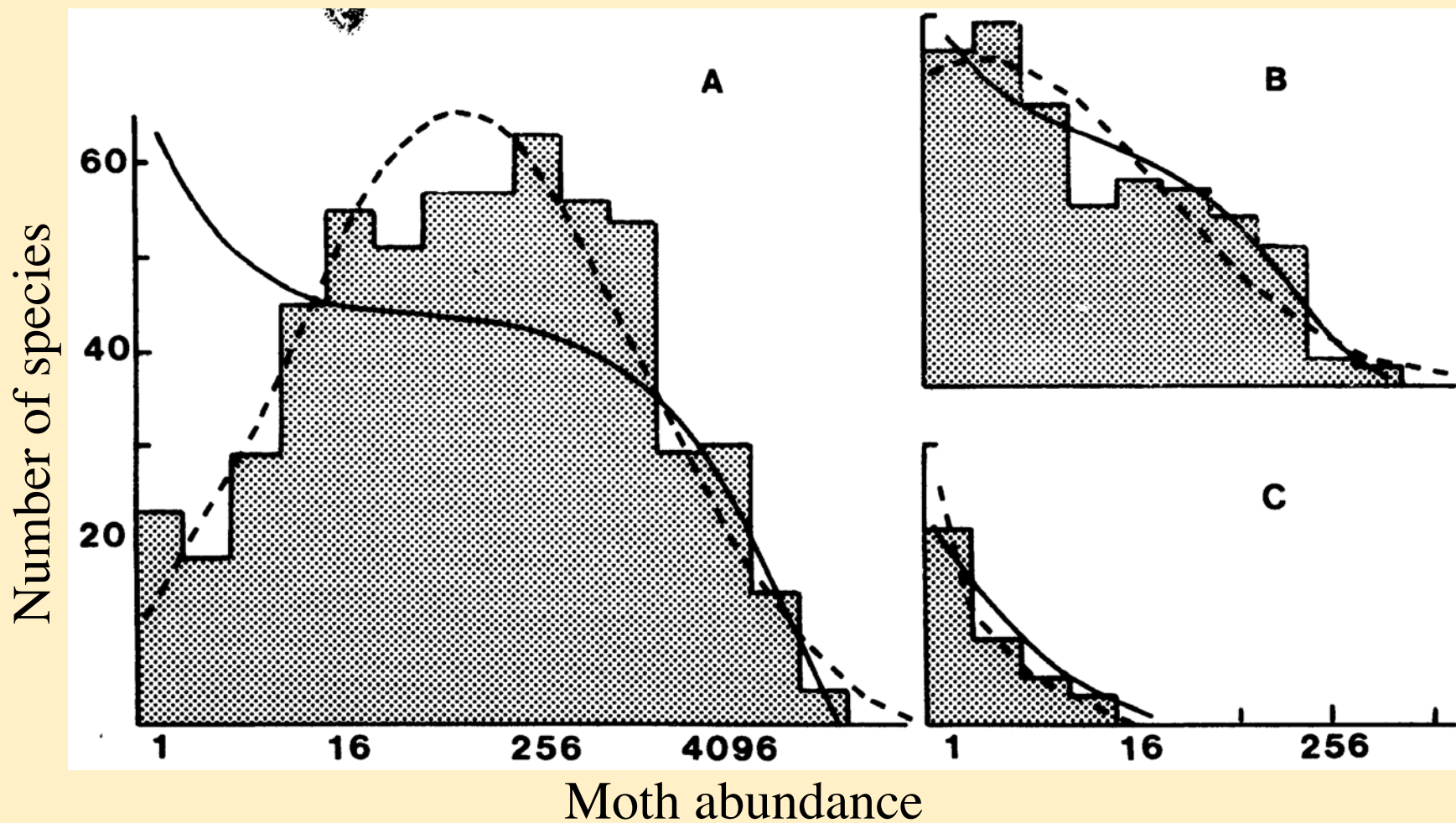
Why do species abundances follow a log-normal distribution?

So ubiquitous that reflect an underlying general mechanism??

No clear answer. May (1975) and others argued that results as consequence of the *Central Limit Theorem* (product of interacting effects of many random processes (*e.g.*, competition, predation, *etc.*)

J. H. Brown (1995, *Macroecology*, pg. 79):
"…just as normal distributions are produced by additive combinations of random variables, lognormal distributions are produced by multiplicative combinations of random variables (May 1975)"
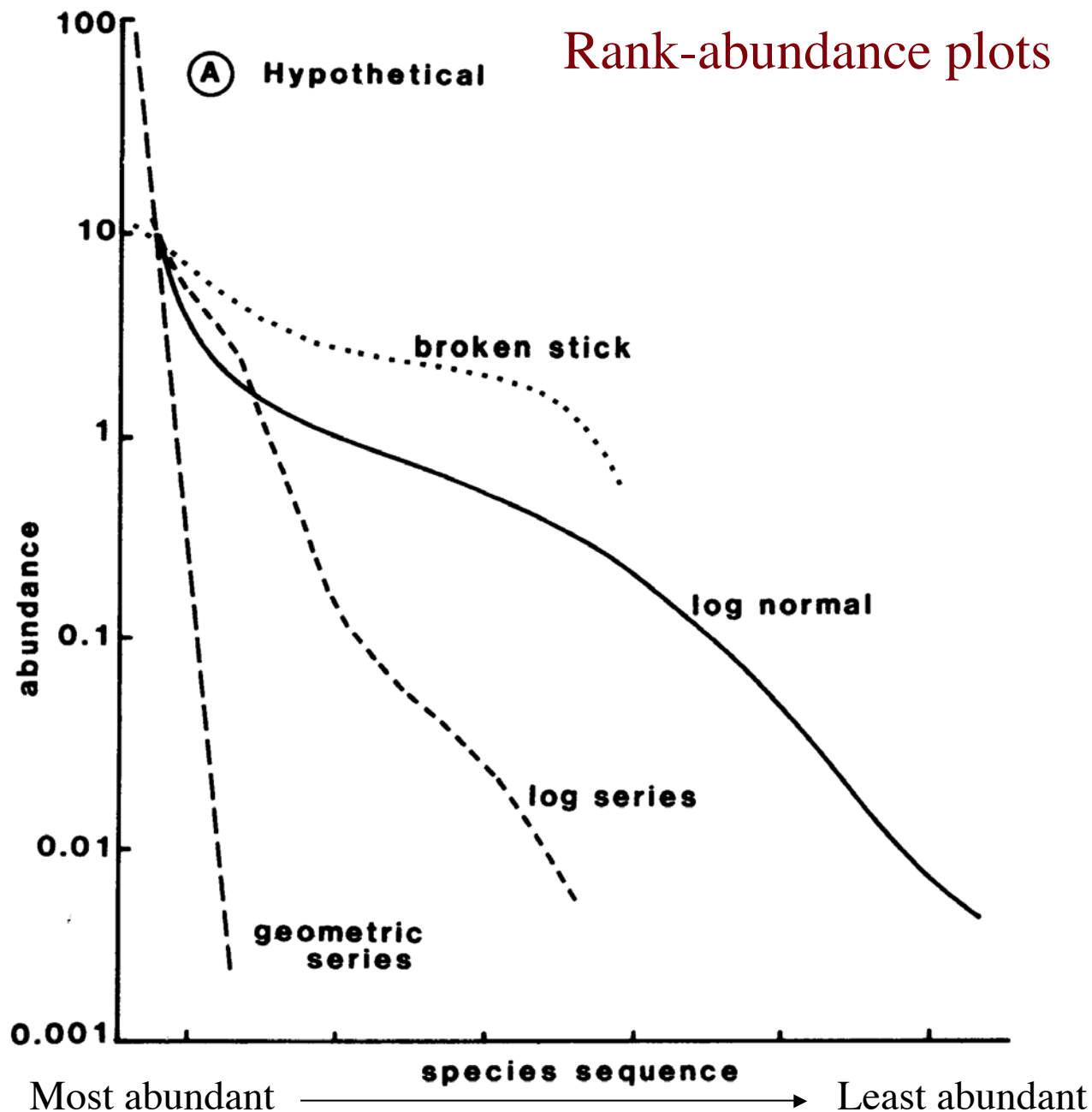
http://www.stat.sc.edu/~west/javahtml/CLT.html

Rank-abundance plots

Rank abundance plots of four spp-abundance models

x axis = *rank* order of abundance (most abundant…least abundant)

y axis = log species abundance

Broken Stick model:

Proposed by MacArthur (1957)

Imagine trophically similar species dividing up a common pool of resources, so that relative abundance is proportional to the fraction of total resources each species uses (rem: geometric series)

Broken stick because imagine placing *S-1 points at random along a resource axis (stick)* and then breaking it into stick sections according to the position of the points… result not a log-normal (abundances are too even…)

Broken Stick:

The sub-division of niche space among species is analogous to randomly breaking a stick into S pieces (MacArthur 1957)

Results in a somewhat more even distribution of abundances among species than the other models, which suggests that it should occur when an important resource is shared more or less equitably among species

Total Available Resources
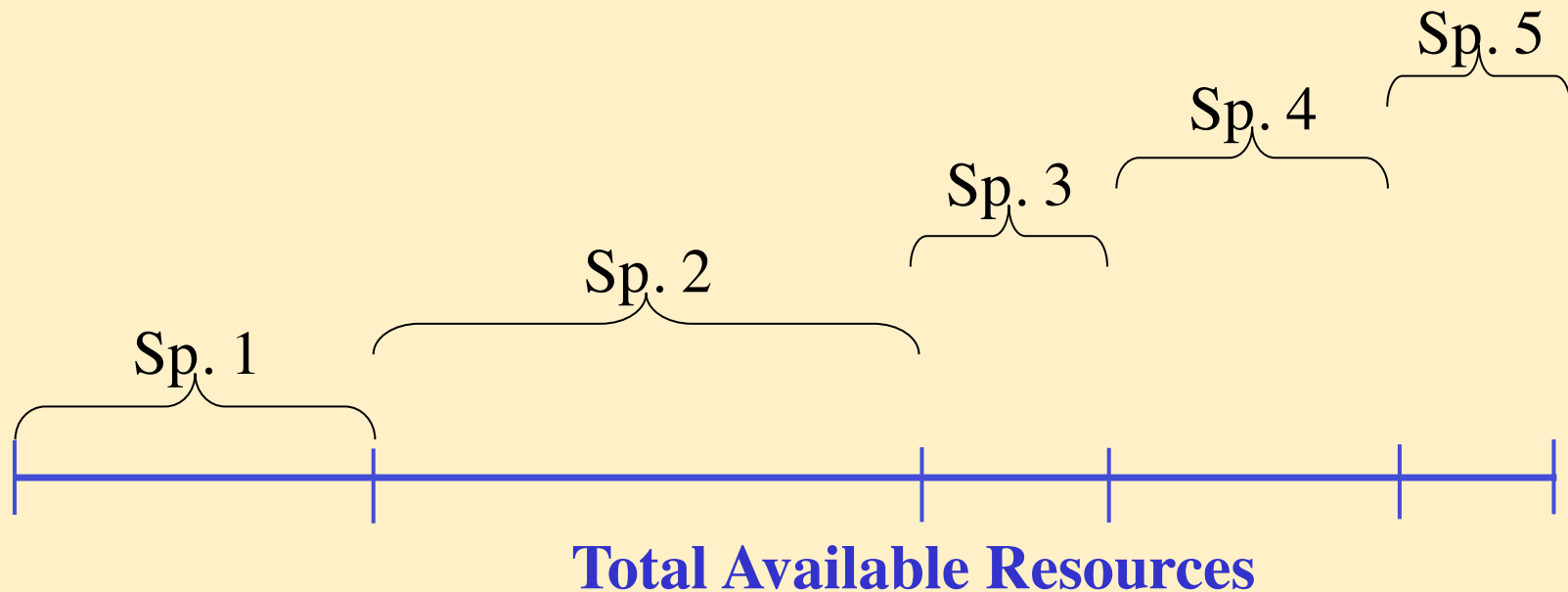
Hubbell (2001) Problems with the development
of theories of species relative abundances

1. Approach is either inductive or "statistical" - fit a model to the data without reference to an underlying mechanism

2. When more deductive (e.g. McArthur's broken stick) the particular mechanism partitioning resources is unclear (what is the stick??!!)

3. *The expected relative species abundances are only determined once the number of species partitioning the resources has been specified*