Species abundance patterns

What characteristics of populations would be useful to know to describe a community and 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*. Unfortunately this is usually difficult to measure (or even estimate!)

Important to distinguish '*richness*' from '*diversity*'. Diversity usually implies a measure of both species number and 'equitability' (or 'evenness') - a measure of how equally abundant those species are in a community.

(One annoying exception: alpha, beta, gamma diversity - which apply specifically to richness).

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. Can consider beta diversity as an *average property of species within a region* (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

Diversity measures are also reflected in the slope and asymptote of the *species-area or species-individuals* curve

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 (Rosenweig 1995)

Islands typically have lower z values compared to mainland areas (no sink species maintained by regular immigration).

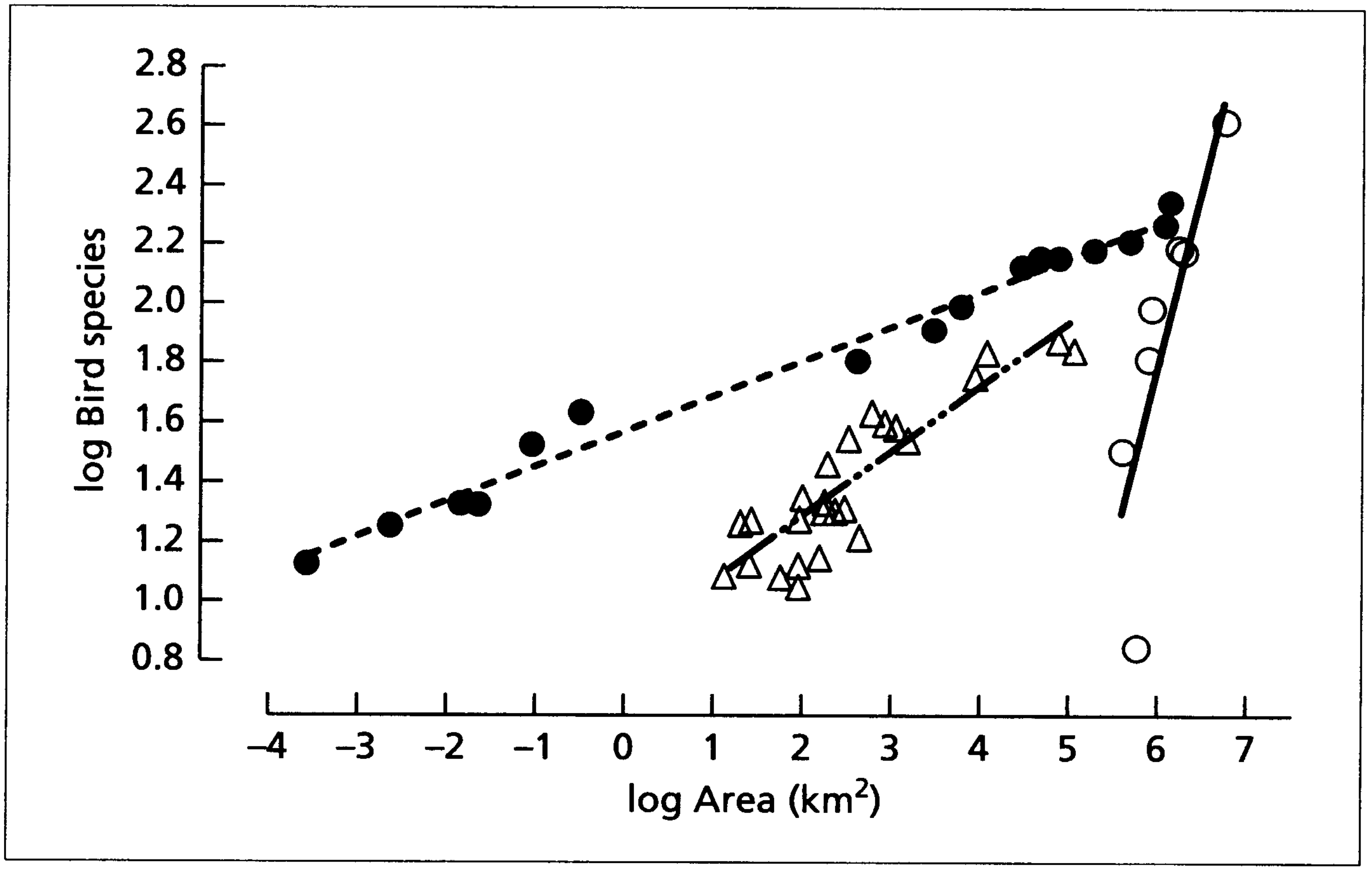


Fig. D7 Three scales of species–area curve for birds. The shallow curve (filled circles) comes from increasingly larger areas within the Mediterranean scrub of Chile; $z = 0.12$. (Data from Cody 1975.) The intermediate curve (open triangles) comes from Caribbean islands; $z = 0.22$. (Data from Wright 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 much larger at scale of biographical regions

Quantifying local species richness

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

- But richness can 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)

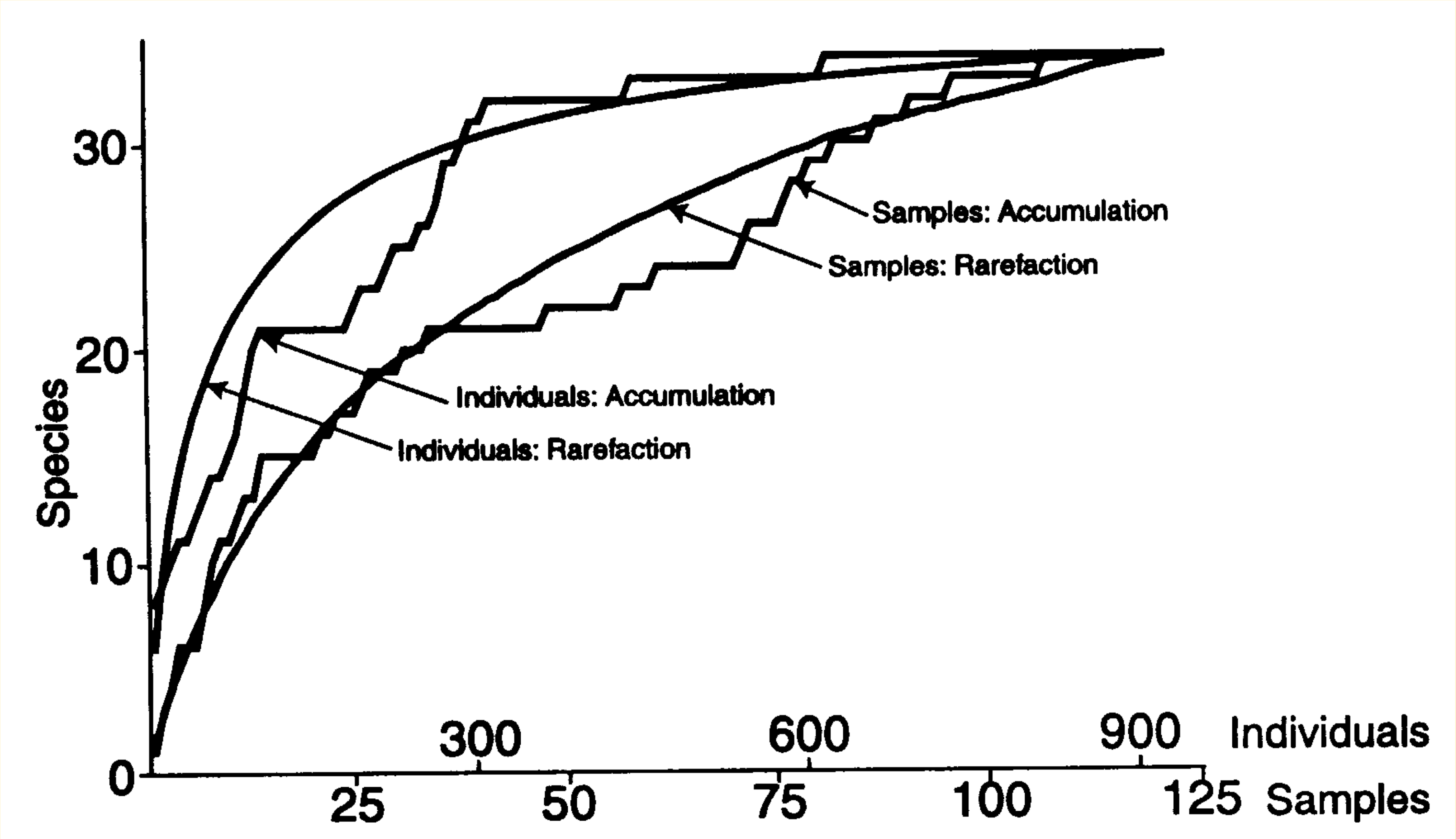
How many tree species are there in the forest??

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)



Sample species richness accumulates more slowly because of spatial autocorrelation. Smoothed lines are ‘rarefactions’

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

How many species are there on earth? Trees? Insects? Fungi?

These approaches are important because some species are very difficult to sample or identify and very diverse (eg insects, microbes) and therefore the asymptotic level of species richness is not reached…

Freeware is now available to generate species accumulation curves and to estimate species richness through rarefaction (Colwell 2000)

viceroy.eeb.uconn.edu/**estimates**

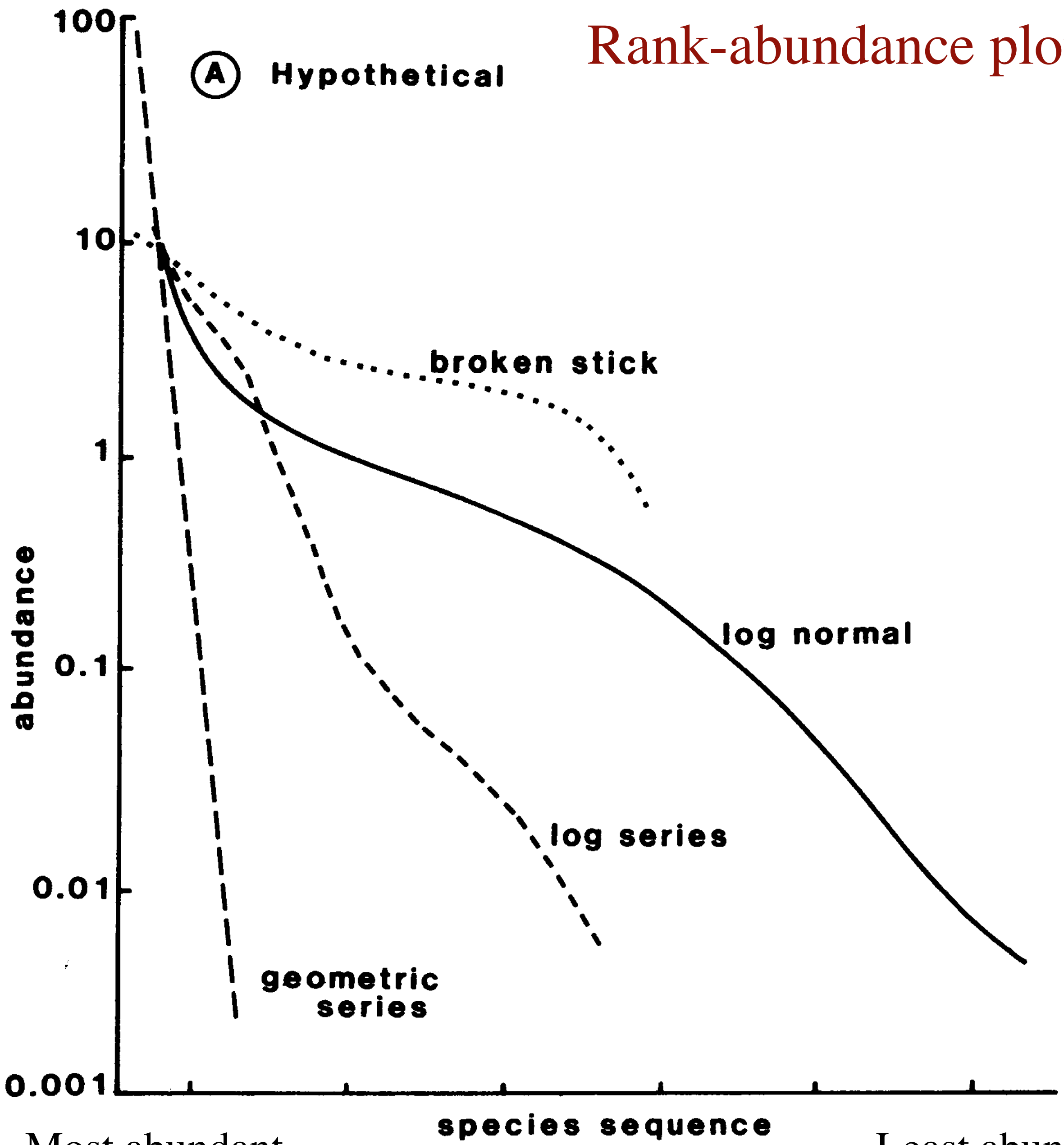
Exploring patterns of diversity

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*

Species abundance data can be described by a family of distributions. Four main models described: log normal distribution, geometric series, logarithmic series, and MacArthur's 'broken stick' model

Much recent theoretical work in this area - stemming from May's (1975) derivation of the species-area power law from the lognormal distribution of species abundances .

Rank-abundance plots

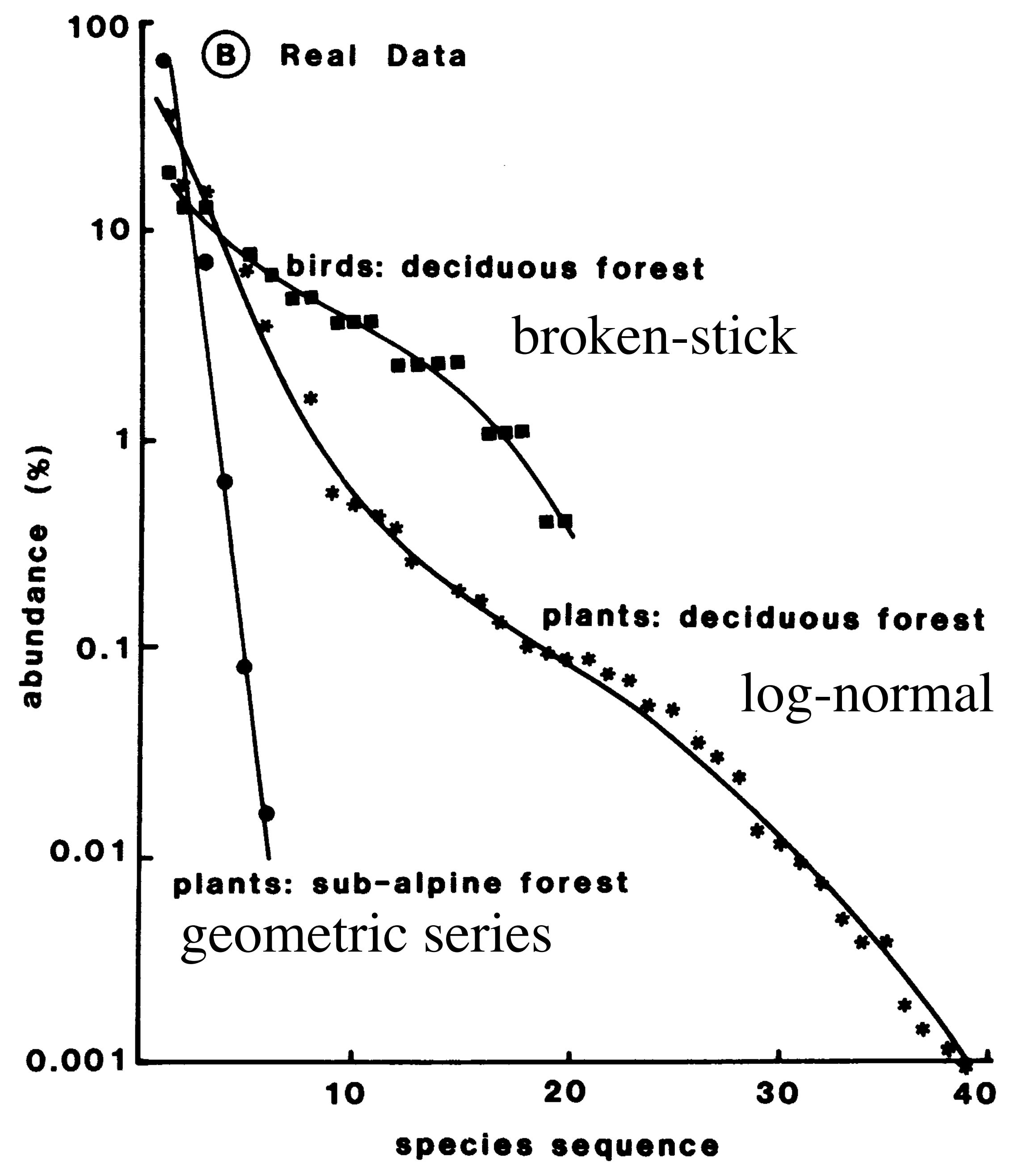


Most abundant → Least abundant

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...

Log series: (aka Fisher's alpha)

First described mathematically by Fisher et al (1943), and derived from a truncated negative binomial distribution

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

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).

On the other hand fitting the logseries will always result in the *singleton category* having the most species

Is this a characteristic of communities??

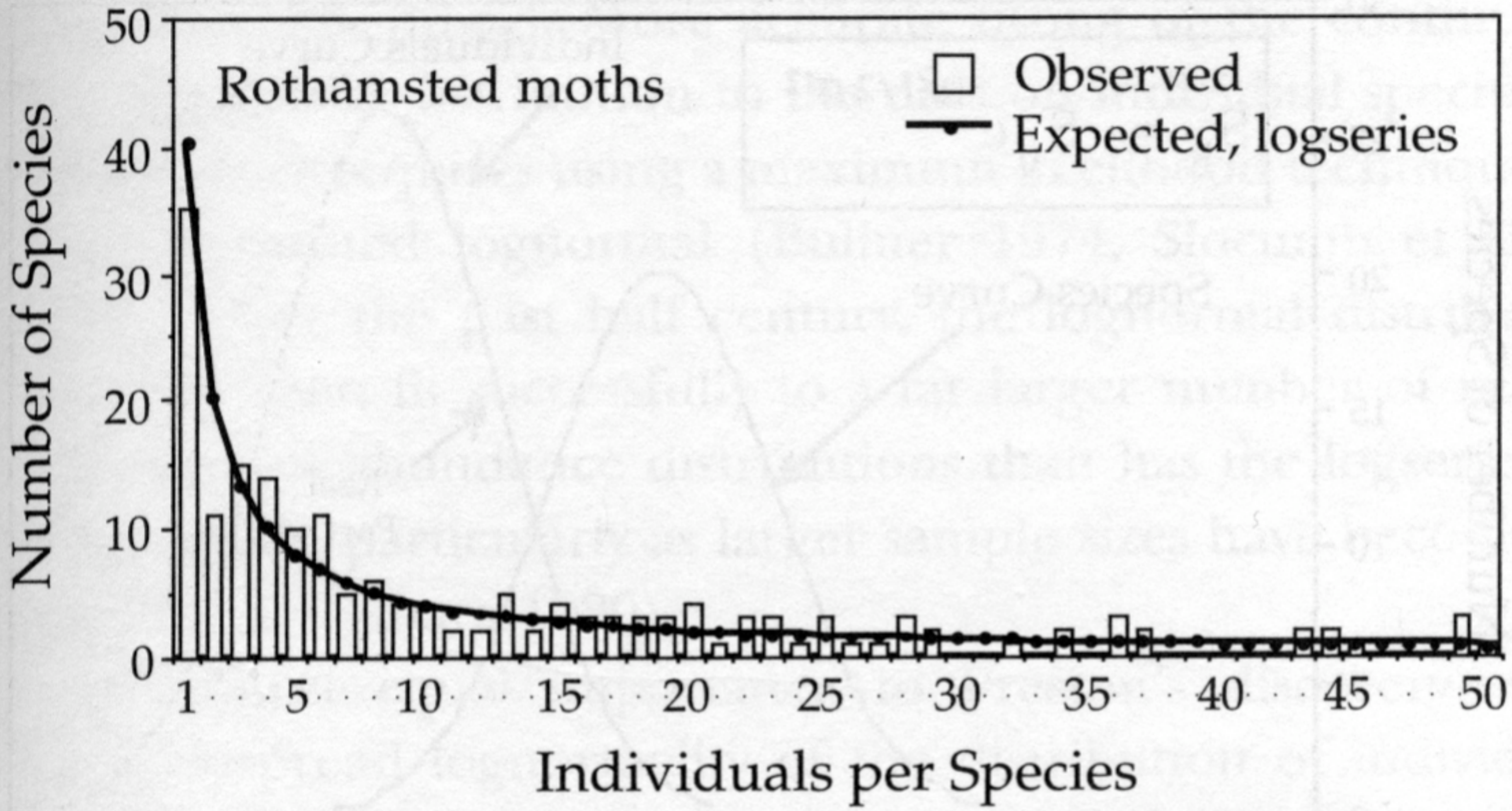


FIG. 2.1. An example of the use of the logseries distribution to fit data on species abundance in collections of months at light trap over a 4-year period at Rothamsted Field Station, U.K. The logseries always predicts that the abundance class of singleton species will be the largest class.

Log-normal distribution:

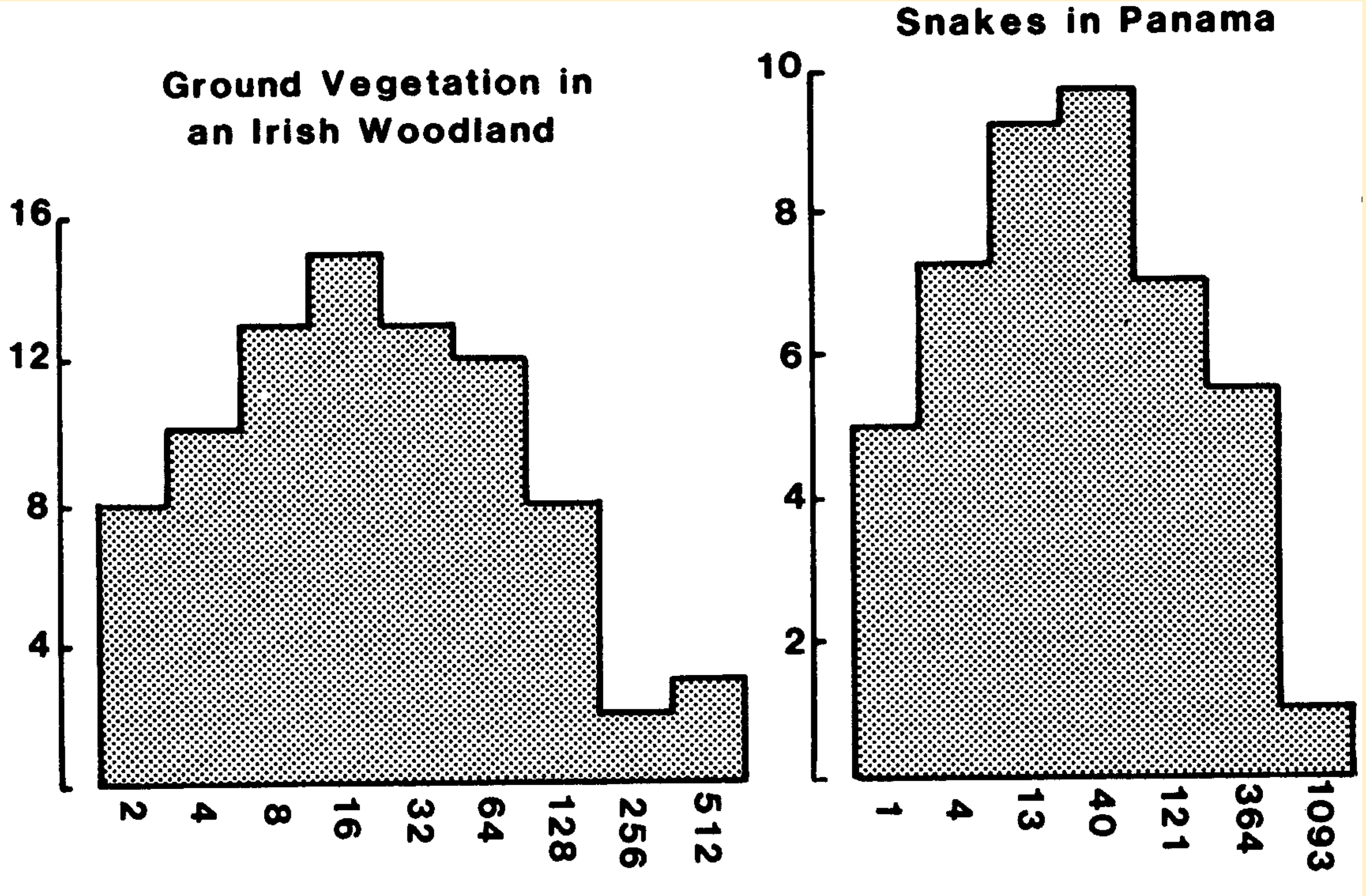
Preston argued that bird species abundance data didn’t fit the log series (*fewer rare species than expected* for logseries). Instead relative abundance distributions were more bell-shaped.

But… abundance distributions were 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 logseries distribution.

In fact, logseries distribution may be an insufficiently sampled log-normal???



Ground Vegetation in an Irish Woodland

Snakes in Panama

Number of spp

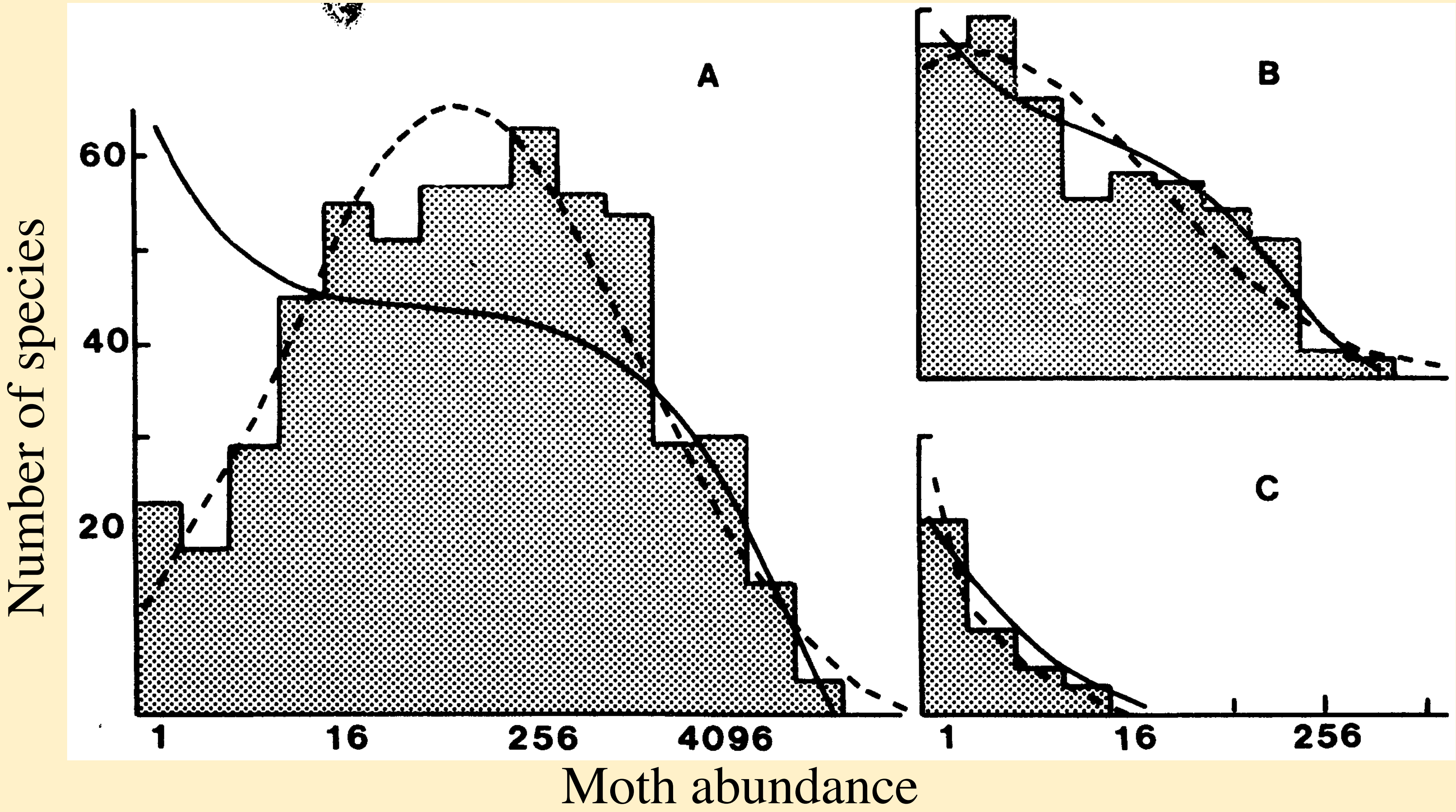
individs $\log_2$

individs $\log_3$

← Octaves →

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

The log normal distribution is a *bell-shaped curve*. If data come from a finite sample *the left hand portion of the curve* (representing rare and unsampled spp) *may be missing*. Preston termed this truncation point the ‘veil line’. For small samples the log series may fit data as well as log normal



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 is a log-normal distribution)

Non-biological systems also have properties of the log-normal (e.g. wealth distribution in the USA; world distribution of human populations), but see Sugihara (1980) for a biological explanation

Broken Stick model:

Proposed by MacArthur (1957) evolved from his search for mechanism generating Preston's log-normal.

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…)

Not many examples of communities with broken stick abundance. Seems to be confined to instances where communities consist of taxonomically related organisms (e.g. birds, minnows, gastropods)

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*

Hubbell (1979) - First development of a neutral (null) model to explain patterns of species abundance

Also considered a *non-equilibrium* theory for the maintenance of diversity

Equilibrium view: Communities are saturated with species which coexist indefinitely as a result of niche differentiation. Competition plays a central role.

Non-equilibruim view: Competition is minimal. Disturbances occur at sufficiently frequent intervals to prevent competitive exclusion

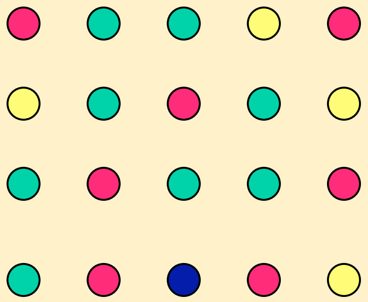
For species rich communities, selection for specialized niches might be weak, and most species "ecologically equivalent" generalists and few selective forces can drive their elimination from a community

Hubbell (1979) Community drift model: Imagine a forest saturated with K trees (all species). Each tree controls one unit of canopy space and resists invasion by other trees until killed

- Suppose a windstorm or landslide kills D trees with mortality randomly distributed across species (loss of each species will be proportional to its current relative abundance)

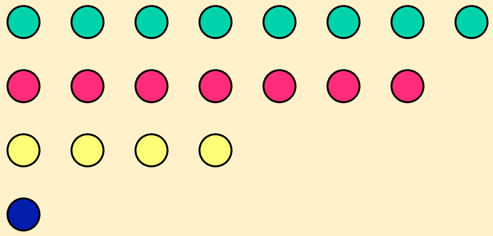
-Let D new trees replace the vacancies, with the proportion of replacement trees contributed by each species *given by the proportional abundance of the species in the community after the disturbance. This is the only assembly rule.*

- Run the model of simulated tree death and replacement over time, what would the outcome be??



Simulated forest
stand K=20

4 species:



Each model iteration: one tree dies. Probability of replacement is proportional to its relative abundance in the community

Probability of replacement by green is 8/20, red is 7/20...

Could apply to any system where dynamics is a ‘*zero sum game*’

Hubbell (1979) Model predictions

Species abundance patterns will take a random walk.

Over the long term, with no immigration or recolonization of the local site, *all but one species will be lost by extinction*.

Over the short term the model leads to lognormal relative abundances, and over the mid-term to a geometric distribution (assuming no immigration or recolonization)

How quickly would species be lost by extinction?

Depends on magnitude of D relative to K

For D=8, K=512, will take 90,000 disturbance events to remove or fix a species with starting population of 256 individuals

For realistic population sizes and mortality rates Hubbell argues that *species can be viewed as essentially immune to extinction over geologically significant time spans* - long enough for speciation to become an important process