

CHAPTER 4

Species Diversity

Background

Species richness is defined as the number of species in a sample unit or other specified area. According to Whittaker (1972), "Diversity in the strict sense is richness in species, and is appropriately measured as the number of species in a sample of standard size."

Although species richness is an intuitive measure of diversity, including inequality in relative abundance as a component of diversity can be intuitive as well. Consider, for example, two plots, each with three species (Table 4.1). Plot 1 has equal amounts of the three species, but Plot 2 has mostly one species and just a bit of the other two. Most people agree that Plot 1 seems more diverse than Plot 2. This intuitive notion of diversity incorporates the **evenness (equitability)** of abundance. A sample unit with more even abundances is, all else being equal, more diverse than a sample unit with abundant and sparse species.

Table 4.1. Which plot is more diverse?

| | species 1 | species 2 | species 3 |
|--------|-----------|-----------|-----------|
| plot 1 | 10 | 10 | 10 |
| plot 2 | 28 | 1 | 1 |

Whittaker (1960, 1965, 1972) defined three levels of diversity.

Alpha diversity: diversity in individual sample units

Beta diversity: amount of compositional variation in a sample (a collection of sample units)

Gamma diversity: overall diversity in a collection of sample units, often "landscape-level" diversity

Each of these can be measured in various ways. There have been numerous reviews of the pros and cons of various diversity measures. Some of the better known and more complete references are Auclair and Goff (1971), Hill (1973a), Hurlbert (1971), Magurran (1988), Peet (1974), Pielou (1966, 1975), Rosenzweig (1995), and Whittaker (1972). A selection of the most popular diversity measures follows.

Alpha diversity

Proportionate diversity measures

Many diversity measures are special cases of a general equation proposed by Hill (1973a) and Rényi (1961). For an observed abundance x_i , (numbers, biomass, cover, etc.) of species i in a sample unit, let

p_i = proportion of individuals belonging to species i :

$$p_i = x_i / \sum_{i=1}^S x_i$$

a = constant that can be assigned and alters the property of the measure

S = number of species

D_a = diversity measure based on the constant a . The units are "effective number of species"

$$D_a = \left(\sum_{i=1}^S p_i^a \right)^{\frac{1}{1-a}}$$

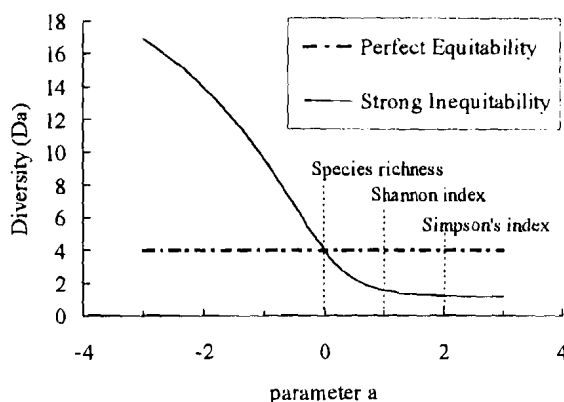


Figure 4.1. Influence of equitability on Hill's (1973a) generalized diversity index. Diversity is shown as a function of the parameter a for two cases: a sample unit with strong inequity in abundance and a sample unit with perfect equitability in abundance (all species present have equal abundance; see Table 4.1).

This equation is one of a small handful of unifying equations (an equation that unifies otherwise disparate-seeming equations) in ecology. As a increases, the index gives more weight to dominant species, less weight to rare species, and sample size (either number or spatial size) is less important (Fig. 4.1).

Although this equation was originally based on information theory, it can also be viewed as the reciprocal of a weighted average. More abundant species are given more weight, and the intensity of this weighting is set by a . The measure D_a is in units of species. You can think of it as equal to the diversity of a community of D_a equally abundant species. It has been called the "effective number of species" (MacArthur 1965, MacArthur & MacArthur 1961).

D_0 = species richness

$$D_0 = \sum_i^s p_i^0$$

When $a = 0$, D_a is simply species richness. Species richness is discussed further below.

D_2 and Simpson's index

$$D_2 = \left(\sum_i^s p_i^2 \right)^{-1} = \frac{1}{\sum_i^s p_i^2}$$

D_2 is another diversity measure, but Simpson's (1949) original index ($1/D_2$) is a measure of dominance rather than diversity. Simpson's index represents the likelihood that two randomly chosen individuals will be the same species. It varies inversely with diversity. The complement of Simpson's index of dominance is

$$\text{Diversity} = 1 - \sum_i^s p_i^2$$

and is a measure of diversity. It is the likelihood that two randomly chosen individuals will be different species. This measure is little affected by addition or loss of rare species and it emphasizes common species. Therefore it is relatively stable with sample size.

Simpson's index applies to an infinite population (i.e., once an individual is sampled, it does not change the probability of getting it as the next individual). There are other versions for finite populations.

D_1 and Shannon-Wiener index. If $a = 1$ then D_1 is a nonsense equation because the exponent is $1/0$. But if we use limits to define D_1 as a approaches 1 then

$$D_1 = \lim_{a \rightarrow 1} a \rightarrow 1 (D_a)$$

$$D_1 = \log^{-1} \left(- \sum_i^s p_i \log p_i \right)$$

The logarithmic form of D_1 is the Shannon-Wiener index (H'), which measures the "information content" of a sample unit:

$$H' = \log(D_1) = - \sum_i^s p_i \log p_i$$

The units for D_1 are "number of species of equal abundance" while the units for H' are the log of the number of species of equal abundance. The minimum value for H' is zero, obtained when one species is present. H' is undefined if $S = 0$. This equation was first used in ecology by MacArthur and MacArthur (1961) and has a basis in information theory. If we put diversity into the context of information theory, then maximum diversity yields maximum uncertainty. Think of it as drawing individuals at random from a community. The higher the diversity, the more uncertainty you will have about which species you will draw next (Box 4.1). Determining the species of an individual drawn from a diverse sample unit relieves more uncertainty (provides more information) than from a sample unit with low diversity.

If you use the antilog form (D_1 or $\log^{-1}(H')$), then the choice of base of logarithms (base e or base 10) makes no difference. Both forms have been commonly used.

D_1 and H' are intermediate between species richness and Simpson's index in its sensitivity to rare species. It is widely used, but has the disadvantage that the numerical value is not as directly meaningful as some other indices, especially species richness.

Whittaker (1972) summarized the interpretation of H' : "There is no particular reason to interpret diversity or equitability as information or uncertainty, but the index has distinctive and appropriate qualities. It is most strongly affected by importances of species in the middle of the sequence. For large samples the index is consequently somewhat damped against effects of differences in quantitative proportions of the first few species. Effects of the rarer species are also damped, rendering the index, like [Simpson's index], relatively independent of sample size... for samples that are not too small."

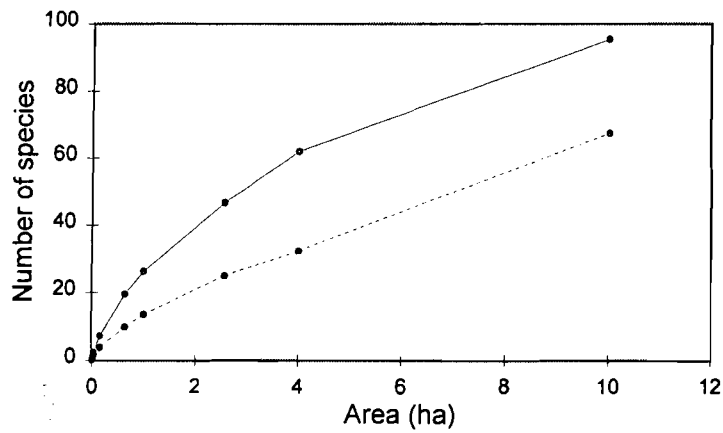
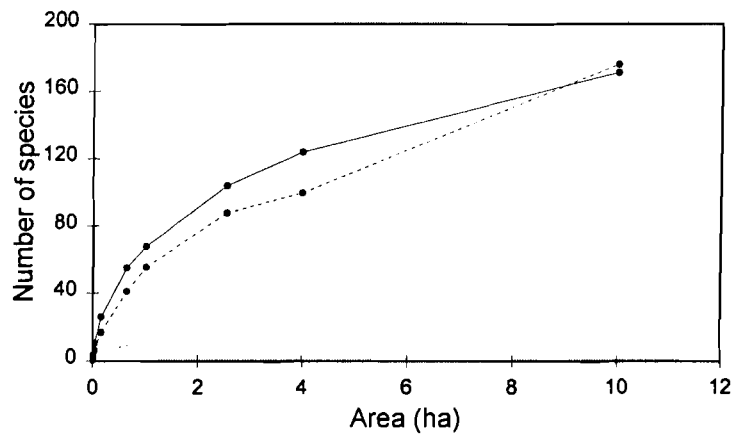
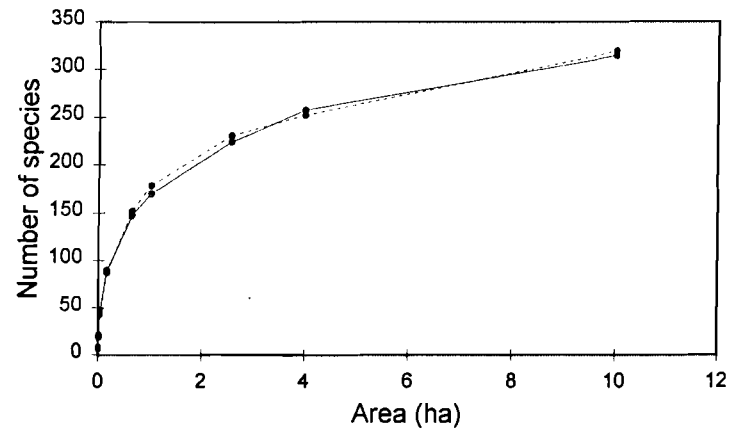


Figure 1.7. Species-area curves of monodominant stands (dotted lines) and of mixed stands (solid lines) in the Ituri Forest.

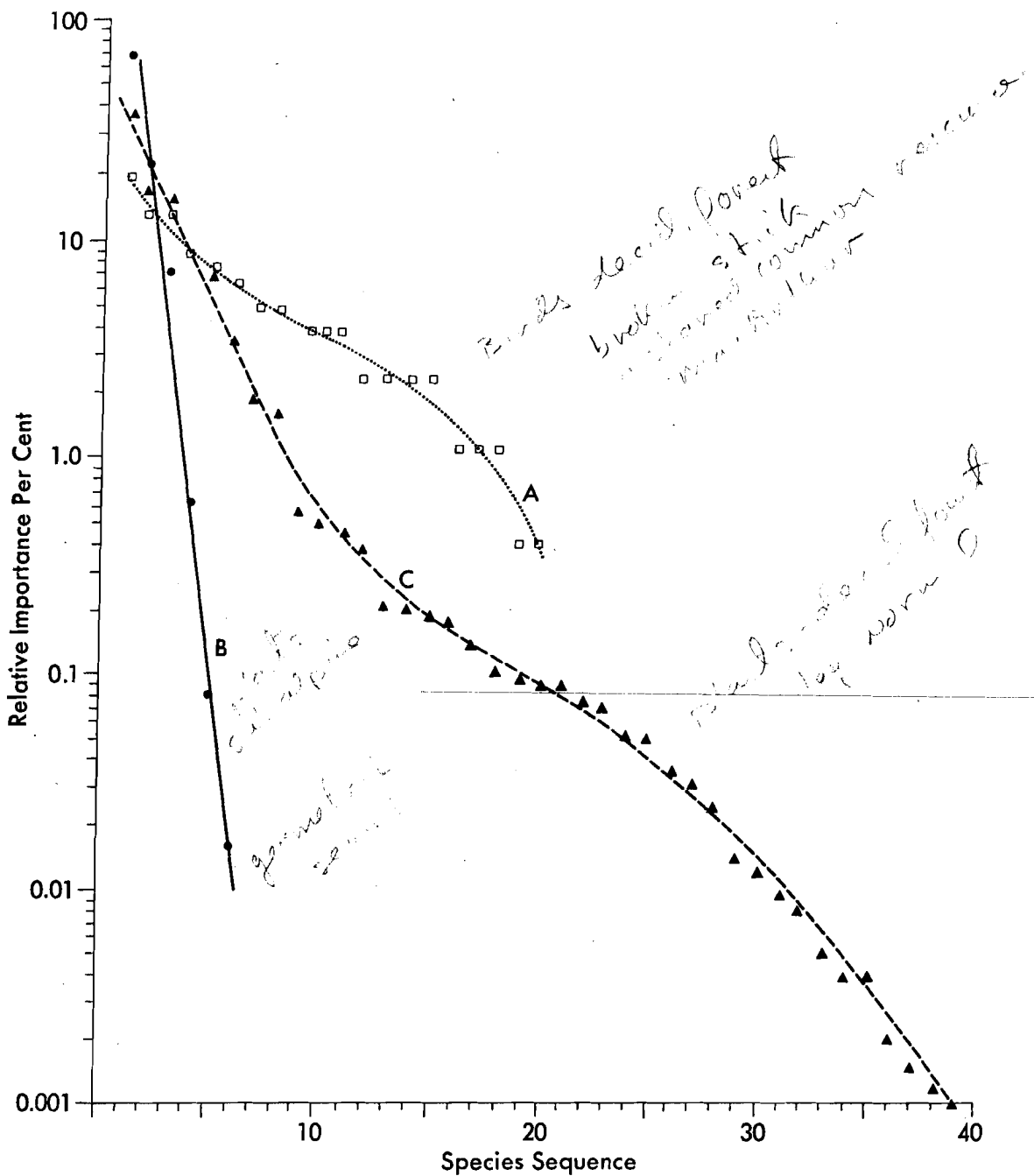


Figure 3.14. Three importance-value curves from natural communities. **A:** Nesting bird pairs (densities) in a deciduous forest, West Virginia; the data fit the random niche-boundary hypothesis as shown in Figure 3.12A. **B:** Vascular plant species by net production in a subalpine fir forest in the Great Smoky Mountains, Tennessee. The data fit the geometric series and niche pre-emption hypothesis as shown in Figure 3.12B. **C:** Vascular plant species by net production in a deciduous cove forest in the Great Smoky Mountains of Tennessee, a community of much higher species diversity. The data approach the lognormal distribution, as shown in Figure 3.12C and (in a different kind of plot) Figure 3.13. Each species is represented by a point located by that species' relative importance (the percentage that that species represents of the total net production, or total density, of all species in the community, on a logarithmic scale) on the vertical axis, and its position in the sequence of species from highest to lowest importance values, on the horizontal axis. Thus in curve *B*, there are points for six species in a sequence of decreasing importance values, from the most important species at the top with 69 per cent, through other species with 23, 7.0, 0.62, and 0.08 per cent, to the least important species sampled, at the bottom, with 0.016 per cent of net primary production for the forest.

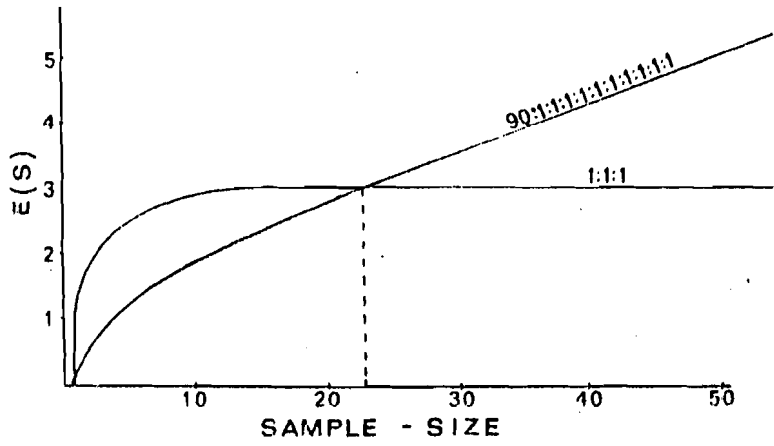


Figure 1 The relationship between the expected number of species and sample size for samples drawn from two hypothetical communities of 1000 individuals.

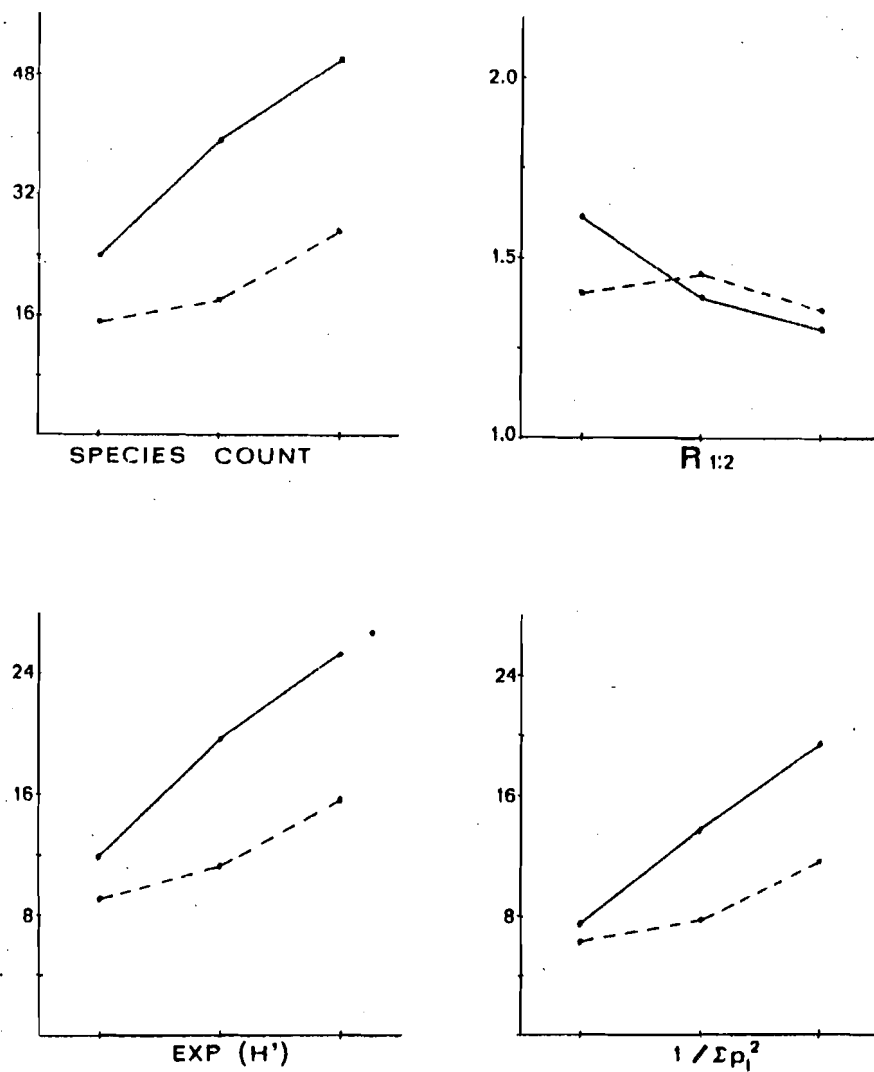


Figure 5 Values of four indices along two gradients in bird species diversity. The broken line represents breeding bird diversity at three points along a north to south latitudinal gradient of Appalachian hemlock-hardwood forests (data from Odum, 47). The solid line represents summer resident bird diversity at three points along a successional sequence in New Jersey (data from Kricher, 26).