CONCENTRATION CURVES AND HAVE-STATISTICS FOR ECOLOGICAL ANALYSIS OF DIVERSITY:

PART II: SPECIES AND OTHER DIVERSITY

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NOTE: This is Part II of a series of three working papers. For a preface, foreword, acknowledgments, and a note about the authors, please see Part I of the series, which is subtitled "Dominance and Evenness in Reproductive Success", IIASA WP-85-72.

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PART II: SPECIES AND OTHER DIVERSITY

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INTRODUCTION

The application of concentration curves and have-statistics to studies of dominance and evenness in reproductive success was discussed in Part I of this series of three papers. Concentration curves and have-statistics can also aid ecologists in studies of species diversity and community structure; a start in this direction was made by Patil and Taillie (1979) and Taillie (1979). Essentially, the method is the same as before except that now the "haves" are species rather than individuals and the "hads" are individuals, biomass, caloric intake, etc., rather than an individual's offspring. In addition, concentration curves and have-statistics can be applied to other ecological topics pertaining to variation and inequality, including the temporal or spatial distribution of some resource, such as food supply or rainfall. Various examples, from studies of diatoms, a community of herbaceous plants, a tropical forest, a model of niche preemption, and temporal variation in the breeding of tropical and temperate bird species illustrate this approach.

THE ANALYSIS OF SPECIES DIVERSITY

Four examples illustrate the use of concentration curves and have-statistics in studies of species diversity.

1. Herbaceous Plants in a Deciduous Woodlot

Figure 1 displays the degree of dominance (i.e., unevenness) in the distribution of 62 herbaceous plant species in a deciduous woodlot; the underlying data are from Pielou (1966b). Each species is weighted in terms of its average biomass (fresh gram weight). The have-statistics for this data set are included in Table 2 of Part III. Note, for example, that less than 12 percent of the species (i.e., seven species) account for half the biomass and that half the species account for close to 95 percent of the biomass. It is apparent from the concentration curve and these measures that the biomass of herbaceous plant material is concentrated in a few species that are dominant in this environment.

2. Diatoms in an Experimental Community

A second example of species concentration, displayed in Figure 2, concerns the populations of individuals in 113 species of diatoms in an experimental community, based on data from Patrick (1968). The figure and the have-statistics clearly indicate that most of the population is concentrated in a few species. Note that the top quarter of the species account for almost 94% of the individuals and that the top half account for 98%. The very low values of the havequarter and havehalf indicate the importance of the most dominant species: scrutiny of the underlying data reveals that the top two species, which have roughly equal populations, account for fully five-eighths of the total population.

Pielou (1975) analyzes the herbaceous plant data and the diatom data from a different perspective. She fits a gamma distribution to the frequency distribution of the biomasses of the herbaceous plants and a truncated lognormal distribution to the populations of diatoms. As Pielou's research illustrates, studies of dominance among species, like studies of dominance among individuals, tend to rely on frequency distributions, often called species-abundance distributions in this context. This approach highlights the relationship between the importance of different species and is useful in answering questions such as "whether, in large communities, rare species are always (or nearly always) more numerous than common ones" (Pielou 1975), i.e., are there more species with small populations than species with large populations. Concentration curves, on the other hand, visually minimize rare species and highlight the importance of the few, common species. Thus, concentration curves and have-statistics are useful in analyzing the dominance of the top species, whereas species-abundance distributions are useful in analyzing how the population of species falls off as species become less populous.

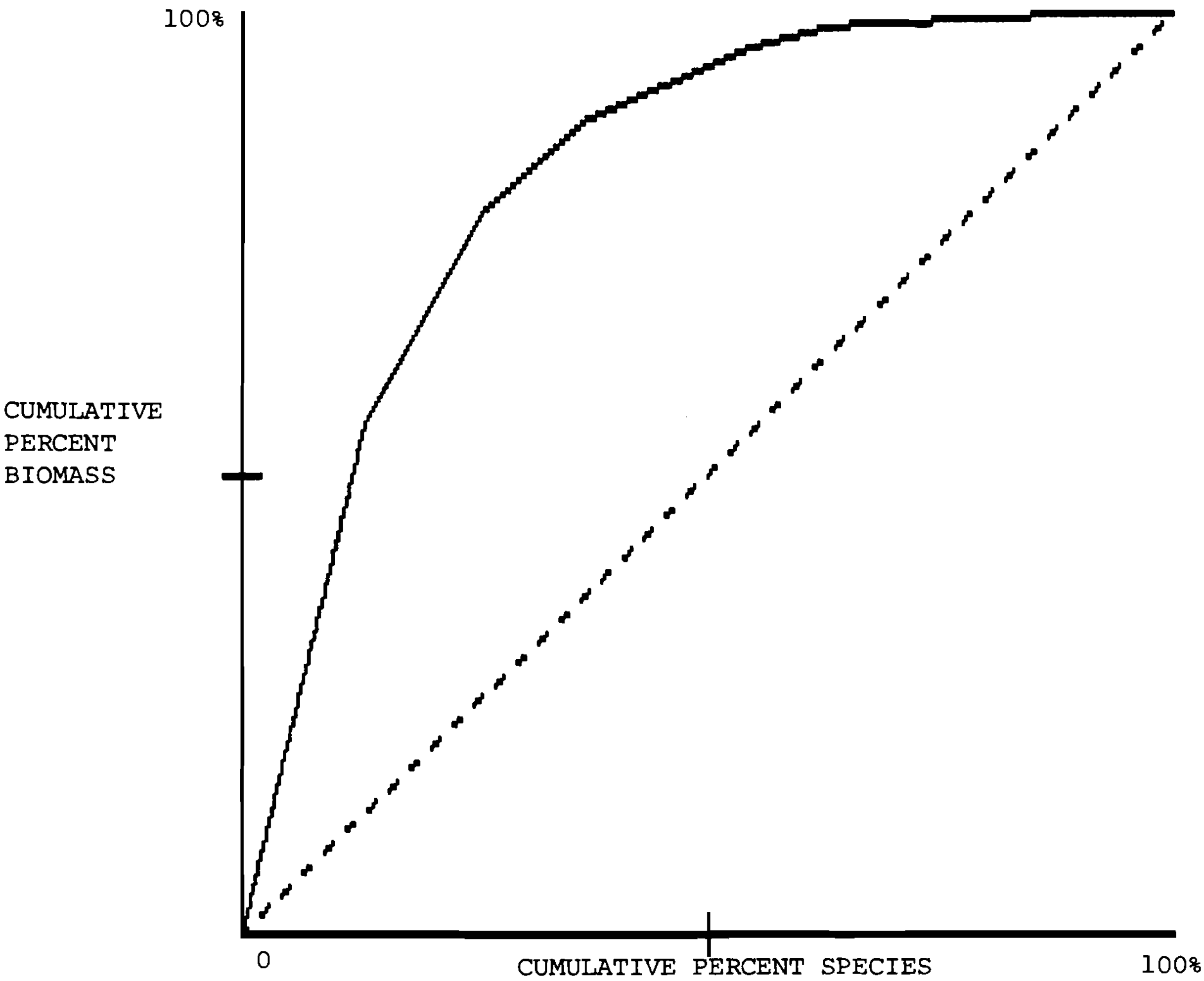

Figure 1: Concentration of biomass (fresh gram weight) within 62 species of herbaceous plants in a 3000 sq.m. deciduous woodlot. (Data from Pielou, 1966b)

3. A Theoretical Model of Niche Preemption

The relationship governing the relative importance of different species can also be analyzed by using a dominance-diversity curve (Whittaker 1965,1972; Odum 1983; Pianka 1983). This curve is similar to a concentration curve in that species are ranked from most dominant to least dominant on the horizontal axis. The vertical axis, however, instead of measuring cumulative population up through the species on the horizontal axis, measures the logarithm of the population of the species on the horizontal axis.

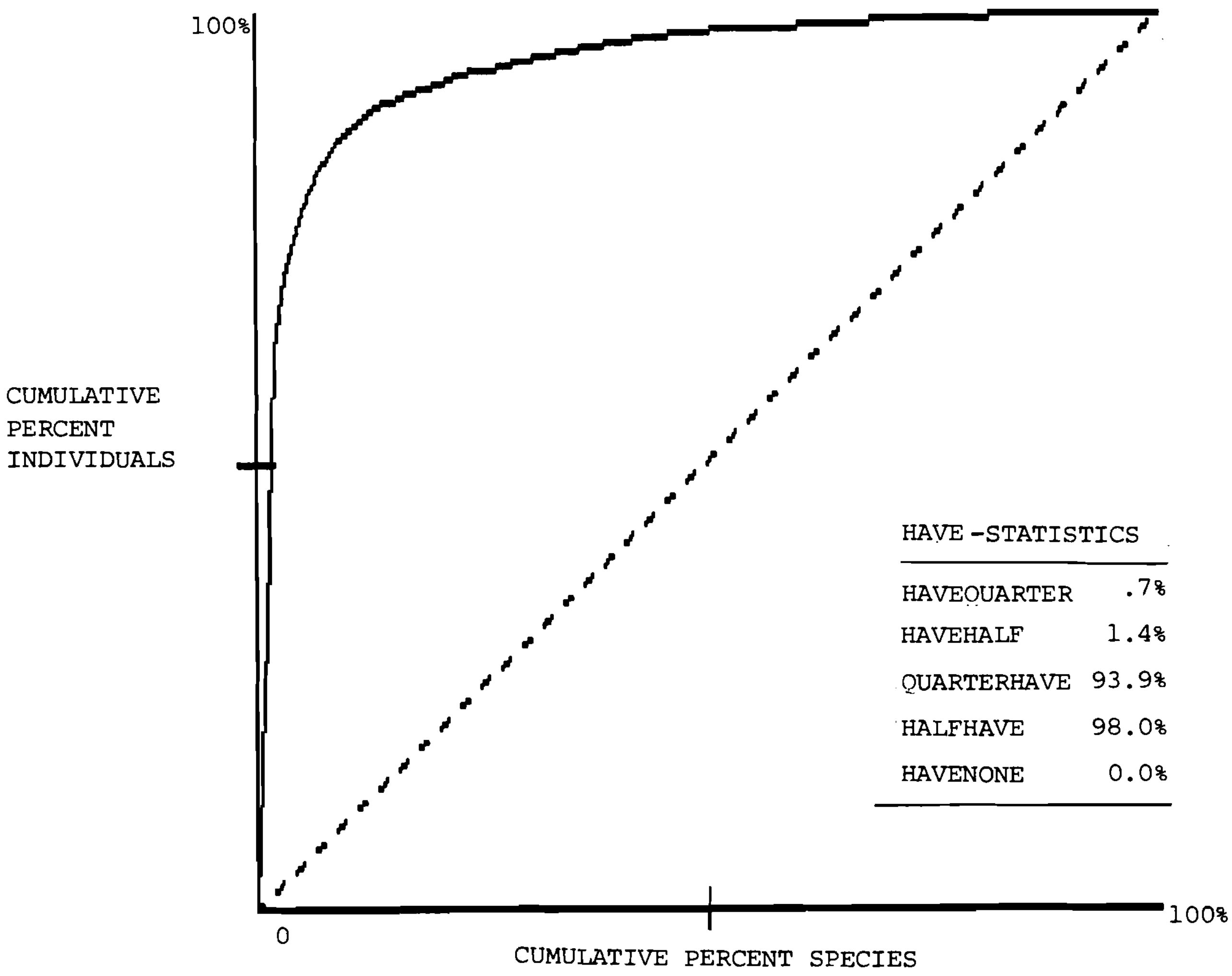

Figure 2: Concentration of individuals within 113 species of diatoms in an experimental community. (Data from Patrick, 1968)

In describing niche preemption, Odum considers a community of species where "the most abundant species is twice as numerous as the next most abundant one, which in turn has twice the density of the third, and so on...". This produces the following relative population sizes for ten species: 512, 256, 128, 64, 32, 16, 8, 4, 2, and 1. This geometric distribution may roughly hold, for example, in some plant communities in harsh environments. As shown in Figure 3a, this pattern results in a declining straight line on a dominance-diversity graph. On the other hand, as shown in Figure 3b, the pattern results in a highly-bowed concentration curve. The concentration curve indicates that the most populous species accounts for half the total population and that the top five species account for 97% of the total population. Thus, dominance-diversity curves and concentration curves reveal two different aspects of an ecological situation: the curves are not substitutes for each other, but complements.

4. Biomass in an Amazonian Forest

In studies of species diversity, it is often useful to consider number of species rather than proportion of species. Hence, the horizontal axis of a concentration curve might be drawn to represent number of species, in rank order. When there are a very large number of species, but only a few have significant populations, the horizontal axis could be truncated at, say, the 100th most populous species or at the least populous species with at least one percent of the population.

As an example, consider the distribution of above-ground biomass in a section of Amazonian forest near Manaus, Brazil. Hubbell (1979) plots a dominance-diversity curve for the top two hundred species in this forest, as shown in Figure 4a. The curve is essentially a straight line, with a slope indicating that the frequency distribution of species' population is negative exponential with a coefficient of roughly 0.035.[1] The corresponding concentration curve indicates that the top 8 species account for a quarter of the total biomass, the top 20 species account for half, the top 66 species account for 90%, the top 100 species account 97%, and the top 200 species account for fully 99.9%. Figure 4b plots the concentration curve for all 200 species; it would also be reasonable to plot the concentration curve out through the top 65 or 100 species.

Note that have-y statistics are meaningful in this context, but x-have statistics are not. If, however, x is taken not as a percentage of the total number of species, but as species rank, then x-have statistics can be calculated. For instance, it might be said that the 100-have is 97% and that the 200-have is 99.9%.

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[1]The deviation from this straight line for the first few species indicates that the first five species or so may be somewhat more numerous than this distribution suggests. Consequently, it is especially important in this instance to stress that the concentration curves and have-statistics we present in this paper should be treated as illustrative rather than as precise.

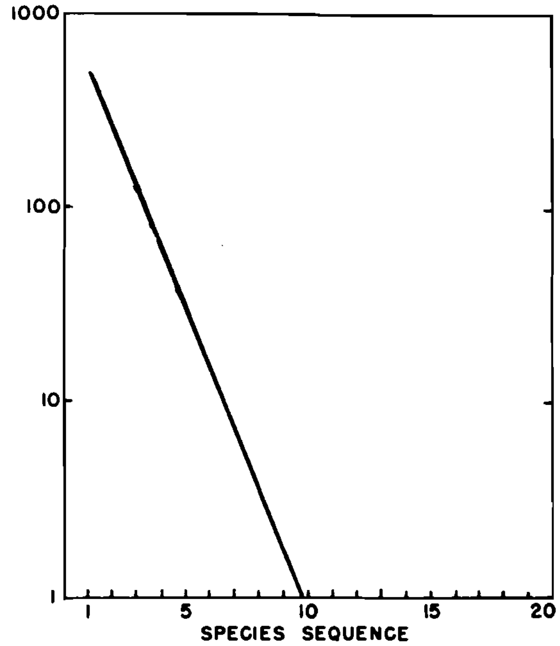

Figure 3a: Dominance-diversity curve for a hypothetical sample of 1000 individuals in 20 species from a community. Number of individuals in the species (ordinate) are plotted against species number in sequence from the most abundant to the least abundant (abscissa). Curve —geometric series with niche preemption.
(From Odum, 1983; after Whittaker, 1965)

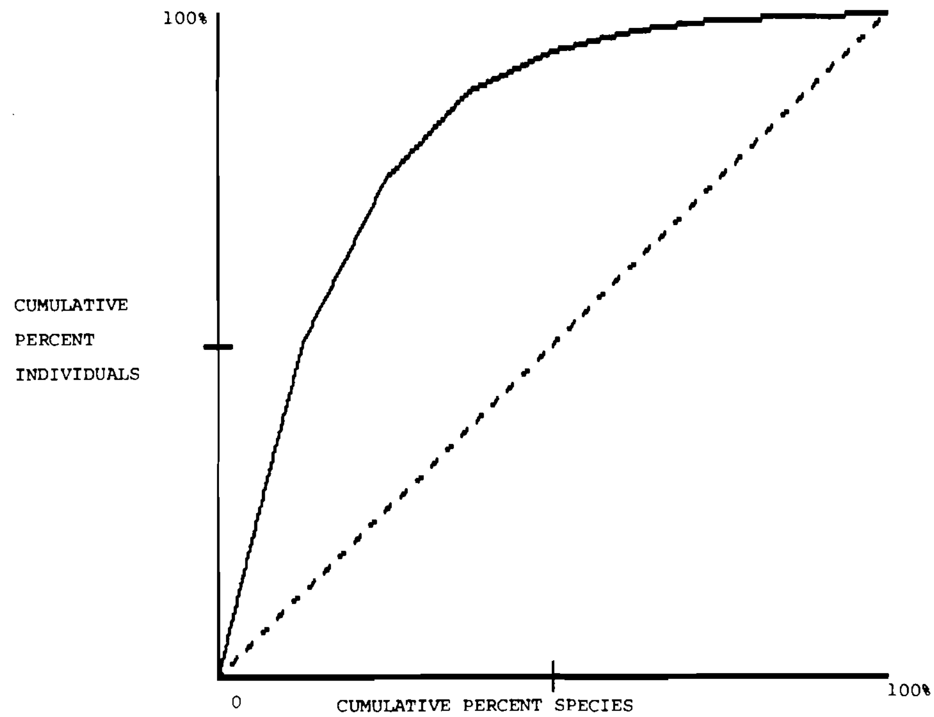

Figure 3b: Concentration of individuals among 10 species in a hypothetical geometrically distributed community.

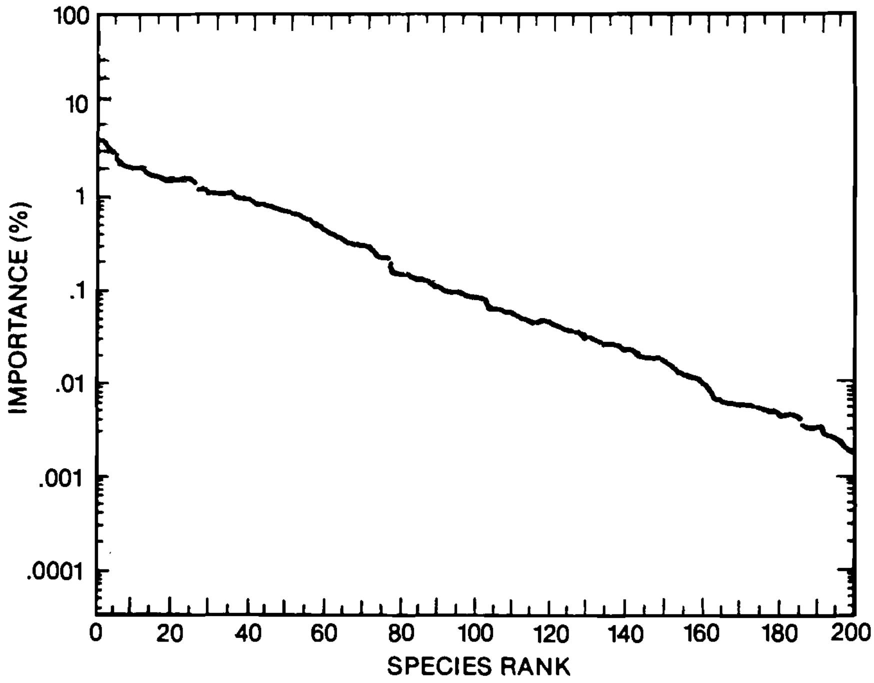

Figure 4a: Dominance-diversity curve for a tropical wet forest (Manaus, Brazil). Importance values based on above-ground biomass. (After Hubbell, 1977)

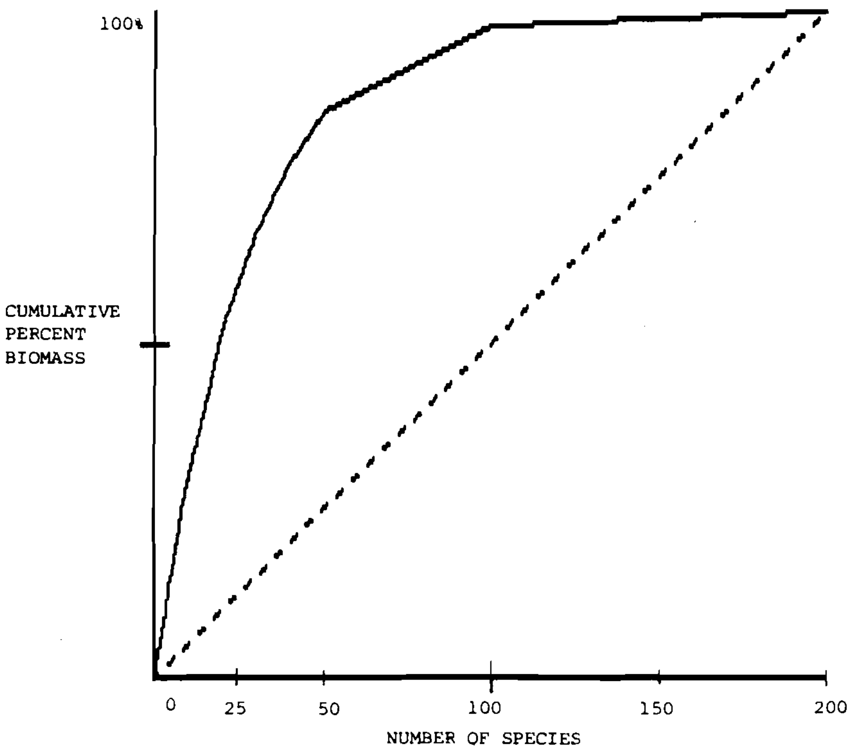

Figure 4b: Concentration of above-ground biomass among 200 tropical forest tree species. (Data from Hubbell, 1979)

APPLICATIONS TO STUDIES OF SPECIES DIVERSITY

As these examples illustrate, the role of concentration curves and have-statistics in analyses of species diversity is to highlight the dominance of the few top species. In particular, in much the same way that concentration curves and have-statistics can be used in comparative analyses of reproduction, they can be used in the description of community structure and the investigation of temporal or spatial differences in the dominance of one or a few species in a habitat, community or ecosystem. Some examples might include the description and analysis of:

- species stratification within different temperature zones in a benthic community;
- altered species dominance as potential indicators of lake eutrophication;
- changes in species concentrations with changing predation levels;
- changes in species evenness or degree of dominance with advancing successional stages.

OTHER APPLICATIONS

The various examples presented in the first part of this series of three papers are concerned some aspect of reproduction. This is an area of prime concern to life scientists. We touched above on the topic of species diversity. There are numerous other applications of concentration curves and have-statistics. As an example consider the temporal distribution of breeding bird pairs in a tropical and a temperate environment.

1. Temporal Diversity: The Monthly Concentration of Breeding Among Birds

MacArthur (1964), presents data from Lack (1950) and Skutch (1950) on the distribution of breeding bird pairs observed, for all species, over twelve months of the year, for samples from England and from Costa Rica. Figure 5a displays the greater temporal concentration of bird breeding in England as opposed to Costa Rica. It is also interesting to note that there is a relatively small difference in the number of months that have half of the breeding pairs.

In Figure 5b we redraw these concentration curves to eliminate the four months in England which had no breeding pair, and the one month that had only a single breeding pair (out of more than 4000 breeding pairs over the course of the year). The concentration curves are now nearly identical. These curves indicate that bird breeding in these sample populations from temperate and tropical zones is similarly distributed over the viable months.

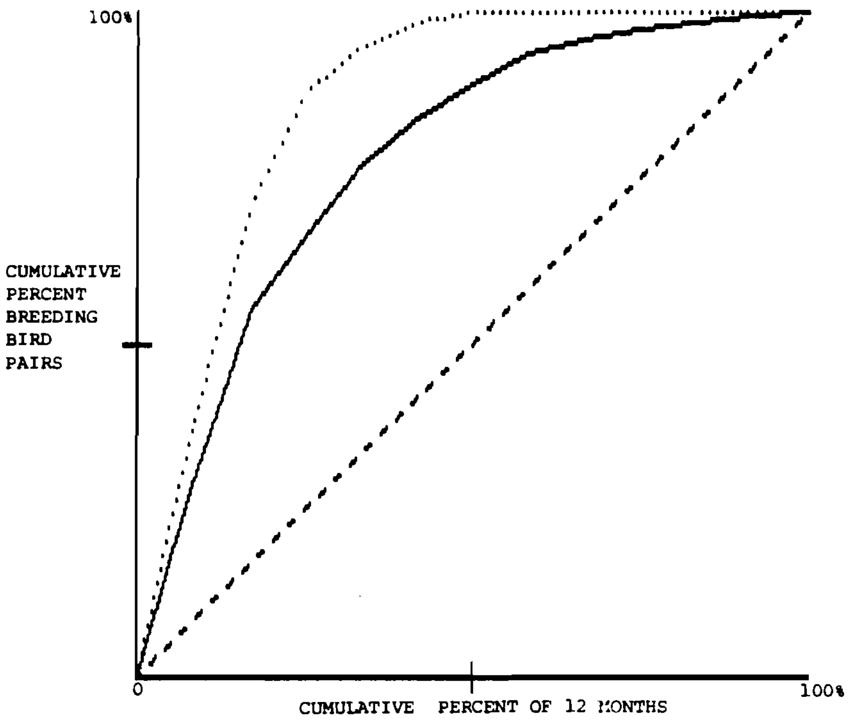

Figure 5a: Monthly concentration of breeding among bird species for:
- England ·······
- Costa Rica ———
(Data from MacArthur, 1964; after Lack, 1950 & Skutch, 1950)

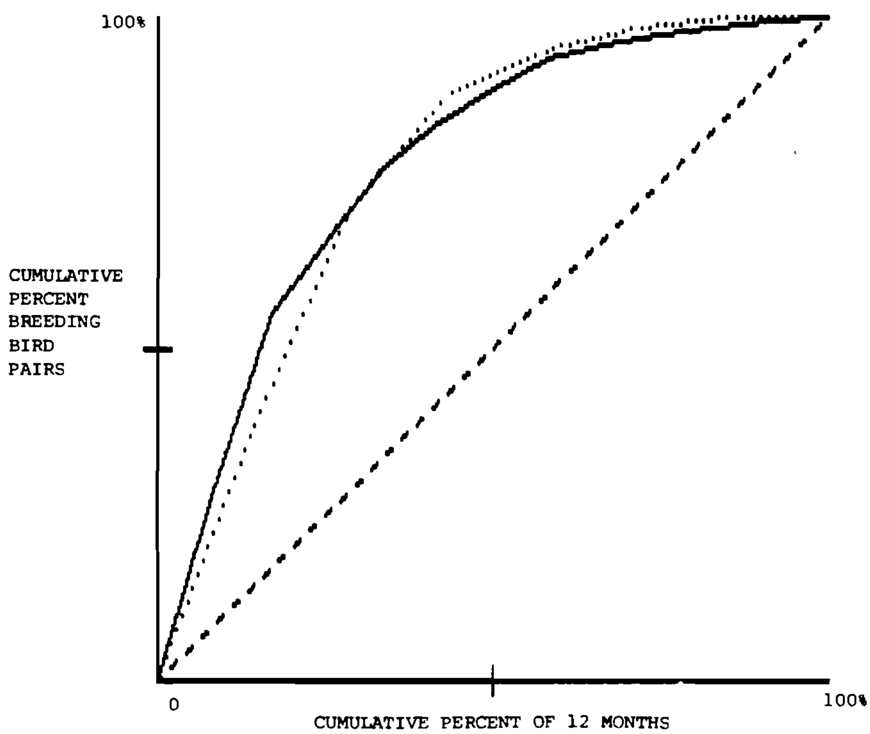

Figure 5b: Monthly concentration of breeding among bird species for:
- England ·······
- Costa Rica ———
(Note: Months with 0 or 1 breeding pairs have been eliminated from England data)

2. An Illustrative List of Other Potential Applications

Logically, concentration curves and have-statistics can be used whenever there is inequality or variation in the distribution of some characteristic: whenever a frequency distribution can be drawn, a concentration curve can also be drawn; whenever an average can be calculated, a havehalf can also be calculated. How meaningful it is to do so, however, depends on the context. Concentration curves and have-statistics seem most appropriate when there is some total amount of something of importance (like offspring or wealth) that is divided up among individuals or among some units (like species or business firms) that can be treated as separate individuals. For instance, concentration curves and have-statistics might be used to analyze:

- spatial distribution of a population (e.g., if a forest is divided into small districts, what proportion of the districts include half of all the maple trees in the forest);
- spatial concentration of food resources (e.g., what proportion of the habitat contains what proportion of the food supply of a population of marshwrens);
- temporal distribution of food resources (e.g., over what proportion of the year is what proportion of a bird species' "preferred" food available);
- concentration of nesting sites (e.g., what proportion of an area contains what proportion of the viable nesting sites of a population of red-winged blackbirds);
- distribution of infant mortality (e.g., what proportion of mothers account for what proportion of deaths of offspring before age one);
- distribution of a prey among some predator (e.g., what proportion of the coyotes account for what proportion of the sheep killed by coyotes in Idaho);
- distribution of reproduction among age classes (e.g., in a species where childbearing extends over many years of an individual's lifespan, what proportion of the years of age account for what proportion of the offspring produced);
- temporal distribution of reproduction (e.g., in a species where the number of offspring born varies over time, perhaps from day to day or from year to year, what proportion of the days or years in some period account for what proportion of the offspring born in that period);
- temporal distribution of mortality (e.g., in a species where the number of deaths varies over time, what proportion of the days or years in some period account for what proportion of the mortality over that period);

- age composition (e.g., what proportion of single-year age categories include what proportion of the population);
- temporal concentration of rainfall (e.g., what proportion of the days, weeks, or months of the year account for what proportion of the annual rainfall in some tropical vs. some temperate area);
- temporal nutrient concentrations (e.g., what proportion of the months account for what proportion of the annual phosphorus load in a lake).

Topics such as species diversity, temporal diversity, and spatial diversity are major focal areas within ecology. The importance of concentration curves and have-statistics depends on their usefulness to ecologists in substantive research on these and other aspects of diversity. We have only sketched some of the potential here but we hope that the relevance of the approach will nonetheless be apparent.

REFERENCES

Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203:1299-1309.

Lack, D. (1950) The breeding seasons of European birds. *Ibis* 92:288-316.

MacArthur, R.H. (1964) Environmental factors affecting bird species diversity. *Amer. Natur.* 98:387-397.

Odum, E.P. (1983) *Basic ecology*. New York: CBS College Publishing.

Patil, G.P. and C. Taillie (1979) An overview of diversity. In *Ecological Diversity in Theory and Practice*, edited by J.F. Grassle, G.P. Patil, W.K. Smith, and C. Taillie. Fairland, Maryland: International Co-operative Publishing House.

Patil, G.P. and C. Taillie (1982) Diversity as a concept and its measurement. *Journal of the American Statistical Association* 77: 548-567.

Patrick, R. (1968) The structure of diatom communities in similar ecological conditions. *Amer. Natur.* 102: 173-183.

Pianka, E.R. (1983) *Evolutionary Ecology* (3rd ed.). New York: Harper & Row.

Pielou, E.C. (1966b) The measurement of diversity in different types of biological collection. *Journal of Theoretical Biology* 13: 131-144.

Pielou, E.C. (1975) *Ecological Diversity*. New York: Wiley.

Skutch, A.F. (1950) The nesting seasons of Central American birds in relation to climate and food supply. *Ibis* 92:185-222.

Taillie, C. (1979) Species equitability: a comparative approach. In *Ecological Diversity in Theory and Practice*, edited by J.F. Grassle, G.P. Patil, W.K. Smith, and C. Taillie. Fairland, Maryland: International Co-operative Publishing House.

Whittaker, R.H. (1965) Dominance and diversity in land plant communities. *Science* 147:250-260.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* 21:213-251.