

RAREFACTION, RELATIVE ABUNDANCE, AND DIVERSITY OF AVIAN COMMUNITIES

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ABSTRACT.—The common practice of expressing community structure in terms of indices of diversity and evenness involves a serious loss of information. Differences attributable to the accumulation of species with increasing area are ignored, differences in the density of individuals are often masked by other factors, and many combinations of species richness and relative abundance can produce the same value of the index. As an alternative we suggest (1) comparing species richness by standardizing samples either to equal numbers of individuals or to the number of individuals expected on equal-sized plots, and (2) expressing the relative abundance of species as a graph of their relative abundances arranged in a decreasing array. We present an analysis of bird census data based on the proposed methods, and we include comparisons with applications of four indices commonly used in ecology, the Shannon-Weaver index of diversity, the J' evenness index, the inverse of Simpson's measure of concentration, and Hill's evenness index.

For 37 Breeding Bird Censuses taken in various terrestrial habitats across the United States and Canada, the proposed methods reveal some very general relationships about the organization of bird communities in different habitats. Equal-sized areas of mature deciduous forest and second-growth habitats may be equally species rich (14–24 species with ≥ 1 breeding territory per 6 ha); the density of individuals (territorial pairs) is generally higher in deciduous forest habitats, and the relative abundance of bird species shows more dominance (less evenness) in the deciduous forest. Mixed coniferous-deciduous forests and dense young deciduous forests have fewer species than mature eastern deciduous forests or second-growth habitats (9–16 and 7–10 species per 6 ha, respectively), although the density of individuals is approximately equal to that in second-growth habitats. Coniferous forests are species-poor (5–8 per 6 ha), and the density of territorial pairs is low (8–12 per 6 ha compared with 40–70 in deciduous forests). Although the proposed methods require assumptions that need to be evaluated carefully, we are optimistic that they will have other useful applications in the analysis of avian communities. *Received 8 October 1980, accepted 15 April 1981.*

A large literature has developed in ecology presenting descriptive analyses of biotic assemblages (Dennis et al. 1979, Patil and Taille 1979). Although one should not infer mechanisms of community regulation from such studies (Pielou 1975), certain patterns recur in vertebrate communities in different habitats (Palmgren 1930, Udvardy 1957, MacArthur and MacArthur 1961, Williams 1964, MacArthur 1964, Karr and Roth 1971, Wiens 1973, Willson 1974), climates (Bock and Lepthien 1974, Rotenberry 1978), seasons (Rotenberry et al. 1979), and geographic areas (Pianka 1966, Recher 1969, Karr 1971, Tramer 1974, Cody 1975, Short 1979). One methodological problem with much of this literature and with community ecology generally since the early 1960's is the expression of community structure in terms of indices of diversity and evenness. Indices such as H' [$-\sum p_i \log p_i$] (Shannon and Weaver 1949, Margalef 1958) and J' [$H'/\log s$] (Pielou 1966a) confound important parameters that should be defined as precisely as possible and examined separately before communities are compared. These are (1) the number of species (species richness), (2) their relative abundance (evenness), (3) the number of individuals or territorial pairs, and (4) the area sampled. To combine any of these variables into a single statistic assures that the relative effects of the contributing parameters cannot be determined. The same value of the index can result from various com-

binations of values of the parameters (Pielou 1975). Here, we recommend that data be standardized to either equal numbers of individuals (in this case, territorial pairs) or equal-sized areas before comparisons are attempted. We propose that rarefaction and relative abundance curves be used as an alternative to diversity indices. In addition to clarifying components of biological interest, these methods avoid many of the mathematical deficiencies of the application of indices. We will examine the community structure of a large set of breeding bird censuses on the basis of the traditional methods and then present four graphic displays of the results of rarefactions (Figs. 1–3) and relative abundance curves (Fig. 4).

METHODS

Data set.—The data consist of 37 Breeding Bird Censuses taken between 1973 and 1977 in a variety of habitats in the United States and Canada (Table 1). The habitats include tundra, desert, coniferous forest, early successional second growth, and deciduous forest. The censuses, published in *American Birds*, were conducted by volunteer observers and are thus subject to individual variation. Nevertheless, the field procedures are clearly defined (Van Velzen 1972, Robbins 1978), and the Williams spot-map method of censusing breeding birds is recognized as one of the most reliable methods available (Svénsson and Williamson 1969, Enemar et al. 1978). The criteria for the selection of censuses were that at least 50 pairs of breeding birds be found in 6 or more hectares, that the census plots be surrounded by similar vegetation, and that the censuses as a set be representative of a wide variety of terrestrial habitats. We give the size of the study plot, the number of territorial pairs of birds, the number of species having at least one breeding territory on each plot, the number of species expected on plots of 6 ha [$E(S_{6ha})$] and its variance [$Var E(S_{6ha})$], the number of species expected in a sample of 50 territorial pairs [$E(S_{50})$] and its variance [$Var E(S_{50})$], the information theoretic diversity index H' [$-\sum p_i \log p_i$], the J' evenness index [$H'/\log s$], the inverse of Simpson's measure of concentration [$D = 1/\sum p_i^2$] (Simpson 1949, May 1975), Hill's (1973) evenness index [$D/\exp(H')$], and a habitat code (Table 1). Throughout this paper the number of individuals refers to the number of territorial pairs. A territory is usually defined by the consistent presence of a singing male, and it is taken to represent a territorial pair. Although the number of territories is substantially lower than the actual number of birds present, it is the standard unit in most terrestrial breeding-bird studies.

Rarefaction.—Rarefaction is a statistical method of estimating the number of species expected [$E(S)$] in a random sample of individuals taken from a census or collection. Given the number of individuals in each species for the census, one can calculate how many species would be expected in a smaller sample of n individuals (Sanders 1968; but see Hurlbert 1971; Fager 1972; Simberloff 1972, 1978, 1979; Heck et al. 1975). By means of a series of predictions for successively smaller numbers of individuals, a rarefaction curve can be defined for the community. A computer program for this procedure is in Simberloff (1978) and is also available from the authors. The method permits comparisons of the species richness among communities when the samples differ in total numbers of individuals (or, in this case, territorial pairs).

The expected number of species [$E(S_n)$] in a random sample of n individuals drawn without replacement from N individuals is given by

$$E(S_n) = \sum_{i=1}^S \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right],$$

where S is the total number of species found in the census and N_i is the number of individuals in species i (Hurlbert 1971). In the right-hand term the numerator is the number of ways that n individuals can be drawn from the census without drawing any individuals of species i , and the denominator is the total number of ways that n individuals can be drawn from N individuals. Hence, the right-hand term is the probability that a sample of n individuals will not include species i . The expected number of species in a random sample of n individuals is thus the summation of the probabilities that each species will be included in the sample. The variance in the number of species expected in a sample of size n is given by Heck and coauthors (1975). Smith and Grassle (1977) have warned that this is not an unbiased estimate

of the population variance, and they provide a rather complex algorithm for estimation of variance. As an alternative, Tipper (1979) recommends that the relative abundances of pairs of communities be compared directly by means of a two-sided Smirnov test. We give $E(S_n)$ and its variance as calculated by Heck and coauthors, and we test differences in species richness and density among communities in six different habitats by an analysis of variance.

In a census of an oak-beech forest in Maryland (Table 1, number 6), taken on 11.6 ha, there were 101 pairs of territorial birds. The distribution of the territories among the 24 species arranged in a decreasing array is:

17 13 12 7 7 6 6 4 3 3 3 2 2 2 2 2 2 1 1 1 1 1 1 1

(One territory was lost by rounding partial territories in the original report.) By rarefaction one can calculate the number of species expected in samples of successively smaller numbers of territories (Table 2). The resultant curve for this census is number 6 in Fig. 1. To compare this census with others on the basis of the number of species expected in a sample of a fixed number of territorial pairs, compare columns 11 and 12 in Table 1 giving the number of species expected in a sample of 50, $E(S_{50})$, and its variance, $Var E(S_{50})$, or examine Fig. 1 at the sample size of 50. With 101 individuals and 24 species distributed as above, one would expect 18.5 species in a sample of 50 territories.

Area.—Frequently, the question of interest is the characterization of a community occupying a given-sized area, even though the data are for different-sized areas. Species-area effects introduce a bias that is difficult to evaluate. The numbers of species observed in the 37 censuses (Table 1, column 5) should not be compared directly, because the numbers of individuals (column 4) and the areas (column 6) of the censuses vary substantially. One solution is to reduce the number of individuals on the larger plot to the number expected on a plot equivalent in size to the smaller plot; multiply the number of individuals on the larger plot by the area of the smaller plot divided by the area of the larger plot; then, by rarefaction, determine the number of species expected in the reduced sample. Thus, if the number of individual territories is reduced to the number expected on 6 ha (column 13), the size of the smallest sample, and then the number of species expected in samples of that size is calculated (column 14) by rarefaction, the communities can be compared. For instance, for the oak-beech community (number 6, Table 1) there were 24 species and 101 territories on 11.6 ha, so we expect approximately 52 territories on 6 ha. By rarefaction we calculate that in this community there will be 18.8 species in 52 territories, and we assume that this is approximately the number of species on 6 ha.

Relative abundance curves.—In looking for patterns among communities, it is important to define the relative distribution (evenness) of birds in addition to their species richness. The shape of rarefaction curves is a function of the relative abundances of the species, but a more direct approach is to examine either the cumulative proportions of individuals (Taille 1979) or the actual relative abundances. Because the patterns of relative abundances in different communities might be complex, we prefer their display to the calculation of a single statistic of evenness. We recommend the examination of plots of the logarithm of the relative abundances of the species arranged in a decreasing array. The logarithmic scale spreads out the less abundant species so that their relative abundances can be examined. On this type of graph the pattern of the relative abundances in a community having equal numbers of all the species present would be represented by a horizontal line. The extent of the deviation from a horizontal line is a function of the difference between this hypothetical case and the community in question. If the total number of individuals is given, the absolute abundances can be retrieved. May (1975) recommends the inclusion of the proportion of individuals in the most common species as a measure of dominance, and Whittaker (1965, 1972) and Hubbell (1979) use this statistic as an "importance value" for plant communities.

RESULTS

Indices.—For the set of 37 censuses, H' varies from 1.52 to 3.57 (Table 1). The large influence of species richness on H' is evident from the fact that the extreme values of H' are also the extreme values of species richness before standardization. Nevertheless, a given value of H' may result from a variety of combinations of species richness and evenness. Compare, for example, census numbers 1 and 28, having similar values of H' (2.71 and 2.70, respectively) but different species richness (19 and 25, respectively). In such a case we expect that the species-poor community (census number 1) will exhibit greater evenness. In fact, a 15-species com-

TABLE 1. Community statistics for 37 Breeding Bird Censuses taken in the United States and Canada in a wide variety of habitats.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|----|-------------------|----------------|--|-------------------|--------------------------|-----------|------|------|---|-------------------------------|-------------|-----------------|-----------|--------------|------------------|---------------------------|
| | State or province | Year of census | Census number in American Birds ^a | Territorial pairs | S ^b (species) | Area (ha) | H' | J' | $D = 1/2\bar{P}_i^2$ Inverse of Simpson's index | $D(\exp(H'))$ Hill's evenness | $E(S_{30})$ | $Var E(S_{30})$ | r_{gha} | $E(S_{gha})$ | $Var E(S_{gha})$ | Habitat code ^c |
| 1 | WV | 73 | 7 | 61 | 19 | 6.0 | 2.71 | 0.92 | 12.9 | 0.86 | 17.7 | 0.97 | 61 | 19.0 | 0.00 | DF |
| 2 | WV | 73 | 9 | 54 | 20 | 6.0 | 2.66 | 0.89 | 10.9 | 0.76 | 19.3 | 0.97 | 54 | 20.0 | 0.00 | DF |
| 3 | SA | 73 | 104 | 70 | 10 | 17.2 | 1.75 | 0.76 | 4.4 | 0.76 | 9.0 | 0.68 | 24 | 7.0 | 1.24 | DD |
| 4 | NY | 74 | 6 | 55 | 23 | 6.0 | 2.96 | 0.94 | 15.7 | 0.81 | 22.4 | 0.48 | 55 | 23.0 | 0.00 | DF |
| 5 | | | | | | | | | | | | | | | | |
| 6 | MD | 74 | 21 | 107 | 27 | 11.6 | 2.84 | 0.86 | 10.8 | 0.63 | 20.3 | 3.02 | 55 | 21.1 | 2.86 | DF |
| 7 | MD | 74 | 25 | 101 | 24 | 11.6 | 2.75 | 0.87 | 11.8 | 0.74 | 18.5 | 2.68 | 52 | 18.8 | 2.60 | DF |
| 8 | TX | 74 | 48 | 215 | 23 | 24.8 | 2.57 | 0.82 | 8.8 | 0.69 | 15.1 | 2.72 | 52 | 15.3 | 2.72 | DF |
| 9 | MN | 74 | 61 | 50 | 14 | 12.0 | 2.26 | 0.86 | 7.3 | 0.76 | 14.0 | 0.00 | 25 | 10.5 | 1.61 | CD |
| 10 | PA | 75 | 8 | 68 | 21 | 6.0 | 2.71 | 0.89 | 11.6 | 0.78 | 18.6 | 1.56 | 68 | 21.0 | 0.00 | DF |
| 11 | WV | 75 | 11 | 61 | 15 | 6.0 | 2.14 | 0.79 | 6.8 | 0.72 | 13.8 | 0.86 | 61 | 15.0 | 0.00 | DF |
| 12 | WV | 75 | 16 | 60 | 21 | 6.0 | 2.67 | 0.88 | 10.6 | 0.73 | 19.3 | 1.14 | 60 | 21.0 | 0.00 | DF |
| 13 | CA | 75 | 109 | 80 | 9 | 12.0 | 1.69 | 0.77 | 3.7 | 0.69 | 8.6 | 0.31 | 40 | 8.2 | 0.57 | DD |
| 14 | BC | 75 | 132 | 89 | 14 | 19.2 | 2.07 | 0.79 | 5.4 | 0.68 | 12.0 | 1.23 | 28 | 9.5 | 1.79 | DD |
| 15 | BC | 75 | 133 | 109 | 25 | 16.0 | 2.73 | 0.85 | 10.5 | 0.69 | 18.4 | 2.91 | 41 | 16.8 | 3.02 | DF |
| 16 | BC | 75 | 140 | 76 | 25 | 18.0 | 2.96 | 0.92 | 14.3 | 0.76 | 21.5 | 2.01 | 25 | 15.1 | 2.63 | CD |
| 17 | NC | 76 | 33 | 90 | 23 | 12.4 | 2.90 | 0.93 | 15.6 | 0.84 | 19.9 | 1.74 | 44 | 19.0 | 2.20 | DF |
| 18 | MA | 76 | 57 | 55 | 27 | 11.6 | 3.04 | 0.92 | 16.5 | 0.79 | 25.5 | 0.95 | 28 | 17.8 | 2.75 | SG |
| 19 | PA | 76 | 61 | 50 | 14 | 8.0 | 2.05 | 0.78 | 4.4 | 0.57 | 14.0 | 0.00 | 38 | 12.7 | 0.88 | CD |
| 20 | | | | | | | | | | | | | | | | |
| 21 | OH | 76 | 83 | 122 | 38 | 28.0 | 3.40 | 0.93 | 24.3 | 0.81 | 26.9 | 3.99 | 26 | 18.2 | 3.12 | SG |
| 22 | CA | 76 | 131 | 68 | 17 | 16.8 | 2.33 | 0.82 | 6.7 | 0.65 | 15.3 | 1.13 | 24 | 10.8 | 2.16 | DF |
| 23 | CA | 76 | 132 | 86 | 14 | 17.2 | 1.92 | 0.73 | 4.5 | 0.66 | 11.3 | 1.53 | 30 | 9.0 | 1.94 | CD |
| 24 | MD | 77 | 24 | 100 | 28 | 12.0 | 2.91 | 0.87 | 12.7 | 0.69 | 20.8 | 3.15 | 50 | 20.8 | 3.15 | DF |
| 25 | NC | 77 | 28 | 103 | 21 | 12.8 | 2.67 | 0.88 | 11.6 | 0.80 | 16.4 | 2.13 | 48 | 16.2 | 2.16 | DF |
| 26 | CT | 77 | 62 | 109 | 24 | 14.0 | 2.67 | 0.84 | 10.3 | 0.72 | 17.3 | 3.01 | 47 | 16.8 | 3.03 | SG |
| 27 | OH | 77 | 72 | 133 | 43 | 28.0 | 3.57 | 0.95 | 30.1 | 0.85 | 29.3 | 4.44 | 28 | 20.3 | 3.25 | SG |
| 28 | OK | 77 | 91 | 135 | 35 | 40.0 | 3.18 | 0.89 | 18.1 | 0.75 | 23.4 | 4.06 | 20 | 13.7 | 2.71 | SG |
| 29 | CO | 77 | 92 | 173 | 27 | 9.6 | 2.70 | 0.82 | 9.4 | 0.63 | 17.8 | 3.43 | 108 | 23.9 | 2.05 | DF |
| 30 | CO | 77 | 93 | 163 | 23 | 51.6 | 2.09 | 0.67 | 4.7 | 0.58 | 13.2 | 3.27 | 19 | 7.7 | 2.44 | DF |
| | CO | 77 | 99 | 62 | 24 | 13.8 | 2.90 | 0.91 | 13.7 | 0.75 | 22.0 | 1.31 | 22 | 15.9 | 2.51 | CD |

TABLE 1. Continued.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|----|-------------------|----------------|--|-------------------|--------------------------|-----------|------|------|---|-----------|-----------------|---------------------|------------------|----------------------|--------------------------|---------------------------|
| | State or province | Year of census | Census number in American Birds ^a | Territorial pairs | S ^b (species) | Area (ha) | H' | J' | D = $\frac{1}{\sum p_i^2}$ Inverse of Simpson's index | D/exp(H') | Hill's evenness | E(S ₉₀) | n _{90a} | E(S _{90a}) | Var E(S _{90a}) | Habitat code ^c |
| 31 | NM | 77 | 104 | 66 | 19 | 36.5 | 2.69 | 0.91 | 12.2 | 0.83 | 17.4 | 1.11 | 11 | 8.0 | 1.31 | C |
| 32 | UT | 77 | 105 | 80 | 11 | 60.0 | 1.94 | 0.81 | 6.0 | 0.82 | 9.8 | 0.80 | 8 | 4.6 | 0.90 | C |
| 33 | CA | 77 | 106 | 63 | 20 | 10.4 | 2.74 | 0.91 | 11.9 | 0.79 | 18.4 | 1.10 | 36 | 16.2 | 1.88 | CD |
| 34 | CA | 77 | 110 | 54 | 11 | 27.2 | 2.00 | 0.84 | 5.4 | 0.73 | 10.8 | 0.14 | 12 | 6.2 | 1.27 | C |
| 35 | UT | 77 | 123 | 58 | 17 | 16.0 | 2.73 | 0.96 | 14.0 | 0.92 | 16.8 | 0.20 | 22 | 12.8 | 1.58 | CD |
| 36 | CA | 77 | 137 | 62 | 8 | 19.8 | 1.52 | 0.73 | 3.1 | 0.75 | 7.8 | 0.16 | 19 | 5.6 | 1.10 | DT |
| 37 | AL | 77 | 168 | 69 | 11 | 24.7 | 2.01 | 0.84 | 5.5 | 0.74 | 10.5 | 0.41 | 17 | 7.3 | 1.32 | T |

^a Published in *American Birds*, volumes 27(6), 28(6), 29(6), 31(1), 32(1).

^b Number having a minimum of one territory.

^c C Coniferous; CD Coniferous-Deciduous; DD Dense deciduous; DF Deciduous forest; DT Deciduous forest; T Tundra.

^d Census 77-92 had 42 Great Blue Herons and 26 House Wrens; census 77-93 had 58 House Wrens and 45 Starlings with a 16% increase in total individuals from the previous year.

TABLE 2. Results of rarefaction^a of a census taken in an oak-beech forest in Maryland having 101 territorial pairs of birds and 24 species (Table 1, number 6). The calculations predict the number of species $E(S)$, and its variance $Var E(S)$, in successively smaller samples of territorial pairs, n .

| n | $E(S)$ | $Var E(S)$ |
|-----|--------|------------|
| 100 | 24.00 | 0.00 |
| 95 | 23.57 | 0.38 |
| 90 | 23.17 | 0.69 |
| 85 | 22.74 | 0.98 |
| 80 | 22.27 | 1.27 |
| 75 | 21.76 | 1.55 |
| 70 | 21.21 | 1.81 |
| 65 | 20.61 | 2.06 |
| 60 | 19.96 | 2.50 |
| 55 | 19.25 | 2.50 |
| 50 | 18.47 | 2.68 |
| 45 | 17.62 | 2.82 |
| 40 | 16.68 | 2.91 |
| 35 | 15.64 | 2.95 |
| 30 | 14.46 | 2.91 |
| 25 | 13.12 | 2.77 |
| 20 | 11.56 | 2.50 |
| 15 | 9.68 | 2.05 |
| 10 | 7.35 | 1.37 |
| 5 | 4.29 | 0.52 |

^a Individuals index in Smith and Grassle (1977).

munity with maximum evenness (equal abundances of all species) would also have an H' of 2.71. It is impossible to sort out the relative importance of species richness and evenness if only the H' values are known.

Indices of evenness have traditionally involved ratios of a diversity statistic to the maximum diversity value that the community would have if all species had equal abundances. To obtain J' , for example, H' is divided by $max H'$ (=log number of species). But this may not be appropriate. Consider two hypothetical communities with the following distributions arranged in an increasing array:

Community 1: 1 2 4 8 16
 Community 2: 1 2 4 8 16 32 64,

in which each species is twice as abundant as the previous species. Here, by definition, the communities have equal evenness. The H' of Community 2 is higher (1.34) than that of Community 1 (1.24) as expected, but the values of J' are not equal (Community 1, $J' = 0.77$; Community 2, $J' = 0.69$). In cases like this, in which the evenness is exactly the same but the communities differ in the number of species, J' is not a reliable index to evenness.

Indices of diversity and evenness are not intended to characterize communities on the basis of area, but their application often leaves the implication that they do. As an example of the ambiguities that can result, compare census numbers 2, 8, 31, and 33 (Table 1), having similar values for the number of species observed (19–23) and H' (2.57–2.74) but taken on different-sized areas (6.0–36.5 ha). In this set, the species richness, H' and J' values increase together. The omission of consideration of the areas occupied results in similar values of H' for the piñon pine-juniper stand in New Mexico (number 31), with 19 species in 66 territories ($H' = 2.69$), and a tulip tree-beech-hickory forest in West Virginia (number 2), with 20 species in 54 territories ($H' = 2.66$). But when standardized to areas of 6 ha, the former has an expected species richness of 8 and the latter of 20.

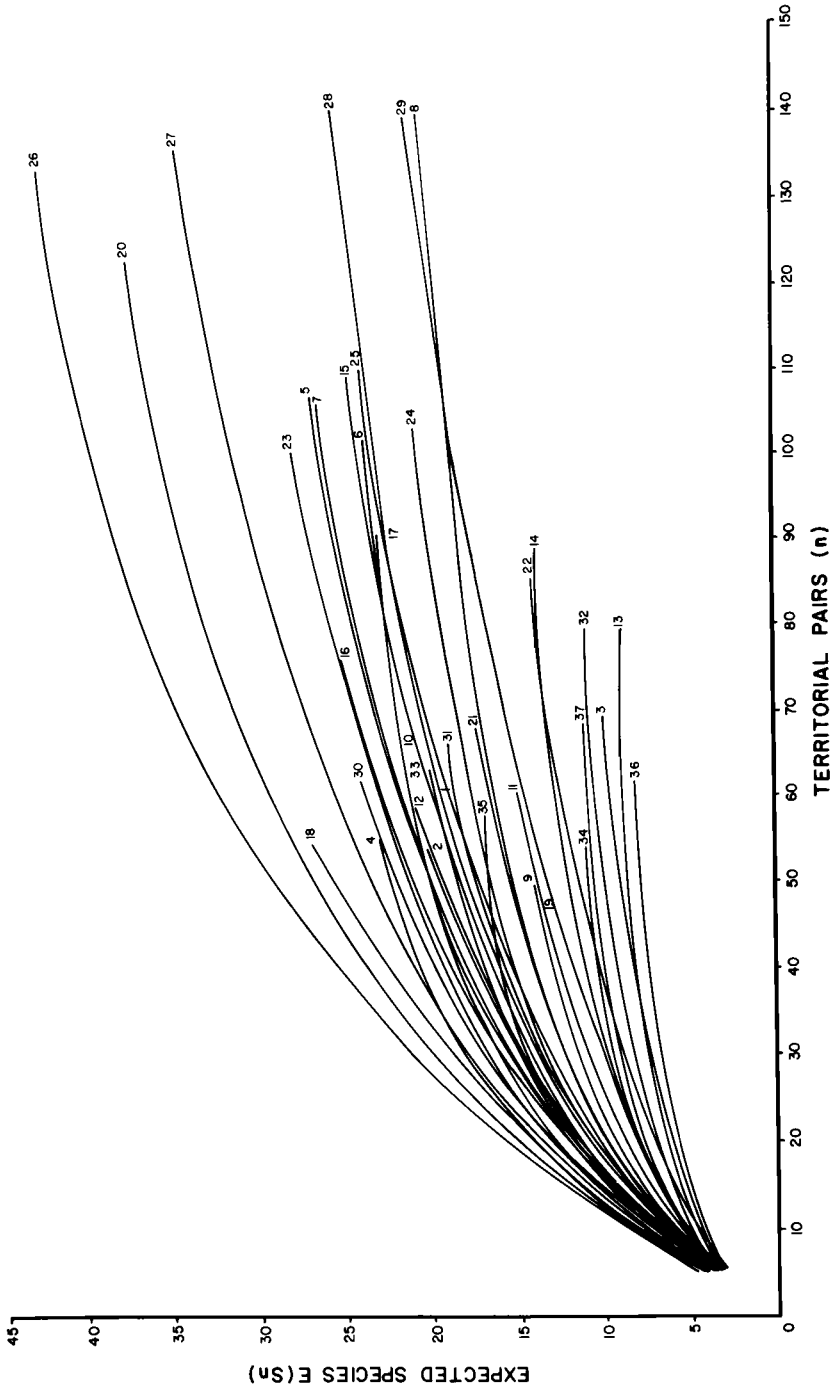


Fig. 1. Rarefaction curves for 37 censuses (Table 1) predict the rate of accumulation of species with increasing number of individuals (territorial pairs) from data for the abundance of each species in the original sample.

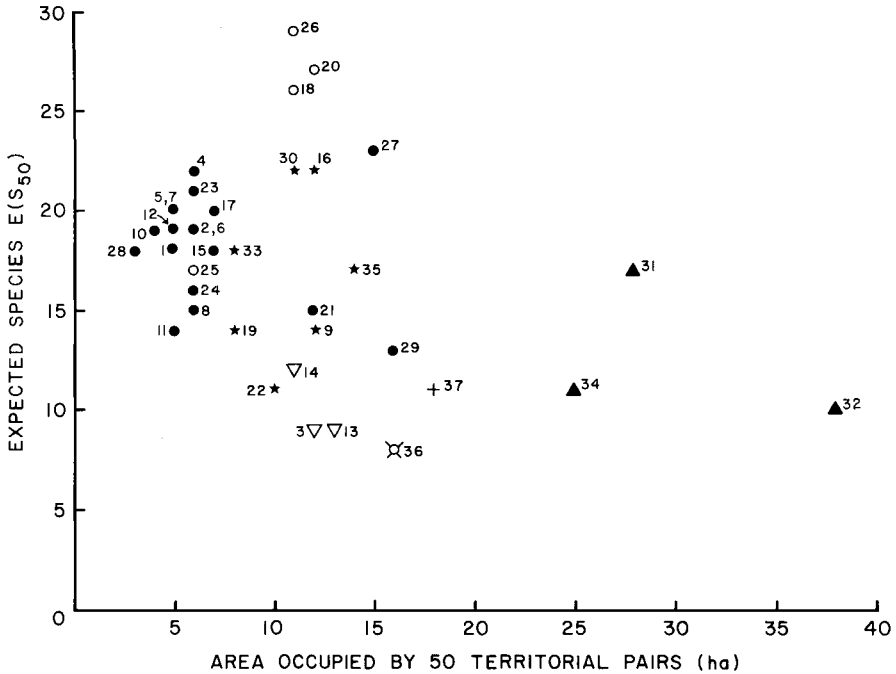


Fig. 2. Standardization of bird census results (Table 1) to the number of species expected in a sample of 50 territorial pairs, $E(S_{50})$, and to the area they would occupy. The habitat codes are: second growth, open circles; deciduous forest, closed circles; coniferous-deciduous, stars; coniferous, closed triangles; young dense deciduous, open triangles; desert, open circle with spines; tundra, plus sign. The area they would occupy is estimated by multiplying the area censused by the fraction 50/total territorial pairs.

The inverse of Simpson's index varies in our data set from 3.1 to 30.1, the extremes being the same censuses as the extremes of H' , species richness on plots of various sizes, and species in a fixed number of individuals. But again these are not the extremes of either the number of individuals or the number of species when the differences in plot size are taken into account (Table 1, columns 14 and 15). Hill's evenness index varies from 0.57 to 0.92. As a compound of Simpson's index and H' , it is subject to all of the criticisms above.

Rarefaction curves.—The species richness of the 37 censuses can be compared in terms of the number of species expected in a fixed number of territorial pairs by moving vertically through Fig. 1 at any fixed number. Thus for $n = 50$, $E(S_{50})$ can be taken as a standard (columns 11 and 12, Table 1) and used to order the censuses in terms of species richness (see also the ordinate of Fig. 2).

One striking result of an examination of the rarefaction curves is that second-growth habitats (numbers 18, 20, 26, 27) have the highest curves. This means that species richness per fixed number of territorial pairs is highest in these habitats. Habitats at the other extreme (low species richness) are desert (number 36), tundra (number 37), dense deciduous stands (numbers 3, 13), and coniferous forest (numbers 32, 34). The overall differences in species richness among six habitats (column 16, Table 1, omitting numbers 36 and 37 and splitting DF into 12 eastern and 6 western deciduous forests) are statistically significant ($F = 8.27$; $df = 5, 29$; $P < 0.01$). We have not made pairwise comparisons, but the SPSS least significant difference pro-

cedure identifies the habitats in increasing order of $E(S_{50})$ as DD, C, CD, WDF, EDF, and SG.

Not only do the curves provide estimates of the number of species expected in successively smaller samples, but the shape of the curves is a graphic display of relative estimated species accumulation rates. The relative evenness of sets of communities can be compared by examination of the steepness of the curves and whether they cross. In cases of crossing, there is no sense in which the intrinsic diversity of one community exceeds the diversity of the other (but see Patil and Taille 1979). Census numbers 4, 17, 31, and 35 appear to have generally steeper rarefaction curves, indicating generally higher evenness compared with most other communities, whereas census numbers 22 and 29 have relatively lower evenness.

Species richness and density.—The result above can be extended to include the effects of density by plotting the number of species expected in a sample of 50 territories against the area that would be occupied by this number (Fig. 2). The bivariate plot can be considered as a two-dimensional ordination of species richness in terms of a fixed sample of individuals on the vertical axis and their density on the horizontal axis. The various habitats represented fall into surprisingly clear patterns. In order of generally increasing species richness, the habitats are desert (7.8), dense deciduous (8.6–12.0) and/or tundra (10.5), coniferous-deciduous (11.3–22.0) or deciduous (13.2–22.4), and second growth (17.3–29.3). With regard to increasing density of individuals, the order of area occupied by 50 pairs of birds from right to left in Fig. 2 is generally coniferous (up to 38 ha), tundra and desert (16–18 ha), second-growth (11–15 ha), coniferous or mixed coniferous/deciduous (8–14 ha), and deciduous forest (3–13 ha).

To summarize, in these data second-growth forests have the highest species richness per sample of a fixed number of individuals (lowest dominance), but deciduous forests have the most individuals per unit area. The density of birds per unit area in coniferous-deciduous forests is not always lower than that of deciduous forests. Pure coniferous stands have the lowest densities of any habitats examined, but their species richness per fixed number of territorial pairs is not lower than that of dense deciduous, desert, or tundra habitats.

Another way to display the species richness of bird communities in terms of the density of individuals in various habitats is to standardize species richness and density to the values expected on equal-sized areas. This procedure requires the assumption that the distribution of the territorial pairs is sufficiently homogeneous that interpolations of the original density to plots of reduced size give reasonably accurate estimated densities. We know intuitively that birds are not regularly distributed in space even in relatively uniform habitats. The amount of bias introduced needs to be evaluated. We will assume for the present analysis that the bias introduced by the assumption of regular distribution will not obscure general patterns. Of course, if samples had been obtained from equal-sized plots, the interpolations would not be necessary. We have reduced the number of individuals (territorial pairs) to the number expected on 6 ha (column 13, Table 1), calculated the number of species expected in samples of that size and its variance (columns 14 and 15), and plotted the results in Fig. 3. Several interesting patterns can be detected. For a fixed area (6 ha), the general relationship is one of regular increase in species and individuals from coniferous forests, desert, and tundra toward coniferous-deciduous and then deciduous forests ($r = 0.77$, $P < 0.01$). (The floodplain area in Colorado (num-

ber 28) contained a rookery of Great Blue Herons and probably should not be compared directly with the other censuses.) Riparian deciduous forests (numbers 21, 27, 29) in the western states have substantially fewer individual birds than other deciduous forests, even those with young dense vegetation (numbers 3, 13, 14). The more heterogeneous upland second-growth habitats have fewer individuals per unit area than deciduous forests, but they are equally species rich. The overall differences in species richness and density among six habitats (column 16, Table 1; omitting numbers 36 and 37 and splitting DF into 12 eastern and 6 western deciduous forests) are statistically significant [$E(S_{6ha})$: $F = 14.83$; $df = 5, 29$; $P < 0.01$; n_{6ha} : $F = 5.86$; $df = 5, 29$; $P < 0.01$]. Again, we have not made all pairwise comparisons, but the SPSS least significant difference procedure identifies the habitats in increasing order of $E(S_{6ha})$ as C, DD, CD, WDF, SG, and EDF, and of n_{6ha} as C, CD, DD, SG, WDF, and EDF.

Relative abundance curves.—Rarefaction can be used to examine the evenness (or its counterpart, dominance) of the distribution of species in assemblages by comparing the steepness of the curves. But a more direct way is to depict relative abundances directly. We present eight relative abundance curves (Fig. 4a–h) in order of increasing species richness per 50 pairs of birds. The objective is to examine relative abundances independently of species richness or density. For these censuses second-growth habitats have the least dominance (highest evenness). The hardwoods-pine-second-growth-meadow (g) and mixed forest-thickets-meadow (h) have the highest evenness. These very mixed habitats may appear to be more evenly assembled because of the inclusion of subhabitats, each of which may have contributed its own dominants. The wax myrtle (a), birch-poplar (b), and arctic tundra (c) have more steeply declining curves. The high relative abundances of the first-ranked species are indicative of generally high dominance patterns in these communities, and the general steepness of the curves indicates low evenness. The fact that species richness also increases from a to h in Fig. 4 indicates that species-rich bird communities have generally lower dominance patterns than species-poor communities. The interpretation of relative abundance curves may be difficult when samples are small because the absence of some rarer species causes a truncation of the curve, making it impossible to determine the shape of the full spectrum of relative abundances. Nevertheless, the differences between species-rich and species-poor communities are not attributable to sampling but rather to real differences in the organization of the communities.

DISCUSSION

One of the alternatives to the applications of indices to species distributions is to fit a particular statistical distribution to the data. This approach is probably not advisable (Hurlbert 1971, Poole 1974), although the recurrence of a seeming log-normal distribution (Preston 1960, 1962) is certainly of interest. The choice of a distribution is difficult, and the assumptions underlying the various choices are rarely met. But to retreat to single nondimensional indices is not a good solution (May 1975). In addition to the fact that it confounds variables that are important to an understanding of community structure, the mathematical properties of the indices are often disregarded (Peet 1974, 1975; Poole 1974; Pielou 1975; Southwood 1978). H' is appropriate only for obtaining the average diversity of a population from a very large random sample (Pielou 1966a, b, c; Bowman et al. 1971). Estimates

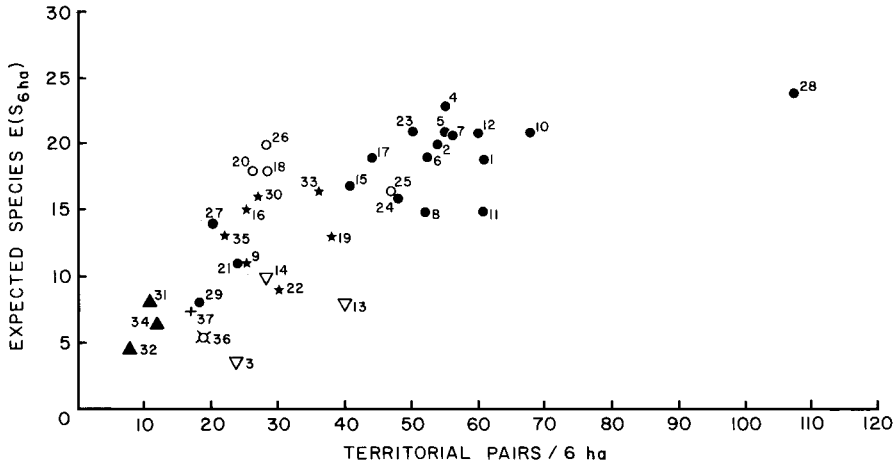


Fig. 3. The number of territorial pairs and species of birds (Table 1) expected on 6 ha (15 acres). Symbols as in Fig. 2.

of H' (Hutcheson 1970, Routledge 1980) reduce some of the bias, but both H' and J' have been shown to be especially sensitive to rare species and this effect varies with sample size (Fager 1972; Tramer 1969; Peet 1974, 1975; Poole 1974). Many ecologists have abandoned information theoretic indices on the basis of their mathematical deficiencies and their dubious biological meaning (Hurlbert 1971, Poole 1974, Goodman 1975, Taylor 1978, Green 1979).

Because they have been applied recently in ecological research (for example, Rotenberry et al. 1979), we have considered two of the several other indices that are available (McIntosh 1967; Pielou 1966a, b, c; Whittaker 1972; Brower and Zar 1977), the inverse of Simpson's measure of concentration and Hill's index. These measures, or more appropriately estimates of them (Simpson 1949, Good 1953, Routledge 1980), avoid some of the biases mentioned above but still confound species richness and evenness and are affected by species/area effects in that larger samples will have more species (Sheldon 1969, May 1975, Connor and McCoy 1979). Unless an index has a specific biological interpretation independent of its parameters, we do not see that it adds to the understanding of community structure. It is not possible to say more than one thing with one number.

Simpson's index and the rarefaction method are related. The expected number of species found by rarefaction of a sample of two (individuals or territories) is 2 minus Simpson's measure of concentration. And Simpson's index is heavily dependent upon the relative abundance of the more abundant species. Rarefaction to samples larger than two is less dependent on the more abundant species (Smith and Grassle 1977). The advantages of rarefaction over Simpson's index, or its sample estimate, are that (1) rarefaction gives a more easily interpretable value (in terms of species units rather than a nondimensional number); (2) rarefaction provides entire curves by which communities can be compared; and (3) in cases in which the data are for different-sized areas, one can use rarefaction to compare communities in terms of density.

In order to satisfy the mathematical properties of the rarefaction method as applied to density, one must assume that the territories are regularly distributed in space. This is certainly not so. Deviation attributable to responses by birds to within-

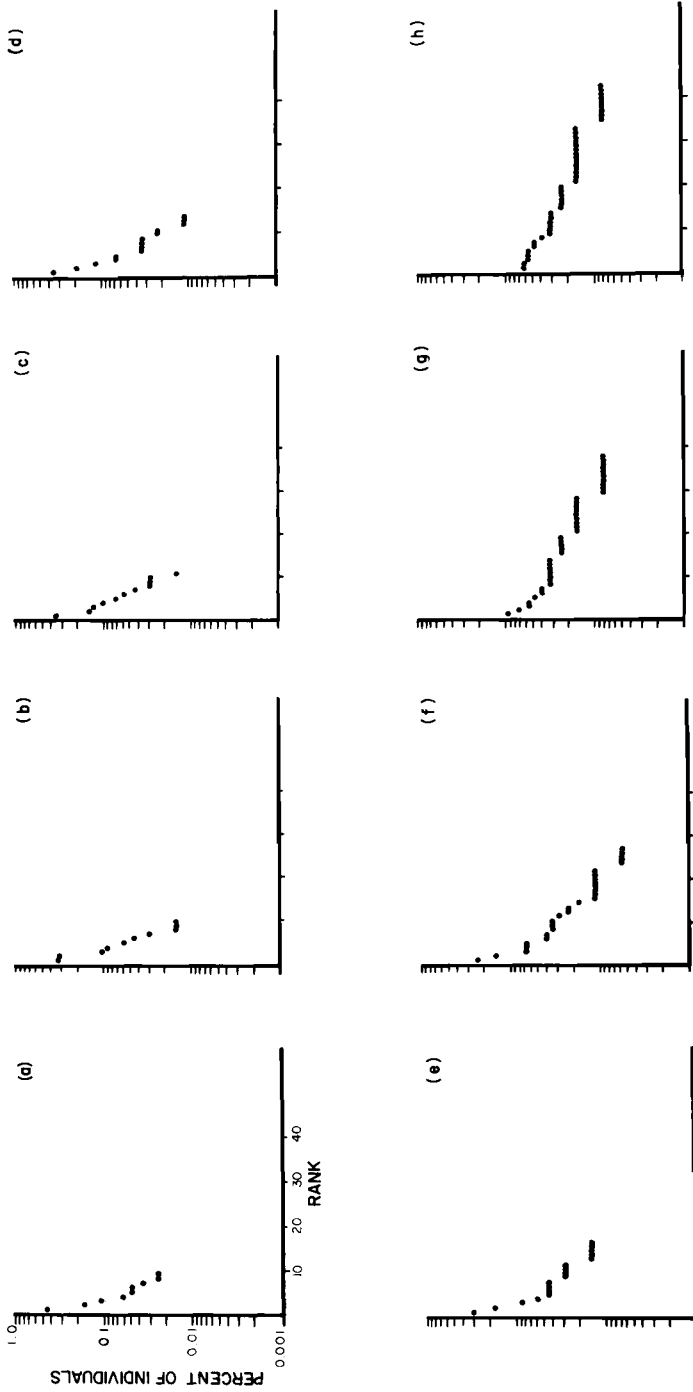


Fig. 4. Relative abundance curves for which the ordinate is the percentage of the total individuals plotted on a logarithmic scale and the abscissa is the rank from the most common to the least common species. The order is (a) wax myrtle, census 13 in Table 1, having $E(S_{50}) = 8.6$; (b) birch-poplar, 3, 9.0; (c) arctic tundra, 37, 10.5; (d) aspen-willow, 14, 12.0; (e) sycamore-alder, 21, 15.3; (f) floodplain with dead cottonwoods, 28, 17.8; (g) mixed hardwoods-pine-second growth-meadow, 20, 26.9; (h) mixed forest-thickets-meadow, 26, 29.3.

habitat variation in vegetation structure, the social organization of the populations, and related factors are important and need to be evaluated. Spatial aggregations cause overestimation of the number of species. In addition, rarefaction curves are not the same as species accumulation rates or relative abundance curves. Fager (1972) and Tipper (1979) discuss this problem and propose the analysis of replicate samples. Future work on local, seasonal, and annual variability and evaluations of the bias incurred by the assumptions of the method are needed. Engstrom and James (1981) show that, even in an apparently uniform habitat, subplot variation in both vegetation structure and avian community structure may be very great. Nevertheless, rarefaction gave good estimates of average species accumulation rates.

Data from breeding bird surveys or mist-net captures should be standardized in terms of either equal field effort or equal numbers of individuals. Certain kinds of point-count data (Blondel et al. 1973, Järvinen 1978a) and transect counts (Järvinen 1978b) can be used to estimate densities. These, or data from areal samples such as the data presented in Table 1, can be standardized to either equal numbers of individuals or to equal-sized areas. The decision should be made on the basis of the objectives of the project. James and Wamer (in press) used both in an analysis of bird communities in relation to the vegetation structure of forests. Even if two censuses are taken on equal-sized areas, it will still be valuable to examine their full rarefaction curves.

We agree with Hurlbert (1971) that "whether two areas differ in species evenness and whether they differ in density are best treated as independent questions." The evenness component of diversity is best characterized by an examination of its full distribution. Although an index to evenness sounds appealing, any reduction of the complex curves of relative abundances obscures potentially interesting biological information. Even then, one should be cautious about interpreting relative abundance curves. In our data, for equal-sized samples of individuals, species-rich communities seem to have less dominance than species-poor communities. But as sample size increases, new species are added and abundance curves lengthened. Although the shape of the initial part of the curve should not change greatly, the general appearance of the curve may change with the relative abundances of the later additions. For example, a steeply sloping curve [such as (a) in Fig. 4] might extend into a more gently sloping curve as additional individuals are censused. If sample size is insufficient there is no means to determine the shape of the latter portion of the curve. We refrain from concluding that biological interactions are more important in communities having steeper curves or that some species are more important than others, although similar results have been so interpreted in the past (MacArthur 1957, 1960; McNaughton and Wolf 1970).

In summary, comparing avian communities in terms of nondimensional indices masks interesting differences in species richness, relative abundance, and density. We recommend that communities be compared on the basis of either equal numbers of individuals or equal-sized areas and that they be analyzed first by the examination of rarefaction curves (Fig. 1) and relative abundance curves (Fig. 4). Neither involves differences in density, but our Figs. 2 and 3 are methods of standardizing community data in terms of density. The properties of rarefaction, the bias incurred by assuming that individuals are distributed evenly (or even that patch size is homogeneous; see Underwood in press), and the problem of defining relative abundance curves in species-poor communities all need further study. But we think that the proposed methods are the best presently available for the characterization of

community structure. Rarefaction has been useful in marine biology (Antia 1977) and paleontology (Raup 1975). For applications in ornithology see Simberloff (1978), Taille (1979), Engstrom and James (in press), and James and Wamer (in press). Relative abundance curves have been useful in plant ecology (dominance diversity curves of Hubbell 1979; Whittaker 1965, 1972). We foresee many other applications to synecological questions about the distribution and abundance of birds. Given standard field procedures, it would be interesting to examine patterns of variation among other habitats, among years, seasons, or geographic areas, or to consider the relative importance of species in terms of biomass and productivity.

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