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BIRD SPECIES DIVERSITY: COMPONENTS OF SHANNON'S FORMULA

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Abstract. Shannon's diversity index $H' = \sum p_i \log_2 p_i$ was calculated for 267 breeding bird censuses. The index was resolved into its components, species richness and relative abundance, to determine which components played a larger role in the determination of diversity patterns. Changes in diversity were correlated closely with species richness ($r = 0.972$), while the relative abundance component remained stable. Among the nine community types represented, diversity and species richness increased with the foliage height diversity. The relative abundance component was strikingly low in the marshes due to the presence of gregarious birds which nest in colonies and feed outside the community. Phytoplankton differ from birds in that the relative abundance component is not stable from one collection to the next. This is attributed to differences in the environmental uncertainty encountered by the two groups, plankton inhabiting relatively uncertain environments and being "opportunistic," while birds occupy predictable environments and are therefore "equilibrium" species. The distribution of relative abundances in birds is more even than in trees, herbaceous-shrub communities, or phytoplankton. Since this is in part the result of intraspecific territoriality, it is predicted that in nonbreeding bird populations, species' relative abundances will be less even than they are during the breeding season. It is suggested that the regulation of diversity by either the species richness or relative abundance components represent alternative strategies which are suited to predictable/nonrigorous and unpredictable/rigorous environments, respectively. Therefore, differences similar to those observed between birds and phytoplankton might be expected in other groups of organisms.

INTRODUCTION

To describe species diversity in natural communities, ecologists have made widespread use of Shannon's function (Shannon and Weaver 1963). This expression is

$$H' = - \sum_{i=1}^S p_i \log_2 p_i \quad (1)$$

where p_i is the proportion of individuals in the i th species ($i = 1, 2, \dots, S$). Lloyd and Ghelardi (1964) have pointed out that this measure has two separate components, species richness and the "equitability" or "evenness" of species abundances. Species richness is simply S , the number of species in the sample. Several expressions have been employed to measure the relative abundance component: here we will use the index

$$J' = H'/H'_{\max} \quad (2)$$

in which H'_{\max} is $\log_2 S$. This index represents the ratio of the observed diversity to the maximum diversity possible for the same number of species. It has a maximum value of unity when all species are equally abundant, while the minimum value is defined by the situation in which all species save the most abundant are represented by only one individual; the more individuals in the sample, the closer J'_{\min} approaches zero.

Since the components of the Shannon formula can vary independently of one another it is obvious that two samples having identical H' values may in fact be very different. Therefore, I resolve the formula into its components when analyzing diversity patterns.

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The purpose of this paper is to present evidence that in breeding bird populations diversity patterns are strongly correlated with variation in the species richness component, the relative abundance component being relatively stable. Furthermore, it will be shown that in most communities the distribution of species abundances in breeding bird populations is unusually even. Some ecological implications of these findings are discussed, particularly regarding the relative effects of the two components on diversity patterns in various types of organisms.

PROCEDURES

Most of the 267 breeding bird censuses used in this study were taken from Audubon Field Notes (1937-1966; formerly Bird Lore and Audubon Magazine). Other sources were Odum (1950), Johnston and Odum (1956), Cody (1966), MacArthur, Recher, and Cody (1966), and seven censuses conducted by the author on forested mountain watersheds at the Coweeta Hydrologic Laboratory near Franklin, N. C. The data included here represent only a fraction of the total number of censuses reported in Audubon Field Notes. This is because many of the censuses in that journal are of heterogeneous vegetation stands or of tracts containing more than one habitat; homogeneity of vegetation structure was the primary criterion applied in the selection of censuses for use here. In addition, tracts censused in more than one year were used only the first time they appeared in the journal. Complete lists of the censuses used are available from the author.

Values of H' and J' were determined for each census and a regression of H' against the logarithm of the num-

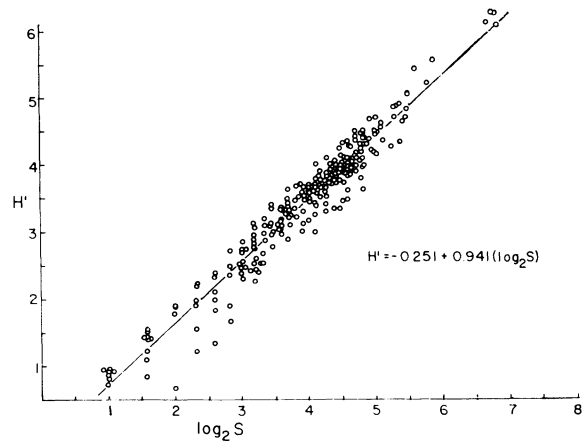


FIG. 1. Regression of diversity, $H' = -\sum p_i \log_2 p_i$, against the logarithm of number of species for 267 breeding bird populations.

ber of species was then calculated. The censuses were then divided among the following nine community types: marshes, grasslands (including early successional fields), shrublands (including overgrown fields), deserts, coniferous forests, mixed (hardwood-coniferous) forests, upland deciduous forests, floodplain deciduous forests, and tropical woodlands. Means and two standard errors of the mean of H' , S , and J' were calculated for each community type.

RESULTS

The regression of H' against $\log_2 S$ (Fig. 1) shows that changes in diversity are closely correlated to variations in species richness. The relationship is expressed by the equation

$$H' = 0.941 (\log_2 S) - 0.251.$$

The data show extremely close fit to the linear form ($r = 0.972$). Since the slope of the regression is $H'/\log_2 S = H'/H'_{\max} = J'$ [formula (2)] the figure demonstrates the stability of the relative abundance component as well as the correlation between H' and species richness.

Table 1 shows means \pm two standard errors of H' , S , and J' for the nine community types (arranged in order of increasing H'). Trends in H' and S from one community to the next are identical (marshes have lower mean H' and higher mean S than grasslands, but these differences are not statistically significant). Marshes and, to a lesser degree, grasslands and shrublands, have somewhat lower mean J' than the temperate zone forest types, while tropical woodlands are slightly higher.

TABLE 1. Means \pm 2 standard errors of H' , S , and J' for breeding bird populations in nine community types. n = number of censuses in sample; $H' = -\sum p_i \log_2 p_i$; S = number of species; $J' = H'/\log_2 S$

Community	<i>n</i>	<i>H'</i>	<i>S</i>	<i>J'</i>
Marshes.....	15	1.79 \pm 0.34	6.33 \pm 1.32	0.718 \pm 0.080
Grasslands.....	38	1.93 \pm 0.24	5.74 \pm 1.00	0.842 \pm 0.034
Shrublands.....	26	3.14 \pm 0.16	14.08 \pm 2.31	0.848 \pm 0.024
Deserts.....	6	3.25 \pm 0.60	14.17 \pm 5.68	0.884 \pm 0.048
Coniferous forests.....	51	3.53 \pm 0.14	17.43 \pm 1.92	0.880 \pm 0.014
Upland deciduous forests.....	62	3.82 \pm 0.08	20.94 \pm 1.34	0.879 \pm 0.012
Mixed forests.....	30	3.92 \pm 0.14	21.87 \pm 2.76	0.893 \pm 0.016
Floodplain deciduous forests.....	18	4.07 \pm 0.16	24.22 \pm 2.84	0.898 \pm 0.020
Tropical woodlands.....	21	5.23 \pm 0.24	55.14 \pm 11.24	0.921 \pm 0.012

DISCUSSION

An obvious consequence of the results is that in a given community, breeding bird diversity can be adequately described by merely counting the number of species present; i.e., their relative abundances can be disregarded. Therefore, we can conclude that the factors which regulate bird species diversity do so by determining the number of species which can coexist in a given habitat.

MacArthur and MacArthur (1961) showed that in temperate regions, bird species diversity is correlated to foliage height diversity. That is, diversity increases with the number of layers in the vegetation and with the evenness of foliage apportionment among the layers. Applying this relationship to the data in Table 1, we find that marshes and grasslands (one-layered) are less diverse than shrublands and deserts (essentially two-layered); coniferous forests (up to three-layered) often have somewhat sparse shrub and herbaceous layers and therefore have diversities in between those of two-layered and other forested (three-layered) communities. Therefore, it is possible that the foliage height diversity determines the number of available niches (at least in the physical sense) and thus the number of species which can coexist within a given community.

Unfortunately the concept of foliage height diversity does not seem to account for the diversity of tropical woodlands, since it appears that birds in tropical forests tolerate narrower niches than their temperate zone counterparts (Klopfer and MacArthur 1961; MacArthur, Recher, and Cody 1966). The high bird species diversity in the tropics is part of a general biological phenomenon which may have a general explanation. Hypotheses as to the causes of tropical diversity have been reviewed by Pianka (1966) and will not be considered here.

While foliage height diversity may explain the correlation of species richness to diversity in temperate communities, it is still not clear why the species abundance component remains so stable. This stability is especially interesting in light of the finding by Sager and Hasler (1969) that diversity patterns in lacustrine phytoplankton are correlated to variations in species relative abundance, while species richness remains stable. Since exactly the opposite situation obtains in birds, this implies a fundamental difference in the control of diversity between birds and phytoplankton which reflects the very different modes of existence in the two groups.

Plankton are "opportunistic" (sensu MacArthur 1960); i.e., a given species can reproduce quickly and become extremely abundant when conditions are favorable. Since their environment is characterized by relatively high climatic and nutrient variability, a species can only achieve high numbers temporarily, and equilibrium numbers only exist as long-term averages taken over a period of many

generations. Therefore, a series of plankton samples taken either at different times or in different communities is likely to have highly variable species abundance distributions.

Birds, on the other hand, are mostly "equilibrium" species whose physical environment and resources are relatively stable from one generation to the next, and whose densities are partly determined by intraspecific territoriality. They lay virtually the same size and number of clutches year after year, and the numbers of birds appear to be more or less at equilibrium from one generation to the next, implying death rates which are also stable. The result is that in most avian communities the available species partition the breeding space in a characteristic way, and a series of samples from the same or from different localities will yield similar distributions of species abundance.

Sager and Hasler (1969) give no tables of J' , but from their graphs it appears that most J' values for plankton are well below those of birds. Pielou (1966a, b) has measured the "evenness" component for trees and herbaceous-shrub vegetation (less than 2 cm in diameter) in Quebec. Her tree plots ranged in evenness from 0.499 to 0.791, while for the herbaceous-shrub community the value was 0.727. These values are also well below those given in Table 1 for breeding birds. The high J' values in Table 1 may be due in part to the well-developed intraspecific territoriality exhibited by breeding birds. Assuming a limit to the compressibility of territories, effect of this behavior would be to place an upper limit on the density of the commonest species in a given census area. No such mechanism is known in the phytoplankton or in terrestrial plant communities.

It is interesting to note that the only avian community having J' values comparable to those of plant communities is the marshes. The reason is that marshes are characterized by gregarious and often polygamous birds which defend only the immediate area of the nest against others of the same species, and which feed largely outside of the census area (Snelling 1968; Horn 1968). This results in high densities of the most abundant species, and therefore lower values of J' .

Birds occupying a given area in the winter or during the migratory season can be expected to have lower values of J' than breeding populations, in part because for most species there is no territorial behavior. It is therefore possible that diversity will be correlated more closely to relative abundance and less to species richness in nonbreeding bird populations as resources become less predictable in their abundance and distribution.

The difference in the importance of the two diversity components in birds and phytoplankton is significant, since it implies two alternative strategies by which diversity can be regulated. It is suggested that these are responses to two general types of environments, rigorous ones which vary widely and often unpredictably in climate and/or resources, and nonrigorous ones in which these variations are small and/or relatively predictable. Although phytoplankton and birds probably represent the extremes of these two situations, it is possible to predict that collections of organisms from rigorous environments will vary in diversity according to their relative abundance distributions while diversity patterns in collections from non-rigorous environments will be a function of the numbers of species. Evidence is currently being gathered to test this prediction.

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