BIRD SPECIES DIVERSITY: THE EFFECT OF SPECIES RICHNESS AND EQUITABILITY ON THE DIVERSITY INDEX[1]

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Abstract. A study of bird species diversity (BSD) on three seral stages characteristic of secondary succession on the New Jersey Piedmont was done during the winter of 1968–69, the spring of 1969, and the summer of 1969. The seral stages studied were a 2- to 3-year-old field (the herbaceous field), a 30-year-old field (the cedar field), and a climax oak-hickory forest (the oak forest). Two study plots, each with an area of 2 hectares, were chosen within each seral stage. Diversity indices were calculated using the Shannon-Weaver information formula, $H' = -\Sigma p_i \log_e p_i$. The species count (species richness) was found to account for many of the differences in BSD between the seral stages. The evenness with which species were numerically distributed (equitability) was found to be lowest and to have its greatest influence on the diversity index in the herbaceous field, due to the presence of large flocks of non-nesting species. Equitability was higher and more constant in the cedar field and oak forest. Territoriality was thought to account for the higher equitabilities observed in summer. In winter, the more rigorous environment was thought to be a factor in lowering the equitability at least in the cedar field. Equitability was not lowered as much in the oak forest, possibly due to aggregations of birds into mixed species flocks. The cedar field and oak forest were quite different in their seasonal patterns of equitability. Both species richness and equitability were concluded to be important parameters in ecological study.

The application of information theory to the study of species diversity has undergone a rapid evolution. Originally, the information statistic, and in particular the Shannon-Weaver formula ($H' = -\Sigma p_i \log_e p_i$), was used as a means of funneling a large amount of data into one figure representative of the diversity of the community (Margalef 1958, MacArthur and MacArthur 1961). Recent authors have questioned what that diversity figure really means ecologically (Lloyd and Ghelardi 1964, Sager and Hasler 1969, Tramer 1969).

One method of investigating the ecological meaning of the information statistic is to dissect it into its component parts. The Shannon-Weaver formula is influenced both by the number of species and by the number of individuals (of each species) in the sample, and therefore the diversity index is confounded by the interaction of these two factors (Pielou 1969). The species content of the sample is referred to as the "species richness" component of diversity, and the distribution of individuals within species is referred to as "equitability" (Lloyd and Ghelardi 1964). Equitability is highest when all species in the sample are as nearly equal in population as is possible. The diversity index is increased both by increasing species richness and increasing equitability.

Equitability may be calculated numerically using various formulae. The formula used in this study was $J' = H'/H'_{\max}$ (Pielou 1966). H' is the species diversity index calculated with the Shannon-Weaver formula; $H'_{\max}$ is the maximum diversity possible for the sample (i.e., when all species are as evenly distributed numerically as is theoretically possible); and J' is the equitability value. $H'_{\max}$ is calculated simply by taking the natural logarithm of the number of species in the sample. Sheldon (1969) has shown the above formula for equitability to be the formula least influenced by species richness.

The purpose of my study was to investigate the bird species diversity of three seral stages which are representative of old field succession on the New Jersey Piedmont. One of my objectives was to evaluate the Shannon-Weaver diversity index in terms of its component parts.

METHODS

Three seral stages representative of early, middle, and late secondary succession were chosen for the study. Each seral stage was divided into two rectangular study plots, A and B. Each plot was 100 m by 200 m, covering an area of 2 ha.

Regular censuses were made during the winter of 1968–69, the spring of 1969, and the summer of 1969.

Each plot was sampled one time per week in winter and spring and twice a week in summer. All bird censuses were made between 7 AM and 10 AM. Each plot was censused for 45 min (1.5 hr per seral stage). Censuses were made by cruising the plots on foot and identifying all birds encountered within the plots. Birds flying overhead were generally not counted. However, swallows (Hirundinidae), swifts (Apodidae), and raptors (Cathartidae, Accipitridae, and Falconidae) were counted since they normally feed or hunt on the wing and would therefore be utilizing

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TABLE 1. Species richness (S), equitability (J'), and diversity (H') values. All values are means per census. Numbers in parentheses are coefficients of variability. In winter, for each plot, $N = 13$; in spring $N = 11$; in summer $N = 20$

	Herbaceous field		Cedar field		Oak forest	
	Plot A	Plot B	Plot A	Plot B	Plot A	Plot B
Winter *S*	—	—	3.08 (55%)	3.00 (41%)	4.08 (41%)	5.08 (49%)
Winter *J'*	—	—	.72 (58%)	.76 (46%)	.87 (12%)	.88 (10%)
Winter *H'*	—	—	.90 (64%)	.88 (51%)	1.15 (33%)	1.30 (43%)
Spring *S*	3.09 (49%)	3.36 (58%)	6.09 (48%)	7.46 (43%)	11.91 (37%)	14.73 (40%)
Spring *J'*	.66 (54%)	.61 (66%)	.92 (6%)	.92 (5%)	.77 (13%)	.78 (15%)
Spring *H'*	.73 (62%)	.82 (70%)	1.56 (29%)	1.76 (25%)	1.85 (17%)	2.07 (27%)
Summer *S*	3.90 (54%)	4.15 (40%)	8.50 (20%)	10.05 (17%)	13.00 (19%)	12.60 (27%)
Summer *J'*	.76 (40%)	.78 (39%)	.91 (10%)	.92 (6%)	.92 (5%)	.92 (4%)
Summer *H'*	.93 (44%)	1.02 (48%)	1.93 (16%)	2.11 (11%)	2.34 (10%)	2.30 (11%)

the area from the air. In summer, censuses were not restricted to nesting species. All species encountered within the plot were counted, including those which used the ecosystem only as a food source.

The study areas were all located near East Millstone, on the New Jersey Piedmont. Plant succession on the Piedmont has been described previously (Bard 1952).

The early successional stage (to be referred to as "the herbaceous field") was sampled when it was 3 years past abandonment. The field was located on the north side of the William L. Hutcheson Memorial Forest, and was composed entirely of herbaceous vegetation, most of which was *Ambrosia artemisiifolia* (common ragweed).

The middle-aged seral stage (to be referred to as "the cedar field") was 1 km from Hutcheson Memorial Forest and was studied in its 30th year since cultivation. Three species, *Juniperus virginiana* (red cedar), *Myrica pensylvanica* (northern bayberry), and *Andropogon scoparius* (little bluestem) dominated the field.

The area chosen as representative of climax (to be referred to as "the oak forest") was the Hutcheson Memorial Forest. Much of the forest is considered to be virgin, and the vegetation has been intensively studied (Monk 1961). The forest is dominated by three species of oak (*Quercus alba, Q. velutina,* and *Q. rubra*) and by *Carya ovalis.* Vertical stratification is quite distinct, the subcanopy being *Cornus florida.* Both plots were located in areas where the shrub cover was *Viburnum acerifolium.*

RESULTS

Bird species diversity (BSD), in all seral stages, was decidedly highest in summer. The herbaceous field was so totally devoid of birds in winter that not enough data were provided even to calculate a mean BSD. At all seasons, BSD increased with the age of the seral stages (H' on Table 1). Statistically significant differences in mean BSD were found among the seral stages at all seasons (Kricher 1970).

Species richness (S) and equitability (J'), the two individual components of the diversity index (H'), were examined separately to determine which was more responsible for the BSD differences observed among the seral stages.

The pattern of bird species richness (mean number of species per census) was quite similar to the pattern of bird species diversity (Table 1). This similarity between the patterns of S and H' was particularly noticeable between plots within seral stages (Table 1). In all cases, regardless of seral stage or season, if the A plot was slightly higher or lower than the B plot with regard to species richness, then it would be likewise with regard to species diversity. Striking seasonal differences in species diversity within seral stages were paralleled by differences in species richness (Table 1).

No such similarities were noted between species diversity and equitability. In the cedar field in winter the differences in H' and J' between the plots were in opposite directions. Plot B, lowest in mean BSD, was highest in the mean J' (Table 1). A similar situation existed in the herbaceous field in spring. Further, in instances where clear differences in BSD occurred between plots (as in the oak forest in winter and cedar field in spring), the plots were virtually equal in equitability (Table 1).

Seasonal differences in equitability within seral stages did not always parallel differences in diversity. In the cedar field, there was no difference between J' in spring and summer although there was a considerable difference in H'. The lowest equitabilities for the oak forest occurred in spring while the lowest diversities occurred in winter (Table 1). Clearly, a closer correlation existed between S and H' than between J' and H'.

The question of how much respective influence S and J' have over H' remains. Some insight may be obtained by examining the amount of variability associated with each component. In each seral stage, summer was the season of least variability in bird species diversity (Table 1). Also, the herbaceous field had a much higher BSD variability than either of the other two seral stages. It is of interest to note that of the two components of the species diversity index, the highest coefficients of variability occurred consistently with species richness. In summer, considering S, J', and H', S was the most variable, J' was the least variable, and H' was in between. This situation was also true in spring for both the cedar field and oak forest, and in winter for the oak forest (Table 1).

The low coefficients of variability found for the equitabilities of the cedar field and oak forest in the summer indicate that most of the day-to-day differences in H' were due to differing species richness. Equitability was generally constant from census to census. A different situation prevailed in the herbaceous field. In that seral stage, both S and J' were highly variable. Further, the herbaceous field was lower in mean J' than the cedar field and oak forest. This difference was found to be statistically significant (Table 2).

A very noticeable characteristic of the bird censuses in the herbaceous field was the sporadic presence of species that utilized the ecosystem only as a food source. These non-nesting birds included the common grackle (*Quiscalus quiscula*), the tree swallow (*Iridoprocne bicolor*), the mourning dove (*Zenaidura macroura*), and particularly the starling (*Sturnus vulgaris*). Flocks of the latter species often exceeded 100 individuals. When any of the above species were present, they tended to be far more numerous than all other species, and equitability was very low. Conversely, when these non-nesting species were absent, most of the birds recorded were territorial and equitability was much increased. Therefore, the occasional occurrence of flocks of non-nesting birds was responsible for (1) an overall decrease in the mean J' and (2) a great increase in variability both with regard to S and J'. While censuses from both the cedar field and oak forest typically contained non-nesting birds, in neither seral stage did the influence of non-nesting species approach that in the herbaceous field (Kricher 1970).

The situation in spring was similar in some ways to summer. Statistically significant differences in mean equitability were found among the seral stages (Table 3).

The lowest equitabilities recorded in the study occurred in the herbaceous field in spring (Table 1). In the herbaceous field, both S and J' were highly variable, again due to the periodic presence of transient species. In spring a notable difference in J' occurred between the cedar field and the oak forest. J' in the cedar field was considerably higher than in the oak forest and was extremely unvariable (Table 1). In other words, virtually all differences in BSD were due to differences in species richness. In the oak forest, J' was lower than at any other season, and slightly more variable than in winter. Its influence over H' was substantially increased over what it was in the cedar field (Table 1).

TABLE 2. Analysis of variance comparing J' means among seral stages, summer 1969

Source	df	SS	MS	F
Seral stages	2	.559	.280	254.2
Plots (seral stages)	3	.003	.001	
Censuses [plots (seral stages)]	114	3.809	.033	
Total	119	4.371		

*$P < .005$.

TABLE 3. Analysis of variance comparing J' means among seral stages, spring 1969

Source	df	SS	MS	F
Seral stages	2	.911	.455	89.3*
Plots (seral stages)	3	.015	.005	
Censuses [plots (seral stages)]	60	3.116	.053	
Total	65	4.042		

*$P < .005$.

There was a marked contrast in J' between the cedar field and oak forest in winter. J' was lowest in the cedar field and far more variable than it was in the oak forest (Table 1). This situation is nearly opposite of the situation in spring. In winter, J' was less constant and more of an influence on H' in the cedar field. The difference in J' between the cedar field and the oak forest was not statistically significant ($P > .10$).

DISCUSSION

The results of the present study show clearly that the seral stages differed in the influence that S and J' had on H'. The relative importances of S and J' varied both with seral stage and with season. It is of interest to ask what the causes of these variations may have been.

The high equitabilities observed in the cedar field and oak forest during the summer were almost undoubtedly results of territoriality. The J' values in these seral stages were extremely constant from census to census. Since nesting passerines tend to distribute themselves evenly among their own species, and since they remain on territory throughout the duration of the breeding season, high and constant J' values in communities containing numerous nesting species should not be surprising. High J' values have been shown to exist for nesting bird communities in several varied habitats (Tramer 1969).

In summer, equitability had its most important influence on the diversity index in the herbaceous field, the early successional stage. The J' values, highly variable from census to census, were strongly influenced by flocks of starlings, tree swallows, and common grackles, which were exploiting an ecosystem unsuitable for reproduction but satisfactory as a food source. These species have been able to take advantage of a temporary and rapidly changing ecosystem. Margalef (1963, 1968) has noted that in disturbed ecosystems, some species tend to gain advantages not shared by others. The abundances of the above three species may represent such a situation. Sager and Hasler (1969), for phytoplankton communities, found that J' accounted for most of the differences in community diversities. These low J' values may have been a response to a disturbed environment (Tramer 1969). In chydorid communities, Goulden (1966) has noted that the lowest equitabilities occurred in the youngest ponds. Low and variable J' would perhaps appear to be a general characteristic either of early succession or of ecosystems containing opportunistic species.

An important point is that both the magnitude and variability of J' in the herbaceous field were strongly influenced by non-nesting species. Previous studies (MacArthur and MacArthur 1961, Karr 1968, Recher 1969) have considered only nesting birds. In this study, only four species (eastern meadowlark, *Sturnella magna;* red-winged blackbird, *Agelaius phoeniceus;* grasshopper sparrow, *Ammodramus savannarum;* vesper sparrow, *Pooecetes gramineus*) nested in the herbaceous field. All other species (total of 16) utilized the ecosystem only as a food source. If only the nesting species had been considered in this study, J' would have been both higher and less variable since only territorial species would have been censused. Although species richness may be an accurate predictor of bird species diversity in ecosystems where the majority of the bird species are nesters (Tramer 1969), it appears from the present study that consideration of all species, both nesters and non-nesters, greatly increases the ecological importance of the equitability measure, particularly in early successional ecosystems.

In winter, S, J', and H' were all considerably less in magnitude and much greater in variability than in summer. It is not difficult to account for lower species richness being the case in winter. All three seral stages presented much more rigorous environments to birds in that season, and although food sources were not measured in this study, food was obviously far less in winter. The ecosystems simply did not provide enough resources to support birds at the level they had in summer. The question of why J' was lower in winter is still to be answered. One obvious answer is that most species were not territorial in winter and ranged, often in flocks, over wider areas. Thus an effect similar to that observed in the herbaceous field in summer was observed. Of interest is the fact that J' was somewhat lower in the cedar field than in the oak forest. Superficial examination of the two ecosystems suggests that the cedar field, being quite open, provided birds with a more rigorous environment than the oak forest. Tramer (1969) hypothesized that winter bird communities have low equitability values because of the effect of an unpredictable and rigorous environment.

The J' values in the oak forest in winter were not greatly less than in summer. An explanation for the similarity in J' between the two seasons may perhaps be found in the characteristic mixed flocks of birds that occurred in the oak forest in winter. Interspecific flocks typically dominated the winter censuses. The numerical distribution of individuals within species in these flocks tended to be quite equitable. While the contribution made by each species to the general welfare of the flock is uncertain, interspecific associations do seem to provide birds with more efficient utilization of food resources and increased protection from predators (Moynihan 1960, 1962, Morse 1970). Further research on the diversity components of mixed flocks is needed to determine (1) if a high equitability is a general characteristic of mixed flocks and (2) what ecological factors are responsible for the high J'.

One could hypothesize that in summer the high J' is an intraspecific response resulting from the partitioning of breeding space. In winter, J' is lowered due to the more rigorous environment. However, this lowering is tempered by the interspecific associations that characterize winter passerine communities.

The seasonal changes in equitability were quite different between the cedar field and the oak forest. In the cedar field, when spring came the equitability increased immediately to its summer value and remained there (as indicated by the low amount of variability). This would seem to imply that a rigorous environment was strongly responsible for the lowered winter J'.

The situation in the oak forest was quite different. Spring was the season of lowest equitability. The lowered J' probably resulted somewhat from periodic influxes of migrating species, but mostly from the presence of a large number of nesting starlings. Species such as the rufous-sided towhee (*Pipilo erythrophthalmus*), the common grackle, the red-winged blackbird, the fox sparrow (*Passerella iliaca*), and the myrtle warbler (*Dendroica coronata*) were present in abundance for short intervals during migration. The starling, which nested in the numerous dead oak trees, nested earlier than other passerines. Therefore, the spring censuses characteristically contained some of the above species that were decidedly more abundant than most of the other species. These few abundant species (in particular the starling since it appeared abundantly on every census) lowered the equitability in the oak forest.

It is apparent then that there exist two different seasonal patterns of equitability between the cedar field and the oak forest. If a lowered J' characterizes an ecosystem containing opportunistic species, then the oak forest, the "climax" stable ecosystem, does indeed contain opportunistic species if only in spring. Most of these species utilize the forest as a food source while migrating (not unlike the situation prevailing in the herbaceous field). However, one species, the starling, has taken advantage of the abundant nest sites present within the forest. This species has successfully invaded the forest, reduced the equitability (and therefore the species diversity), and has provided an example of how mature ecosystems are not necessarily invulnerable to opportunistic species.

The significance of the foregoing discussion lies in the fact that definite and explainable rates of change of equitability do occur. Even though species richness would seem to be all that is required to describe diversity in many cases, the factors affecting equitability may be of great ecological interest. Thus it is concluded that both components of the diversity index are necessary to adequately describe species diversity.

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