Summer Bird Species Diversity in Relation to Secondary Succession on the New Jersey Piedmont

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ABSTRACT: Bird species diversity was studied in three seral stages characteristic of secondary succession on the New Jersey Piedmont during the summers of 1968 and 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 near climax oak-hickory forest (the oak forest). Two study plots each with an area of 2 ha were chosen within each seral stage. Diversity indices were calculated using the Shannon-Weaver information formula, $H' = -\Sigma p_i \log_e P_i$.

Bird species diversity (BSD) and age of the seral stage were positively correlated, and the greatest increase in the diversity index occurred between the herbaceous field and the cedar field. BSD in the oak forest was consistently higher than in the cedar field, although the mean values were not greatly different. BSD variability decreased with the age of the seral stage. The highest variability estimates were for the herbaceous field. Much of the variability in the herbaceous field was due to the importance of nonnesting birds which fed in the field. The importance of nonnesting birds decreased with the age of the seral stage. The suggestion is made that variability is an important parameter and should be examined more closely in future species-diversity studies. Although no cause-effect mechanism between species diversity and habitat stability was found, the trends observed suggest that low species diversity and high variability characterize unstable habitats.

INTRODUCTION

Species diversity is an attribute of all biological communities. Ecologists have long recognized that the number of species which characterizes a community differs from one community to another. Why one community should contain more or fewer species than another is as yet poorly understood, and numerous hypotheses regarding the functional role of species diversity have been proposed (Elton, 1958; Hutchinson, 1959; Connell and Orias, 1964; MacArthur, 1965; Pianka, 1966).

Species diversity changes in relation to succession have been studied by Margalef (1963, 1968). Many of Margalef's conclusions are now considered to be characteristic of autotrophic succession in general (Odum, 1963, 1969). Karr (1968) has recently described species diversity and avian succession in Illinois. Prior to that, studies on avian succession have not specifically considered species diversity (Odum, 1950; Johnston and Odum, 1956).

Evaluation of many previous studies of species diversity is difficult for several reasons. Often, studies are restricted to only a single ecosystem. Those that are not often fail to supply such information as sample size per ecosystem and sample number per ecosystem, making

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statistical comparisons between ecosystems very difficult. Many studies of species diversity are devoid of estimates of variability and statistical analysis.

Previous studies of bird species diversity have considered only nesting species. In terms of ecosystem energetics, however, if two species both feed in an ecosystem but only one of the two nests, it would certainly be an error to exclude the nonnesting species from consideration.

The purpose of this study was to investigate the bird species diversity of three seral stages which are representative of old-field succession on the New Jersey Piedmont. A principal objective was to correlate bird species diversity (BSD) with the age of the seral stage in such a manner as to make possible statistical comparisons among seral stages. Particular attention was paid to assessing BSD variability in each seral stage. A further objective was to compare the contributions of nesting and nonnesting birds to the total index of bird species diversity.

THE INFORMATION STATISTIC

Numerous mathematical relationships have been used as measures of species diversity (Hairston, 1959). Margalef (1956, 1957, 1958) proposed that species diversity be measured using the information statistic, and information theory has since been used widely by ecologists for measuring diversity. Information theory, in its modern sense, was developed for use in communications work (Shannon, 1948; Shannon and Weaver, 1949). The theory does not require that species conform to any strict numerical distribution.

The information formula measures the degree of uncertainty involved in predicting what the next message encountered will be. When the information formula is used in ecology, the term "species diversity" is equated with the amount of uncertainty attached to the species identity of an individual chosen at random for the community (Pielou, 1966c). This definition means that, for a given community, an increase in the total number of species and/or the numerical evenness with which the species are distributed will increase the diversity index. Two formulae, that of Brillouin and that of Shannon and Weaver, are used to calculate species diversity with information theory. The mathematical derivations of the Brillouin and Shannon-Weaver formulae and the specific relationship between them are discussed by Shannon in Shannon and Weaver (1949), Brillouin (1960), Patten (1959, 1962) and Pielou (1969).

Because it is least sensitive to sample size, the Shannon-Weaver formula, $H' = -\Sigma p_i \log_e p_i$, has been used in the present study. In this formula, H' is species diversity and p_i is the proportion of individuals belonging to the ith species. p_i is estimated by dividing the number of individuals of species i in the sample (n_i) by the total number of individuals of all species present in the sample (N). The Shannon-Weaver formula has been used extensively in studies of bird species diversity (MacArthur and MacArthur, 1961; MacArthur, *et al.*, 1962; Karr, 1968; Recher, 1969).

The formula assumes that the data are samples taken at random from a large collection (Pielou, 1966a, 1966b, 1966c, 1966d, 1969). This assumption was not violated in the collection of data for this study. The data collected were assumed to be representative samples taken inside study plots within the seral stage. The seral stage was regarded as the collection and the bird censuses made within the plots represented the samples.

METHODS

Three seral stages representative of early, middle and late secondary succession were chosen for the study. To provide an estimate of variability in BSD within a seral stage, each seral stage was divided into two rectangular study plots, A and B. Each plot was 100 m by 200 m (2 ha).

Regular censuses were made during the summers of 1968 and 1969 throughout the nesting and postnesting seasons. All bird censuses were made between 7 AM and 10 AM. No area was censused more at one time than at another. Usually, both plots within a seral stage were sampled on the same day. Each plot was censused for 45 min (1½ hr per seral stage). In 1968, 46 censuses were made per seral stage, from 26 June to 31 August. In 1969, 40 censuses per seral stage were made, from 3 June to 8 August. The above figures do not include censuses conducted in the spring for the purpose of mapping territories of nesting species.

Censuses were made by cruising the plots on foot and identifying all birds encountered within the plots. Birds flying overhead were not counted, with the exceptions of swallows, swifts and raptors which normally feed or hunt on the wing and would therefore be utilizing the area from the air. Nesting birds were determined by use of spot-mapping (Williams, 1936) and by observations of birds either building nests, incubating or feeding young.

Bird species diversity data were analyzed by analysis of variance and Student's *t* test following procedures described by Steel and Torrie (1960). Prior to each Student's *t* test, the variance of the two means were tested for significant difference at the .05 probability level using the **F** statistic. No significance was found in any case, and therefore all variances were pooled. Variability estimates were expressed as ± one standard error. Prior to statistical analysis, all data were tested for normality.

Importance values were calculated for all bird species per study plot per year. The importance value was defined as the relative density per census plus the relative frequency (number of censuses on which the species appeared). The maximum importance value that a species could have was 200.

Similarity between the bird communities of the study plots within a seral stage was expressed as the coefficient of community, $C=2W/A+B$, where W is the sum of the importance values for species shared by the two study plots; A is the sum of the importance values for the

A plot; and B is the sum of the importance values for species occurring on the B plot (Bray and Curtis, 1957).

STUDY AREAS

The study areas were all located near East Millstone in Middlesex Co. on the New Jersey Piedmont. The vegetation changes during secondary succession on the New Jersey Piedmont have been described previously (Bard, 1952). The early successional stage (the "herbaceous field") was sampled when it was 2 and 3 years postabandonment. The field was located on the N side of the William L. Hutcheson Memorial Forest (HMF), and had an area of 7 ha, 4 of which comprised the study plots. The field was composed entirely of herbaceous vegetation, under 1.5 m in height. The "cedar field" was a 5-ha field 1 km from HMF, in its 29th and 30th summers since cultivation. Three species, *Juniperus virginiana* (red cedar), *Myrica pensylvanica* (northern bayberry) and *Andropogon scoparius* (little blue-stem) dominated the field. The area chosen as representative of approaching climax (the "oak forest") was the William L. Hutcheson Memorial Forest. The forest is approximately 26 ha and is surrounded by cultivated and abandoned fields. Much of the forest is considered virgin and the vegetation has been described by Monk (1961). The forest is dominated by three species of oak (*Quercus alba, Q. velutina* and *Q. rubra*) and red hickory (*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* (Monk, 1957). The study areas are described in greater detail in Kricher (1970).

RESULTS

Differences among seral stage means.—The mean values for bird species diversity obtained in each seral stage were extremely similar for the 2 summers of the study (Table 1). The similarity occurred even though the period of sampling in 1968 (26 June-31 August) did not completely overlap that of 1969 (3 June-8 August).

During the summer of 1968, the oak forest was consistently highest in BSD and the herbaceous field was consistently lowest (Fig. 1). A hierarchic analysis of variance was used to test for significant differences among seral stage means. The design was completely balanced with respect to the total number of censuses per seral stage and per study plot but was unbalanced with respect to the number of censuses per study plot per seral stage per week. A given study plot was some-

TABLE 1.—Mean BSD (H') per seral stage per season per year plus or minus one standard error

Season, year	Herbaceous field	Cedar field	Oak forest
Summer, 1968	0.936 ± 0.081	2.013 ± 0.035	2.293 ± 0.038
Summer, 1969	0.978 ± 0.071	2.021 ± 0.046	2.323 ± 0.038

times censused only one time per week and sometimes as often as six times per week. The analysis of variance (Table 2) indicated that significant differences existed ($p<.05$) among the seral stage means. The calculation of the least significant difference (Steel and Torrie, 1960), and from that, the least significant interval (Shure, 1971) showed that the means of both the cedar field and oak forest were significantly different from the herbaceous field mean, but the cedar field and oak forest were not significantly different from each other ($s^2=0.7367$, LSD=0.5695, LSI=0.2848).

The pattern of bird species diversity observed in the summer of 1968 was repeated in the summer of 1969 (Fig. 2). The experimental design used in 1969 was completely balanced (*i.e.*, equal numbers of censuses per study plot per seral stage per week). A partially hierarchic

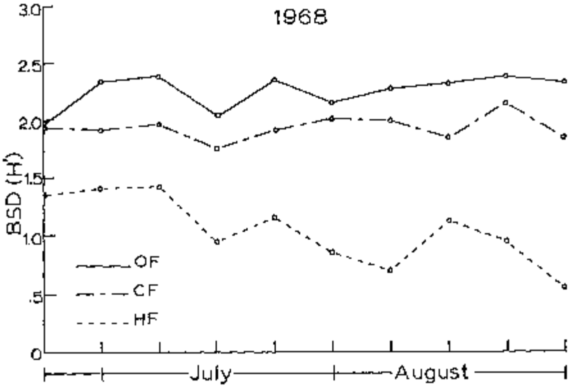

Fig. 1.—Mean BSD per seral stage per week in 1968. HF is herbaceous field, CF is cedar field and OF is oak forest

TABLE 2.—Summer 1968 nested ANOVA comparing BSD means between the three seral stages

	Summer 1968 analysis of variance				
Source	df	s.s.	m.s.	e.m.s.	F
Total	137	66.40			
Seral stage	2	47.20	23.6000	$\sigma^2 + \sigma^2_S + 3.19\sigma^2_T + 23\sigma^2_P + 46\sigma^2_{SS}$	32.0347**
Plots (S.S.)	3	2.27	0.7367	$\sigma^2 + \sigma^2_S + 3.19\sigma^2_T + 23\sigma^2_P$	4.1434*
Time [P(S.S.)]	54	9.60	0.1778	$\sigma^2 + \sigma^2_S + 2.20\sigma^2_T$	1.8775*
Samples {T[P(S.S.)]}	78	7.39	0.0947	$\sigma^2 + \sigma^2_S$	

** $p < .01$
* $p < .05$

analysis of variance (Table 3) indicated that highly significant differences existed among seral stage means at the .005 probability level. Calculation of the least significant interval showed that the means of the herbaceous field, the cedar field, and the oak forest were all significantly different from one another at the .05 probability level ($s^2=0.1390$, LSD=0.2654, LSI=0.1327). The increased significance
be attributed to a better balanced and therefore more sensitive experi-
in the differences between the means in 1969 over those in 1968 can
mental design employed in 1969.

Differences between study plots.—Differences in mean BSD between

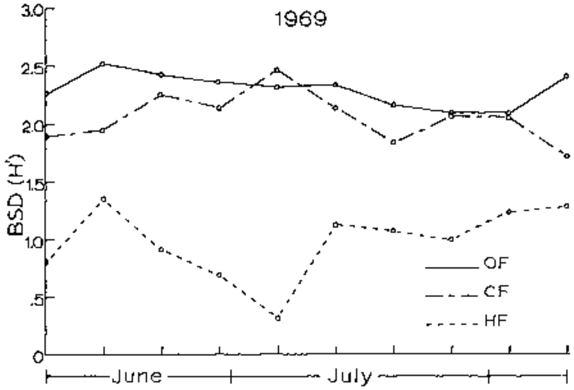

Fig. 2.—Mean BSD per seral stage per week in 1969

TABLE 3.—Summer 1969 partially hierarchic ANOVA comparing BSD means between the three seral stages

	Summer 1969 analysis of variance				
Source	df	s.s.	m.s.	e.m.s.	F
Total	119	53.35			
Seral stage	2	39.86	19.9315	$\sigma^2 + \sigma^2_{STPS} + 20\sigma^2_{PS} + 40\sigma^2_{S}$	143.495***
Plots (S.S.)	3	0.42	0.1390	$\sigma^2 + \sigma^2_{STPS} + 20\sigma^2_{PS}$	1.515
Time	9	0.99	0.1111	$\sigma^2 + \sigma^2_{STPS} + 2\sigma^2_{TPS} + 12\sigma^2_{T}$	1.445
T. X. S.S.	18	4.49	0.2500	$\sigma^2 + \sigma^2_{STPS} + 2\sigma^2_{TPS} + 4\sigma^2_{TS}$	3.254*
T. X. p. (S.S.)	27	2.07	0.7700	$\sigma^2 + \sigma^2_{STPS} + {}^{S}\sigma^2_{TPS}$	0.928
Samples [T X p. (S.S.)]	60	5.00	0.0833	$\sigma^2 + \sigma^2_{STPS}$	

*** $p < .005$
* $p < .05$

the A and B study plots in each seral stage were analyzed using Student's t test for the 1968 data and analysis of variance (Table 3) for the 1969 data. Generally, the A and B plots were extremely similar in mean BSD for each seral stage (Figs. 3, 4, 5). Only in 1968 was there any significance difference in mean BSD between plots within a seral stage. This difference occurred in the herbaceous field ($d = 0.4141$, $s^2_{\text{pooled}} = 0.2670$, $t = 2.6903$, $p < .02$), and was not repeated in 1969 (Table 3, plots m.s. is not significant).

To examine the similarity of species compositions between plots, the coefficient of community was calculated. A coefficient of 1.0 indicates complete similarity. The coefficients indicated that the avian communities of plots A and B were essentially identical in all seral stages during both summers (Table 4). Plots A and B were therefore replicate samples in terms of their species compositions.

The effect of time.—Analyses were made to determine if BSD in any seral stage changed during the course of the summer. The effect

TABLE 4.—Coefficients of community based upon avian importance values. Coefficients indicate degree of similarity in community composition between A and B plots within a seral stage

Season, year	Herbaceous field	Cedar field	Oak forest
Summer, 1968	0.93	0.93	0.95
Summer, 1969	0.88	0.95	0.96

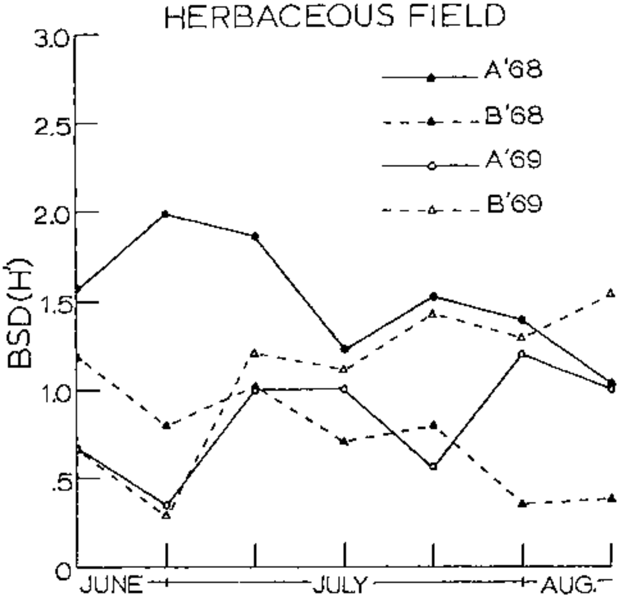

Fig. 3.—Mean weekly BSD of each plot in the herbaceous field during both summers. Note the high variability between plots and between years

of time was statistically significant in the herbaceous field in the summer of 1968 (Table 2), but not in the summer of 1969 (Table 3). Both plots in the herbaceous field showed steady declines in BSD from late June through early August in 1968 but not in 1969 (Fig. 3). No trends toward declining or increasing BSD with time were observed

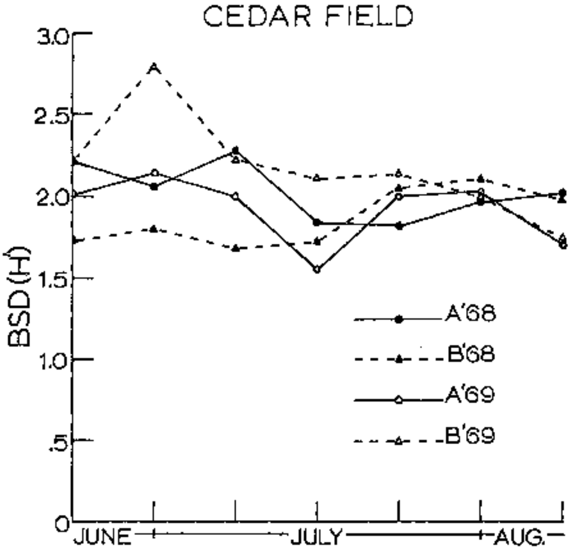

Fig. 4.—Mean weekly BSD of each plot in the cedar field during both summers

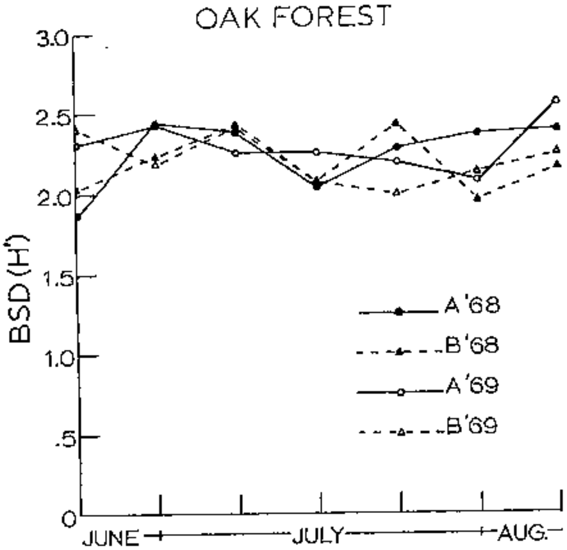

Fig. 5.—Mean weekly BSD of each plot in the oak forest during both summers

in any plot in either of the other two seral stages (Figs. 4 and 5).

The time by seral stage interaction was evaluated in 1969 and found to be statistically significant (Table 3). The interaction indicated that the differences between seral stage means changed relative to one another sometime during the summer. This change was greatest in early July, when the cedar field was higher in BSD than the oak forest and the herbaceous field was lower in BSD than usual (Fig. 2).

Bird species diversity variability.—For each seral stage, BSD variability (standard error) estimates were essentially equal in 1968 and 1969 (Table 1). Further, there were essentially no differences between plot variability estimates within seral stages in either year. Variability in mean BSD was by far the highest in the herbaceous field. The cedar field and oak forest had nearly equal variability estimates (Table 1). Figures 3, 4 and 5 show a general decline in weekly BSD variability (as indicated by the smoothness of the curves) with increasing age of the seral stage. This decline is quite obvious between the herbaceous field and cedar field but slight between the cedar field and oak forest.

The importance of nonnesting birds.—The importance of nonnesting birds differed in each seral stage (Table 5). The presence of nonnesting birds was extremely important in the herbaceous field, moderately important in the cedar field, and unimportant in the oak forest (Table 5). The nonnesting birds were either species which nested elsewhere (in another seral stage) but fed occasionally in the study area or migrants which were temporarily in the area.

Nonnesting birds were most important in the herbaceous field and accounted for the high BSD variability observed in that seral stage. The only nesting species were grasshopper sparrow, vesper sparrow, eastern meadowlark, and red-winged blackbird (Table 6), which were all territorial with, at most, two pairs inhabiting the entire field. Since the herbaceous field was structurally very simple, it was by far the easiest seral stage to sample and nesting birds were detected on virtually every census. In contrast, large flocks of starlings, common grackles and tree swallows, in addition to smaller numbers of field sparrows, song sparrows, mourning doves, flickers and indigo buntings, sporadically fed in the field. The presence of these feeding birds was in large part an edge effect. The herbaceous field was bordered by a small 10-year old-field, a 5-year old-field, a hedgerow of sycamore trees (*Platanus occidentalis*), and a 1-year-old experimental field. The oak forest was approximately 100 m from the field. The majority of the species encountered in the herbaceous field nested in these sur-

TABLE 5.—Importance of nonnesting species expressed as a per cent of the total importance values for all species found in the study plot (*i.e.*, total I.V. for nonnesting species/total I.V. for all species x 100)

	1968		1969		
	A	*B*	*A*	*B*	Mean
Herbaceous field	80.6	90.0	74.4	77.7	80.7
Cedar field	26.1	40.3	32.4	22.8	30.4
Oak forest	16.6	19.9	12.2	10.3	14.8

rounding ecosystems. The occurrence of these species in the herbaceous field was quite unpredictable from day to day. The significant difference in mean BSD between A and B plots in 1968 could have been a result of there being more edge species whose feeding territories overlapped the A plot than the B plot. The significant decrease in BSD over time in the herbaceous field in 1968 was a result of nonnesting species. Bird species diversity decreased constantly in both plots during July (Fig. 3). Simultaneous with this decrease was an increase in the number of migrating tree swallows feeding by skimming over the field. These swallows were the most abundant birds recorded on many censuses, and their disproportionate abundance lowered the diversity index. The fact that these trends were not repeated in 1969 is further indication of the variable nature of BSD in the herbaceous field.

TABLE 6.—Mean importance values of bird species identified during the study (all scientific names according to A.O.U. check-list)

	Herbaceous field	Cedar field	Oak forest
Eastern Meadowlark (*Sturnella magna*)	8.8*	....	....
Grasshopper Sparrow (*Ammodramus savannarum*)	14.1*	....	....
Red-tailed Hawk (*Buteo jamaicensis*)	0.4	....	....
Rough-winged Swallow (*Stelgidopteryx ruficollis*)	0.4	....	....
Savannah Sparrow (*Passerculus sandwichensis*)	0.7	....	....
Vesper Sparrow (*Pooecetes gramineus*)	8.9*	....	....
Barn Swallow (*Hirundo rustica*)	9.2	6.2	....
Cedar Waxwing (*Bombycilla cedrorum*)	0.4	5.9*	....
Eastern Kingbird (*Tyrannus tyrannus*)	5.5	1.9	....
Indigo Bunting (*Passerina cyanea*)	6.7	0.2	....
Purple Martin (*Progne subis*)	0.4	0.8	....
Ring-necked Pheasant (*Phasianus colchicus*)	3.1	0.9	....
Song Sparrow (*Melospiza melodia*)	5.2	9.3*	....
Tree Swallow (*Iridoprocne bicolor*)	27.4	24.8	....
American Goldfinch (*Spinus tristis*)	5.7	11.4*	0.2
Cardinal (*Richmondena cardinalis*)	0.4	3.8*	4.9*
Chimney Swift (*Chaetura pelagica*)	2.8	4.2	0.4
Yellow-shafted Flicker (*Colaptes auratus*)	3.2	3.0	13.0*
Common Grackle (*Quiscalus quiscula*)	6.9	2.8	12.4
Mourning Dove (*Zenaidura macroura*)	2.6	2.3*	5.9*
Red-winged Blackbird (*Agelaius phoeniceus*)	8.1*	....	0.5
Sparrow Hawk (*Falco sparverius*)	2.1	0.4	0.5*
Starling (*Sturnus vulgaris*)	63.7	0.4	6.1*
Field Sparrow (*Spizella pusilla*)	18.4	28.6*	0.1
Brown-headed Cowbird (*Molothrus ater*)	....	5.6*	.... **
Chipping Sparrow (*Spizella passerina*)	....	0.3	....
Mockingbird (*Mimus polyglottos*)	....	1.4*	....
Prairie Warbler (*Dendroica discolor*)	....	4.5*	....
Turkey Vulture (*Cathartes aura*)	....	0.2	....
Yellowthroat (*Geothlypis trichas*)	....	14.0*	....
American Redstart (*Setophaga ruticilla*)	....	0.2	1.9
American Woodcock (*Philohela minor*)	....	0.2	0.9
Baltimore Oriole (*Icterus galbula*)	....	2.4	4.2*
Black-capped Chickadee (*Parus atricapillus*)	....	0.9	3.3*
Blue Jay (*Cyanocitta cristata*)	....	3.7	25.6*
Blue-winged Warbler (*Vermivora pinus*)	....	2.0*	1.0

The effect of nonnesting birds in the cedar field was much less than in the herbaceous field. On the average, nearly 70% of the total of all importance values belonged to nesting species (Table 5). These species ranged in abundance from six pairs to one pair over the entire seral stage (combining both study plots). Populations of nonnesters utilizing the habitat (blue jay, downy woodpecker, black-capped chickadee) were not numerically important, with the exception of the tree swallow (Table 6). No large flocks of species other than the tree swallow occurred in either summer. The reduced importance of nonnesting birds acted to reduce greatly the variability estimates. Most of the birds were on territory and appeared on almost every census.

Nonnesting birds were least important in the oak forest (Table 5). The vast majority of the species present were nesting species (Table 6). Nonnesting birds were slightly more important in 1968 (Table 5) because censusing continued throughout August. Because

TABLE 6.—(continued)

	Herbaceous field	Cedar field	Oak forest
Brown Thrasher (*Toxostoma rufum*)	....	5.9	1.3
Catbird (*Dumetella carolinensis*)	....	17.3*	1.9*
Common Grackle (*Corvus brachyrhynchos*)	....	0.5	2.8
Downy Woodpecker (*Dendrocopos pubescens*)	....	1.4	9.9*
House Wren (*Troglodytes aedon*)	....	7.6*	9.5*
Ovenbird (*Seiurus aurocapillus*)	....	0.2	5.8*
Robin (*Turdus migratorius*)	....	4.4	8.6*
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	....	0.4	3.9*
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	....	21.1*	11.1*
Tufted Titmouse (*Parus bicolor*)	....	0.6	11.0*
Black and White Warbler (*Mniotilta varia*)	....	....	1.7
Blackburnian Warbler (*Dendroica fusca*)	....	....	0.2
Black-throated Green Warbler (*Dendroica virens*)	....	....	0.2
Blue-gray Gnatcatcher (*Polioptila caerulea*)	....	....	0.2
Canada Warbler (*Wilsonia canadensis*)	....	....	1.5
Carolina Wren (*Thryothorus ludovicianus*)	....	....	0.2
Cooper's Hawk (*Accipiter cooperii*)	....	....	0.2
Eastern Wood Pewee (*Contopus virens*)	....	....	6.3*
Empidonax Flycatcher (*Empidonax* sp.)	....	....	0.5
Golden-winged Warbler (*Vermivora chrysoptera*)	....	....	0.2
Great Crested Flycatcher (*Myiarchus crinitus*)	....	....	5.1*
Great Horned Owl (*Bubo virginianus*)	....	....	0.2*
Hairy Woodpecker (*Dendrocopos villosus*)	....	....	2.4
Kentucky Warbler (*Oporornis formosus*)	....	....	0.1
Magnolia Warbler (*Dendroica magnolia*)	....	....	0.3
Red-bellied Woodpecker (*Centurus carolinus*)	....	....	6.4*
Red-eyed Vireo (*Vireo olivaceus*)	....	....	0.3
Scarlet Tanager (*Piranga olivacea*)	....	....	4.8*
Screech Owl (*Otus asio*)	....	....	0.2
White-breasted Nuthatch (*Sitta carolinensis*)	....	....	9.2*
Wood Thrush (*Hylocichla mustelina*)	....	....	13.8*
Yellow-billed Cuckoo (*Coccyzus americanus*)	....	....	0.2
Yellow-throated Vireo (*Vireo flavifrons*)	....	....	0.2
Yellow Warbler (*Dendroica petechia*)	....	....	0.1

* — nesting species
** — brood parasite, "nested" in spring, not present in summer

of the continued sampling, some species of autumn migratory warblers were recorded in 1968 but absent in 1969 (Table 6). In general, however, nonnesting species were unimportant. As in the cedar field, the lower importance of nonnesters reduced BSD variability.

Complete lists of the importance values of each species per plot per summer are available from the author by request.

DISCUSSION

The pattern of bird species diversity.—This study represents an analysis of three discrete points unequally distributed in a continuous process lasting over 100 years. The interval from the 2- to 3-year-old herbaceous field to the 29- to 30-year-old cedar field is 27 years, while the interval from the cedar field to the oak forest is in excess of 100 years. The average change in diversity (H′) from the 2- to 3-year-old to 29- to 30-year old-field was approximately 1.06, while from the 29- to 30-year old-field to the oak forest the change was only 0.29. If the change is directional and continuous, it indicates an extremely rapid increase in BSD during early succession and a very gradual change in BSD from year 30 to approaching climax. A similar pattern was observed by Karr (1968) in Illinois. Such a pattern is generally similar to that suggested by Margalef (1963), who hypothesized that species diversity increases most rapidly during early succession.

The present study was limited to only three seral stages in order to permit thorough statistical analyses. However, Johnston and Odum (1956) provide data on avian succession for nine seral stages on the Georgia Piedmont. When these data are reanalyzed using the Shannon-Weaver formula, the pattern revealed is that of a rapid increase in BSD during early succession and a gradual increase in later stages (Fig. 6). Margalef (1963) has suggested that species diversity may decline slightly during the final stages of succession. However, for avian succession on the Georgia Piedmont, as well as in the present study, no diversity peak is reached prior to near climax (Fig. 6).

BSD variability and habitat instability.—What factors are responsible for the trends in variability observed in this study? Variability is simply the failure of any given individual bird to be recorded on every census. If a bird is absent from a census, it is because (1) the bird

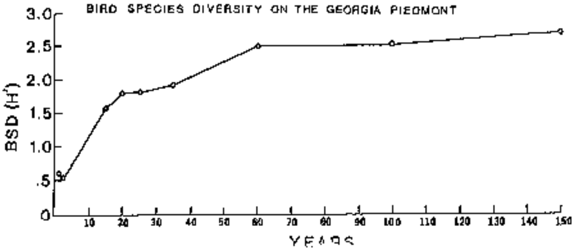

Fig. 6.—Bird species diversity changes during succession on the Georgia Piedmont (from Johnston and Odum, 1956)

was not present in the study area at the time of the census or (2) the bird was present and the observer overlooked it.

The presence or absence of any given bird in a seral stage is determined by the use the bird makes of the habitat. A bird may use a habitat for nesting or feeding or both. In the present study, all birds occurring in the habitat were included on the census. Importance values showed that nonnesting species were of considerable importance, especially in the herbaceous field.

The failure of the observer to detect a bird present in the study area is a function of the habitat complexity. It is naturally more difficult to find all birds in a structurally complex habitat than in a structurally simple habitat. The three seral stages studied differed greatly in their structural complexities, the herbaceous field being the simplest and the oak forest being the more complex. However, if the BSD variability observed in this study was caused mostly by the failure of the observer to detect the bird, then the variability would be greatest in the oak forest and least in the herbaceous field. Exactly the opposite occurred.

If, on the other hand, the variability resulted from movement of the bird in or out of the habitat, then the variability would be expected to be the least in the oak forest, since the oak forest contained the highest percentage of nesting species. These species were territorial and therefore static compared with nonnesting species. The most variability would be expected in the herbaceous field, since the most important species were nonnesters that moved freely in and out of the habitat.

The specific cause of BSD variability in each seral stage may now be examined. In the herbaceous field, this variability probably resulted almost entirely from movement of nonnesting species in and out of the habitat. In the cedar field, BSD variability probably resulted in part from increased habitat completely causing some birds to be missed, but the movement of nonnesting birds was still a relatively important cause of variability. Nonnesting birds were much less important in the cedar field, and, since the habitat was not difficult to sample, the variability was much reduced. Nonnesting birds were even less important in the oak forest, but the structural complexity of the habitat was much increased over the other seral stages. The increased complexity of the habitat caused some birds to be missed on each census and this probably accounted for most of the variability. If it were not for the increased complexity of the oak forest causing increased difficulty in sampling, the oak forest would be expected to have shown distinctly less variability than the cedar field.

How does variability in BSD relate to succession theory? Variability reflects change and change is an outstanding characteristic of early old-field succession. Rapid temporal change is a criterion for calling early successional stages "unstable." The day-to-day variability in BSD may be a reflection of the rapidity of habitat change. The emerging pattern of BSD in early old-field succession is one of change and oscillation due to the periodic presence or absence of flocks of feeding birds. These birds are opportunistic in the sense that although the ecosystem fails to offer them suitable nesting conditions, it does offer a food source for at least some part of the summer and the birds avail themselves of this source. Day-to-day abundances vary as species move both locally from field to field and as they move through the area during migration. Although few species are adapted to breed within the ecosystem, the avian food web is quite complex. A marked variability due to nonnesting birds (which may be the most "important" birds in the ecosystem from an energetics standpoint) may characterize an unstable ecosystem. As succession proceeds and change becomes less rapid, BSD variability decreases because more nesting areas become available, and possibly because food sources become more constant.

There is some question as to whether a seral stage actually does constitute an unstable ecosystem, since a seral stage is merely a component in the succession process. What seems to be at issue is not the definition of stability *per se*, but the period of time involved. Loucks (1970) is of the opinion that stability should be considered over a much longer period of time than is required for succession, and that the term unstable is inappropriate in reference to seral stages. Simpson (1969), considering stability in terms of geologic time, has concluded that long-range stabilization of earth's ecosystems has not as yet been reached.

The process of succession, although predictable and perhaps cyclic (Loucks, 1970), is nonetheless a progressive *development* of as stable an ecosystem as is possible on the site in question (Odum, 1969). The fact that a stable ecosystem is in the process of developing implies clearly that such stability must be preceded by instability. The biotic community present at any given time as succession proceeds does in fact exist in an unstable system as far as most of the organisms are concerned. As succession continues, the degree of instability, as measured by the rapidity of change in the biotic components (a definition similar to that of MacArthur, 1955), decreases steadily. It does not seem unreasonable to describe seral stages as unstable communities when viewed in the frame of reference of the individual species populations involved.

Attempts have been made to prove that species diversity and ecosystem stability are, if not cause and effect, at least intimately related (MacArthur, 1955; Hutchinson, 1959; Connell and Orias, 1964; Hairston *et al.*, 1969). Species diversity is supposedly lowest where the ecosystem is least stable. However, it has been shown that low BSD is found in relatively stable ecosystems, such as the North American grasslands (Cody, 1966, 1968).

The BSD data in the present study do not provide an answer as to what cause-effect relationships exist between species diversity and ecosystem stability, but they do not conflict with the hypothesis that stability is least where diversity is lowest (or vice versa). The entire question of how diversity and stability are related could prove to be an ecological "chicken or the egg." Concerning succession, a reasonable argument would seem to be that once the process is initiated, a strong positive feedback exists between diversity and stability. Each is both a cause and an effect. Such characteristics as larger organisms, longer, more complex life cycles, and narrower niches develop as ecosystems reach maturity (Odum, 1969). These characteristics may serve as negative feedbacks which progressively slow the succession process.

What relates BSD to instability is not the magnitude of the diversity index itself, but the variability of the index. Variability changes should be just as intensely studied as diversity changes. Although low species diversity may not always indicate an unstable ecosystem, low species diversity plus high diversity index variability may. In terms of bird species diversity, variability is due to nonnesting birds. Therefore, the lower the percentage of nesting birds to total bird species found in the ecosystem, the more unstable may be the ecosystem. Perhaps variability and instability are really the same thing.

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REFERENCES

A.O.U. CHECK-LIST COMMITTEE. 1957. Check-list of North American birds. 5th ed. Amer. Ornithol. Union.

BARD, G. E. 1952. Secondary succession on the Piedmont of New Jersey. *Ecol. Monogr.,* **22**:195-215.

BRAY, J. R. AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ibid.,* **27**:325-349.

BRILLOUIN, L. 1960. Science and information theory. 2nd ed. Academic Press, New York. 320 p.

CODY, M. L. 1966. The consistency of intra- and inter-continental grassland bird species counts. *Amer. Natur.,* **100**:371-376.

———. 1968. On the methods of resource division in grassland bird communities. *Ibid.,* **102**:107-147.

CONNELL, J. H. AND E. ORIAS. 1964. The ecological regulation of species diversity. *Ibid.,* **98**:399-414.

ELTON, C. S. 1958. The ecology of invasions by plants and animals. Methuen and Co., London. 181 p.

HAIRSTON, N. G. 1959. Species abundance and community organization. *Ecology,* **40**:414-416.

———, J. D. ALLAN, R. K. COLWELL, D. J. FUTUYAMA, J. HOWELL, M. D.

LUBIN, J. MATHIAS AND J. H. VANDEMEER. 1969. The relationship between species diversity and stability: An experimental approach with protozoa and bacteria. *Ibid.,* **49**:1091-1101.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *Amer. Natur.,* **93**:145-159.

JOHNSTON, D. W. AND E. P. ODUM. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. *Ecology,* **37**:50-62.

KARR, J. R. 1968. Habitat and avian diversity on strip-mined land in East Central Illinois. *Condor,* **70**:348-357.

KRICHER, J. C. 1970. Bird species diversity in relation to secondary succession on the New Jersey Piedmont. Ph.D. Thesis, Rutgers Univ., New Brunswick, New Jersey. 123 p

LOUCKS, O. L. 1970. Evolution of diversity, efficiency, and community stability. *Amer. Zool.,* **10**:17-25.

MACARTHUR, R. H. AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology,* **42**:594-598.

———, ——— AND J. PREER. 1962. On bird species diversity — Prediction of bird census from habitat measurements. *Amer. Natur.,* **96**:167-174.

———. 1965. Patterns of species diversity. *Biol. Rev.,* **40**:510-533.

MARGALEF, D. R. 1956. Información y diversidad específica en las comunidades de organismos. *Invest. Pesq.,* **3**:99-106.

———. 1957. La teoria de la información en ecologia. *Mem. Real Acad. Cienc. Artes Barcelona,* **32**:373-449.

———. 1958. Information theory in ecology. *Gen. Systems,* **3**:36.

———. 1963. On certain unifying principles in ecology. *Amer. Natur.,* **97**: 357-374.

———. 1968. Perspectives in ecological theory. Univ. of Chicago Press, Chicago. 111 p.

MONK, C. D. 1957. Plant communities of the Hutcheson Memorial Forest based on shrub distribution. *Bull. Torrey Bot. Club,* **84**:198-206.

———. 1961. The vegetation of the William L. Hutcheson Memorial Forest, New Jersey. *Ibid.,* **88**:156-166.

ODUM, E. P. 1950. Bird populations of the highlands (North Carolina) plateau in relation to plant succession and avian invasion. *Ecology,* **31**:587-605.

———. 1963. Ecology. Holt, Rinehart, Winston, New York. 152 p.

———. 1969. The strategy of ecosystem development. *Science,* **164**:262-270.

PATTEN, B. C. 1959. The diversity of species in net phytoplankton of the Raritan estuary. Ph.D. Thesis, Rutgers Univ., New Brunswick, New Jersey. 111 p.

———. 1962. Species diversity of net phytoplankton of Raritan Bay. *J. Mar. Res.,* **20**:57-75.

PIANKA, E. R. 1966. Latitudinal gradients in species diversity — a review of concepts. *Amer. Natur.,* **100**:33-45.

PIELOU, E. C. 1966a. Species diversity and pattern diversity in the study of ecological succession. *J. Theor. Biol.,* **10**:370-383.

———. 1966b. The measurement of diversity in different types of biological collections. *Ibid.,* **13**:131-144.

———. 1966c. Shannon's formula as a measure of specific diversity: Its use and misuse. *Amer. Natur.*, **100**:463-465.

———. 1966d. The use of information theory in the study of the diversity of biological populations. *Proc. 5th Berkeley Symp. Math. Statist. Probab.*, **4**:163-177.

———. 1969. An introduction to mathematical ecology. John Wiley and Sons, New York. 286 p.

RECHER, H. F. 1969. Bird species diversity and habitat diversity in Australia and North America. *Amer. Natur.*, **103**:75-80.

SHANNON, C. E. 1948. A mathematical theory of communication. *Bell Syst. Tech. J.*, **27**:379-423, 623-656.

——— AND W. WEAVER. 1949. The mathematical theory of communication. Univ. Illinois Press, Urbana. 117 p.

SHURE, D. J. 1971. Insecticide effects on early succession in an old field ecosystem. *Ecology*, **25**:271-279.

SIMPSON, G. G. 1969. The first three billion years of community evolution, p. 162-176. *In:* Brookhaven National Laboratory. Diversity and stability in ecological systems. U.S. Dep. of Commerce, Virginia.

STEEL, R. G. D. AND J. H. TORRIE. 1960. Principles and procedure of statistics. McGraw-Hill, New York. 481 p.

WILLIAMS, A. B. 1936. The composition and dynamics of a beech-maple climax community. *Ecol. Monogr.*, **6**:317-408.

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