DIVERSITY IN TWO WINTERING BIRD COMMUNITIES: POSSIBLE WEATHER EFFECTS

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THE study of bird species diversity has thus far been concerned primarily with nesting bird communities (MacArthur and MacArthur 1961, Karr 1968, Recher 1969, Kricher 1973). Comparable studies on winter bird communities are less frequent (but see Emlen 1972, Austin and Smith 1972). This is unfortunate because winter presents a very distinct series of stresses to avian populations, differing from those of the nesting season. In winter, birds in north temperate latitudes are concerned only with individual survival. There is no singing, courtship display, or nesting activities. Acquisition of food is of prime importance to birds occupying a winter environment characterized by short daylight hours and an ambient temperature usually many degrees below body temperature (Gordon et al. 1968). Migration testifies to the rigors of the temperate winter environment. Recent studies of avian population biology (Lack 1966, 1968; Fretwell 1969, 1972) emphasized the possible importance of the winter season as a regulator of population size.

The objective of this paper is to examine the patterns of winter bird species diversity over a 2-year period in two ecosystems of the New Jersey Piedmont. Considerable attention has been paid to possible relationships between weather factors and avian population and diversity changes. It is hoped that the elucidation of patterns in winter bird species diversity will contribute a greater understanding to the importance of the winter season relative to population regulation and will also contribute to an increased understanding of how ecosystems function.

METHODS

The two ecosystems studied were a 30-year-old successional field and a mature oak-hickory forest. Both were near East Millstone, New Jersey, on the New Jersey Piedmont, and about 1 km apart.

The 30-year-old field (to be referred to as "the cedar field") provided an ecosystem representative of near midpoint in the pattern of secondary succession on the Piedmont (Bard 1952). It was a semiopen field dominated by red cedar (*Juniperus virginiana*), northern bayberry (*Myrica pensylvanica*), and little bluestem (*Andropogon scoparius*). The most distinct characteristic of the field was the horizontal patchiness of the vegetation. Open growths of *Andropogon* were interspersed with dense patches of *Myrica*. *Juniperus*, while found throughout the field, also tended to grow in dense patches, often with deciduous trees (*Acer rubrum, Quercus palustris*). The field was 5 ha in area and was bordered by cultivated fields and successional fields of similar age.

The forest studied (to be referred to as "the oak forest") was the William L.

Hutcheson Memorial Forest, 26 ha in area and surrounded by cultivated and abandoned fields. Much of the forest is considered virgin and the vegetation has been described (Monk 1961). The forest is dominated by three species of oak (*Quercus alba, Q. veluntina, Q. rubra*) and red hickory (*Carya ovalis*). Vertical stratification is quite distinct, the subcanopy being *Cornus florida.*

Within each study tract, two rectangular study plots, A and B, were used for taking bird censuses. Each plot was 100 by 200 m covering an area of 2 ha. Two plots within each study tract were used to provide an estimate of variability within it. Regular censuses were made during the winters of 1968–69 and 1969–70. Each plot was sampled once per week from 17 December through 13 March, a 13-week period. As each tract had two plots, each study area was sampled a total of 26 times per winter (twice a week). All bird censuses were made between 0700 and 1000. The design was such that no plot was censused more at one hour than at another. Censuses were made by cruising the plots on foot and identifying all birds encountered within the plots. Each census period lasted 45 min.

Data on air temperature were taken at 0830 at each census. In addition, data on air temperature and precipitation taken at 0730 were available for all days of both winters from the records of the Hutcheson Forest weather station.

Bird species diversity was calculated using the Shannon-Wiener information formula $H' = -\sum_i p_i \log_e p_i$. Species diversity data were analyzed by the analysis of variance and Student's *t*-test following procedures described by Steel and Torrie (1960). Prior to each Student's *t*-test, the data were tested for normality and the variances of the two means were tested for significant differences at the 0.05 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. All diversity indices were normalized by transformation, using the formula $x' = \sqrt{x + 1}$.

Importance values were calculated for all bird species per study plot per winter. The importance value was defined as the relative density per census plus the relative frequency (percent of the total number of censuses on which a given species appeared) (Kricher 1973). Since both relative density and relative frequency are percent values, the maximum importance value a species could have was 200. The importance value allows one to consider species that are periodically common along with species that may be consistently uncommon but nonetheless regular members of the community. Importance values were employed only to assess similarity between bird communities using the formula for the coefficient of community (Kricher 1973).

Results

In the two-winter study, totals of 25 and 22 species were identified in the cedar field and oak forest respectively (Table 1). These totals represent only species richness. With regard to mean bird species diversity (H′), in both winters, the oak forest exceeded the cedar field (Table 2). Compared with other seasons, winter was clearly the season of lowest species diversity in both ecosystems (Kricher 1972).

To test for significance of differences in diversity due to years, seral stages, time, and the various interactions among these variables, a partially hierarchic analysis of variance was performed. The analysis of variance and F statistic (Table 3) indicated that significant differences

TABLE 1

MEAN IMPORTANCE VALUE OF ALL SPECIES RECORDED DURING THE STUDY[1]

Species	Cedar field	Oak forest
Red-tailed Hawk (*Buteo jamaicensis*)	2.5	3.8
Red-shouldered Hawk (*Buteo lineatus*)	—	0.6
Marsh Hawk (*Circus cyaneus*)	2.1	—
American Kestrel (*Falco sparverius*)	2.1	—
Ring-necked Pheasant (*Phasianus colchicus*)	4.0	0.6
Mourning Dove (*Zenaida macroura*)	1.1	1.7
Screech Owl (*Otus asio*)	1.7	—
Great Horned Owl (*Bubo virginianus*)	—	0.6
Saw-whet Owl (*Aegolius acadicus*)	1.0	—
Common Flicker (*Colaptes auratus*)	1.1	2.8
Red-bellied Woodpecker (*Centurus carolinus*)	—	7.0
Hairy Woodpecker (*Dendrocopos villosus*)	—	7.4
Downy Woodpecker (*Dendrocopos pubescens*)	5.6	28.8
Blue Jay (*Cyanocitta cristata*)	9.6	3.6
Common Crow (*Corvus brachyrhynchos*)	1.1	8.4
Black-capped Chickadee (*Parus atricapillus*)	37.9	24.4
Boreal Chickadee (*Parus hudsonicus*)	1.1	—
Tufted Titmouse (*Parus bicolor*)	1.1	29.9
White-breasted Nuthatch (*Sitta carolinensis*)	—	17.8
Brown Creeper (*Certhia familiaris*)	—	10.5
Mockingbird (*Mimus polyglottos*)	1.0	—
Robin (*Turdus migratorius*)	3.5	—
Eastern Bluebird (*Sialia sialis*)	2.8	—
Golden-crowned Kinglet (*Regulus satrapa*)	8.7	4.0
Starling (*Sturnus vulgaris*)	2.0	10.7
Yellow-rumped Warbler (*Dendroica coronata*)	39.4	—
Cardinal (*Cardinalis cardinalis*)	6.9	4.9
Purple Finch (*Carpodacus purpureus*)	6.9	—
Common Redpoll (*Acanthis flammea*)	1.0	—
American Goldfinch (*Spinus tristis*)	—	.8
Dark-eyed Junco (*Junco hyemalis*)	29.8	28.0
Tree Sparrow (*Spizella arborea*)	24.5	1.5
White-throated Sparrow (*Zonotrichia albicollis*)	—	2.8

[1] All scientific names according to A.O.U. (1957, 1973).

in bird species diversity (H′) existed between the cedar field and oak forest. In addition, highly significant effects were found for time and the interactions of time with years and with seral stages.

The only variable not testable with the analysis of variance was the

TABLE 2

PLOT MEANS AND STANDARD DEVIATIONS FOR BIRD SPECIES DIVERSITY FOR THE TWO WINTERS OF THE STUDY

Year	Cedar field		Oak forest	
	Plot A	Plot B	Plot A	Plot B
1968–69	0.897 ± 0.160	0.884 ± 0.126	1.150 ± 0.105	1.300 ± 0.156
1969–70	0.612 ± 0.132	0.385 ± 0.105	1.183 ± 0.161	1.332 ± 0.143

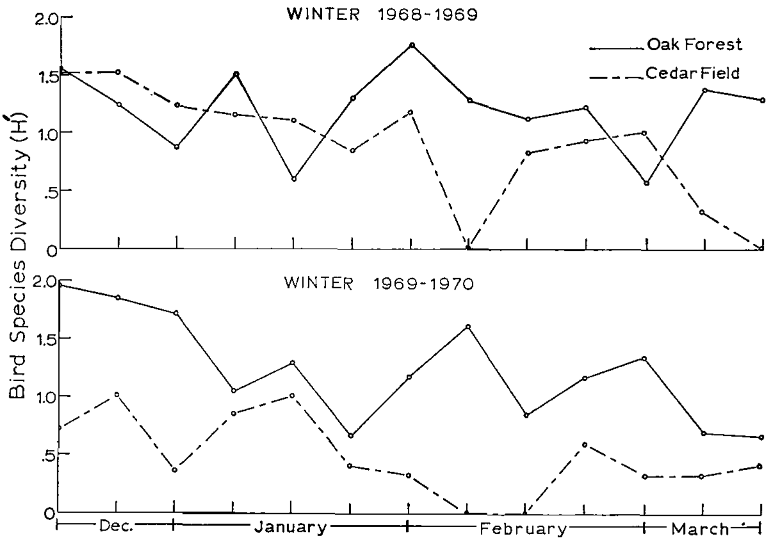

Fig. 1. Mean weekly BSD in cedar field and oak forest in winters of 1968–69 and 1969–70.

difference between plot means (Table 2) within a seral stage. Student's *t*-tests showed that the A and B plot means were not significantly different in either seral stage in either year of the study. Bird species diversity decreased as each winter proceeded (Fig. 1). This temporal decrease was disproportionate between years and between seral stages (hence the highly significant interactions shown in the analysis of variance). The oak forest in 1968–69 showed oscillation in diversity from week to week but no absolute decline, but in 1969–70, the oak forest showed a

TABLE 3

Comparison of Analysis of Variance (ANOVA) Results for H' and S

		Shanon-Wiener (H')			Species richness (S)		
Source	DF	SS	MS	F	SS	MS	F
Total	103	4.7585	–	–	467.65	–	–
Years	1	0.1614	0.1614	2.68	6.50	6.50	1.09
Seral stages	1	1.1159	1.1159	18.54[1]	124.96	124.96	20.93[1]
Y × SS	1	0.1361	0.1361	2.26	11.11	11.11	1.86
Plots (Y × SS)	4	0.2409	0.0602	–	23.88	5.97	–
Time	12	1.0036	0.0836	76.00[2]	86.40	7.20	28.99[2]
Y × T	12	0.2670	0.0222	20.18[2]	39.25	3.27	13.17[2]
SS × T	12	0.4168	0.0347	31.54[2]	20.79	1.73	6.97[2]
Y × SS × T	12	1.3616	0.1135	103.18[2]	142.79	11.90	47.71[2]
Plots (Y × SS × T)	48	0.0552	0.0011	–	11.97	0.25	–

[1] $0.025 > P > 0.010$.
[2] $P < 0.005$.

TABLE 4

MEAN SPECIES RICHNESS (S)

	Oak forest				Cedar field			
	1968–69		1969–70		1968–69		1969–70	
	A	B	A	B	A	B	A	B
First 4 weeks	4.75	5.25	6.00	6.25	5.00	4.00	3.00	2.25
Second 4 weeks	3.25	6.25	4.00	5.75	2.25	3.00	1.50	1.75
Third 5 weeks	4.20	4.00	3.40	3.60	2.20	2.20	2.00	1.00

clear decline in avian diversity as winter proceeded. The cedar field showed clear declines in diversity throughout both winters (Fig. 1).

Declining diversity can be explained in several different ways, because two components, species richness and equitability, interact within each diversity index. The relationship between these two components and the relative influence of each on the diversity index has been discussed by Tramer (1969) and Kricher (1972). Essentially the diversity index increases if an increase occurs in species richness (S) or equitability (J') or both. Two communities, one with say 10 species and the other with 15 species, could have equal species diversities if the 10 species of the first community were considerably closer to having equal population sizes (higher equitability) than the 15 species of the second community. The significant drop in diversity in both winters could have resulted from (1) decreased species richness (fewer species observed per census), (2) lowered equitability (one or a few species became more abundant relative to the total number of birds observed), or (3) both the above.

Decreasing species richness appears to be the major reason for the temporally decreasing diversity index. Table 4 divides each winter into nearly equal thirds and shows the mean species richness for each third. Decreases in species richness occurred both winters in both ecosystems. Though some decreases in mean equitability were noted (Table 5) there were no clear trends toward decreasing equitability, as there were for species richness. Equitability values stayed consistently high.

The same analysis of variance that was performed on the diversity index data was performed on the species richness data (Table 3). The F values, though generally more robust for the diversity data, were nonetheless strikingly similar. Tests of significance yielded exactly the same probability estimates in both analyses (Table 3). This means that the trends described by the diversity index could have been just as adequately detected by merely counting the species present, without regard to population numbers. The numbers of species present in the study tracts decreased significantly as time proceeded each year. The fact that only

TABLE 5

MEAN EQUITABILITIES (J′)

	Oak forest				Cedar field			
	1968–69		1969–70		1968–69		1969–70	
	A	B	A	B	A	B	A	B
First 4 weeks	0.92	0.86	0.95	0.95	0.93	0.86	0.86	0.78
Second 4 weeks	0.90	0.86	0.75	0.89	0.92	0.95	1.00	0.88
Third 5 weeks	0.81	0.91	0.90	0.80	0.97	0.89	0.95	0.49

species richness decreased (not equitability) could indicate that the decrease in species was not selective, i.e. otherwise different proportions would occur and this would be reflected in fluctuating equitabilities. Decreasing richness without decreasing equitability would also suggest that fewer total birds were being recorded, as was indeed the case (Table 6). Few species and fewer individuals were noted per week throughout each winter.

The analysis of variance and F tests indicated that significant interactions between time and years and time and seral stages existed (Table 3). This means that the differences in diversity (and/or species richness) that occurred over time were not the same from one year to the next nor were they the same, in a given year, from one seral stage to the other. Decline in species over time was more severe in the cedar field than in the oak forest (Fig. 1) and the cedar field experienced a marked decrease in species diversity in 1969–70 (Table 2). The oak forest experienced no such decrease. One asks what caused the decreasing diversity and species richness through the course of each winter, and why was the decrease more severe in the cedar field?

In winter the severity of local weather would be expected to influence the food and shelter requirements of birds. Microclimate (as perceived by birds) probably differed in the two seral stages because of their differing structural complexities. The oak forest was a well-stratified ecosystem with many tree cavities and patchy but often dense undergrowth. The cedar field was more exposed though the *Juniperus virginiana* and

TABLE 6

MEAN NUMBER OF BIRDS PER CENSUS

	Oak forest		Cedar field	
	1968–69	1969–70	1968–69	1969–70
December	10.0	12.2	10.3	14.0
January	11.3	10.0	5.3	3.0
February	7.0	8.0	4.0	3.0

TABLE 7
MEAN TEMPERATURES, STANDARD DEVIATIONS, AND CO-EFFICIENTS OF VARIABILITY FOR THE TWO WINTERS OF THE STUDY

	1968–69	1969–70
December	26.1 ± 10.1 (39%)	27.2 ± 8.8 (32%)
January	24.7 ± 10.2 (41%)	17.1 ± 11.0 (64%)
February	26.0 ± 7.3 (28%)	27.6 ± 9.0 (32%)
March	32.0 ± 7.7 (24%)	32.4 ± 5.9 (18%)

Myrica pensylvanica gave the birds some food and shelter; *Andropogon* and related grass species gave them seeds but no shelter.

The two winters of the study clearly differed in the severity of local weather conditions. In 1968–69, the mean temperature prior to each census of the oak forest was 29.7° F ± 1.40° F (N = 13). In 1969–70, it was 22.7° F ± 3.04° F (N = 13). The coefficients of variability were 17 and 48, respectively. The lowest temperature recorded in 1968–69 was 21° F, while in 1969–70, the lowest temperature was 2° F.

In addition to the above readings standard temperature and precipitation readings were taken daily at 0730 at the Hutcheson Forest weather station. Those data indicate that the two winters of the study differed in temperature principally during January (Table 7). The mean difference was tested for significance using Student's *t*-test and found to be significant at the 0.01 probability level. With regard to precipitation, in 1968–69 snow covered the ground for 39 days, including an uninterrupted 34-day period from 9 January to 14 March. In 1969–70, however, the ground was snow-covered for a total of 50 days including an uninterrupted 36-day period from 26 December to 30 January. On the evening of 1 January 1970 a severe ice storm coated trees, bushes, and grass with up to 0.5 inches of ice for the following 4 days before extensive thawing occurred. No ice storms occurred in the winter of 1968–69.

It could be argued that the temperature data were recorded at discrete intervals and to examine a continuous variable in a discrete way is invalid. However bird censuses themselves represent discrete samples of what amounts to a continuous variable and few object to discussing means and variabilities of census data. The temperature data indicate simply that the winter of 1969–70 was, on the average, colder and subject to more temperature fluctuations than the previous winter. Also the winter of 1969–70 produced more snow and ice than the previous winter.

The statistically significant temporal decreases in bird species diversity, species richness, and total numbers observed in the cedar field in both winters and in the oak forest in 1969–70 could have been an effect of

TABLE 8

COEFFICIENTS OF COMMUNITY COMPARING THE SIMILARITY FROM ONE YEAR TO THE OTHER OF EACH STUDY PLOT

	Cedar field	Oak forest
Plot A	0.65	0.94
Plot B	0.86	0.91
Mean	0.76	0.93

weather on winter bird populations. Although neither microclimate nor available food sources were measured, temperature and precipitation did indicate that the overall climate was more severe in 1969–70, which could account for (1) the much lower diversity in the cedar field in 1969–70 and (2) the decrease in the oak forest diversity in 1969–70. As the diversity of the cedar field decreased significantly during both winters, it could be hypothesized that the field's more rigorous local climate caused greater mortality and/or dispersion than in the oak forest.

The cedar field and oak forest differed in one other major respect. The species most often recorded in the cedar field tended to occur in small conspecific flocks. Uniform flocks of Yellow-rumped Warblers, Dark-eyed Juncos, Tree Sparrows, Black-capped Chickadees, and Golden-crowned Kinglets occurred there during both winters. Mixed species flocks were unusual in the cedar field, but in the oak forest mixed flocks were the rule rather than the exception. Black-capped Chickadees, Tufted Titmice, White-breasted Nuthatches, Downy Woodpeckers, Brown Creepers, and Golden-crowned Kinglets all tended to forage in each other's presence. Members of the genus *Parus* consistently dominated (a pattern identical to that noted by Austin and Smith 1972). Mixed flocks of the above species were recorded on 61% of the censuses in the oak forest in 1968–69 and on 42% of the censuses in 1969–70.

The coefficient of community was calculated for each study plot in both ecosystems to compare the similarity of avian communities in each plot from one year to the other. These figures (Table 8) show clearly that the oak forest avian communities were considerably more similar during the two year period than those of the cedar field.

DISCUSSION

Viewed in light of current succession theory, the difference between the results found for the cedar field and oak forest could be interpreted as indicative of the differing degree of stability present in each ecosystem. The fact that species diversity was significantly higher in the oak forest is consistent with the hypothesis that more mature ecosystems have higher diversity (Margalef 1968; Odum 1969, 1971). The higher avian diversity in the oak forest was probably a reflection of the increased structural complexity of that ecosystem. Emlen (1972) found that species diversity in wintering avian communities in Texas was highest in ecosystems with trees and shrubs, lowest in prairies, and intermediate in brushlands.

In several ways the data suggest strongly that the cedar field is a less stable ecosystem than the oak forest. Not only was species diversity lower in the cedar field, but the variability in species diversity was distinctly higher (Table 2). Kricher (1973) has argued that species diversity variability is indicative of ecosystem instability. In addition, the avian communities in the cedar field plots showed less similarity from one year to the other than did those of the oak forest. Such a difference is to be expected for two ecosystems differing in degree of stability.

The clear presence of mixed species flocks in the oak forest and their absence in the cedar field has implications relative to stability. The mixed species flocks of the forest could indicate a longer evolutionary association. This association could result in a more efficient exploitation of the available resources of the ecosystem (Morse 1970, 1971). One would expect mixed species flocks to be more characteristic of mature ecosystems.

Finally the oak forest underwent less severe perturbation in species diversity. The oak forest declined temporally in diversity, species richness, and total numbers only in the more severe of the two winters. That decline was not nearly so dramatic as that in the cedar field. The avian community of the cedar field clearly underwent wider oscillations, a characteristic of a less stable ecosystem (Elton 1958).

The other aspect of this study that deserves attention is the trends in diversity (and its parameters) relative to possible weather influences. Without question a 2-year study is too brief for drawing firm conclusions, but the data indicate some correlations of possible interest.

It is clear that diversity, species richness, and total numbers per census declined significantly as winter proceeded in the cedar field during both years and in the oak forest in 1969–70. In addition the mean diversity was much reduced in the cedar field in 1969–70 compared with the previous winter. One is tempted to suggest that the declines in diversity, richness, and numbers reflect changes brought about by mortality and dispersion. The increased effects that occurred in 1969–70 could be attributed to the increased severity of that winter.

Some recent studies suggest that species wintering in temperate latitudes are highly responsive to weather influences. Willson (1970) showed that distinct winter foraging patterns exist between males and females within a species as well as between species of the "scansorial guild." Such a pattern indicates that rather precise resource division must be occurring, something that would be predicted for species coexisting in a rigorous environment. Morse (1970) showed that members of the genus *Parus* increase the time spent foraging on the ground when snow is thinner and also pointed out the importance of ice storms to avian mortality. Morse (1970, 1971) concluded that mixed species flocks are an adaptive strategy to cope with difficult conditions while providing for maximum resource exploitation. Morse (1967) has suggested that foraging patterns between two species would be most distinct under more severe environmental conditions. Hadow (1973), studying the winter ecology of *Asyndesmus lewis*, found that aggressive encounter displays toward both heterospecifics and conspecifics increased in frequency on "snowy" days (when the temperature dropped below 0°C and the ground was snow-covered).

The substance of the argument presented here is that the avian communities of the cedar field and oak forest were affected by weather, and each was affected in a particular way. It is impossible to know whether the decreases were due to mortality or dispersion. It is not unreasonable to suppose that both were involved. Even if dispersion was the principal cause of the losses such losses do represent a sort of "mortality" to the ecosystem. Also those birds must have gone somewhere. Emigration from an ecosystem usually increases mortality risks.

If mixed flocks do serve to provide for maximum resource exploitation in stressed situations, as Morse suggests, it would not be surprising that the oak forest would be less subject to avian declines than the cedar field. Mixed flocks occurred frequently in the oak forest but only rarely in the cedar field. What is surprising is that mixed species flocks were least frequent in the oak forest in the more severe of the two winters. One seemingly would have predicted just the opposite.

The question of the effect of winter weather on temperate bird populations has been debated before. Lack (1966) argued convincingly that only very severe winter weather directly affected the populations of *Parus major* in Marley Wood and concluded that winter population sizes in relation to food supply could be of major importance in regulating bird populations. Lack (1968) suggested that winter survival of birds is determined in a density dependent way by the amount of food present on the wintering grounds. Both Lack's (1966) and Fretwell's (1972) analyses of the Marley Wood data concluded that *Parus major* was limited by winter resources but that the mortality seems to occur before winter even begins. Fretwell (1972) suggested the possibility of group selection acting within the species.

It does not seem unreasonable to hypothesize that winter weather and food supply act in a synergistic manner to affect avian populations.

Despite the conclusions from the Marley Wood data, Lack (1966) noted that winter cold did appear to affect a Dutch population of *Parus major* between 1912 and 1943. Weather severity and food availability are two variables of tremendous importance to birds in winter. The present study has shown that significant decreases occurred in species diversity, species richness, and total numbers in two avian communities in the course of two winters, the most severe decreases occurring in the more severe winter. Perhaps what was happening in these ecosystems was described by Darwin (1859) in chapter III of the "Origin": "I estimated that the winter of 1854–55 destroyed four-fifths of the birds in my own grounds; and this is a tremendous destruction, when we remember that ten per cent is an extraordinarily severe mortality from epidemics with man. The action of climate seems at first sight to be quite independent of the struggle for existence; but in so far as climate chiefly acts in reducing food; it brings on the most severe struggle between the individuals, whether of the same or of distinct species, which subsist on the same kind of food."

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SUMMARY

Two ecosystems, a mature oak-hickory forest and a 30-year-old successional red cedar field, were studied with regard to their winter bird communities. Species diversity was found to be highest in the oak-hickory forest. Significant decreases in bird species diversity over time were observed in both winters of the study and these decreases were more severe in the red cedar field. Differing severity of weather between the two winters of the study correlated with some of the diversity and population trends. The results, studied in the light of current succession theory, support the contention that the red cedar field represents a less stable ecosystem than the oak-hickory forest, and suggest the possibility that bird populations are at least partially regulated by winter factors.

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