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BREEDING BIRD POPULATIONS IN THE GREAT SMOKY MOUNTAINS, TENNESSEE AND NORTH CAROLINA

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The analysis of bird populations in mountain systems, such as the Great Smoky Mountains, is of special interest because of the relations of these populations to the mosaic of vegetation types and to variations in climate and physical conditions that occur. The Great Smoky Mountains of eastern Tennessee and western North Carolina lie at the southern end of the Appalachian Mountain System, escaped glaciation during the Pleistocene epoch, have sufficient elevation to provide a considerable gradient of temperature and contain a variety of slope exposures with striking contrasts in moisture conditions (Shanks 1954, Whittaker 1956).

The many different types of vegetation in the Great Smoky Mountains National Park are in nearly virgin condition. The deciduous plant communities have remained relatively undisturbed since the early Tertiary, and their diversity of plant species is the richest within the deciduous forest biome. Coniferous forests of different types and past history occur at both low and high elevations.

Breeding bird censuses were taken in 26 areas, representing 8 types of climax or relatively stable vegetation and 4 seral stages. The fieldwork was carried out during June and July 1947 and from May through July 1948.

PLANT COMMUNITIES

The vegetation shows a continuum of change with elevation and slope exposures (Fig. 1). For convenience, however, separate plant communities are recognized, based on their dominant species (Whittaker 1956).

Cove hardwoods occur characteristically at lower elevations in moist shaded coves and on north-facing slopes. Eastern hemlock (*Tsuga canadensis*) occurs in some cove forests in mixed or nearly pure stands. Chestnut oak (*Quercus prinus*) (chestnut) and oak-hickory forests prevail on east and west slopes, while on exposed, drier south and southwest slopes, subject also to more frequent fires, southern pine (*Pinus* spp.) forest or pines with an undergrowth of heath predominate.

At intermediate elevations, cove forests extend up into beech forests in gaps between mountains or on sheltered slopes, northern red oak (*Q. rubra*) (chestnut) and white oak (*Q. alba*) (chestnut) forests replace the chestnut oak (chestnut) forest, while on exposed ridges grassy balds replace trees. Chestnut (*Castanea*) is, of course, no longer a dominant, although at the time of this study many dead stubs scattered through the forest indicated their former importance. At cooler high elevations, spruce (*Picea*)-fir (*Abies*) forests predominate, although they give way to heath balds on xeric exposed ridges.

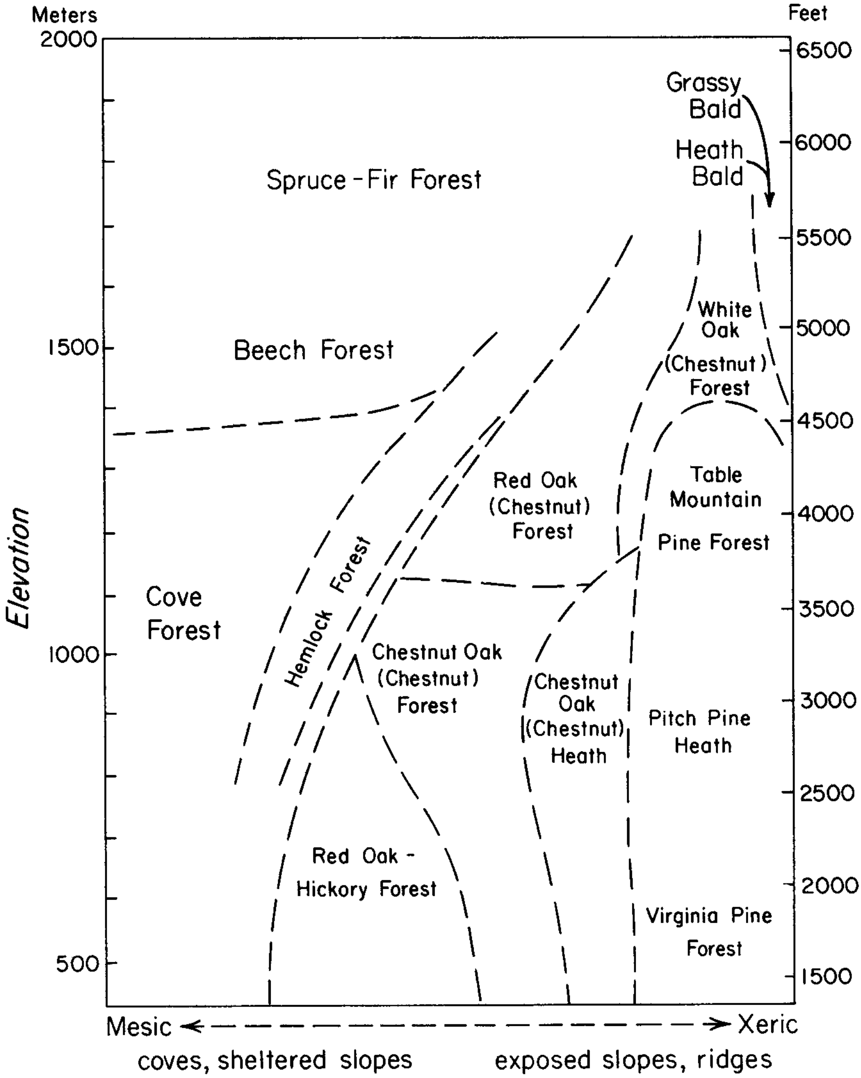

FIG. 1. Mosaic of plant communities showing variations with elevation and slope exposure (modified from Whittaker 1956).

METHODS OF ANALYSIS

Bird populations.—The spot-map method for censusing breeding birds was used where the terrain and available time permitted. Areas varied in size and shape depending on terrain and slope. They ranged from 6–12 ha (Table 1), which are rather small areas, but since each major vegetation type was censused at different localities, the total area covered in each vegetation type was at least 23 ha and usually over 40 ha. Boundaries were measured with a steel tape or by pacing and mapped to scale. Use was made of natural landmarks and of numbered white cards nailed to trees at 50-m intervals for locating birds, especially singing males, on maps. In several instances, areas were long strips along trails and only 1 line of markers was used. Bird counts were obtained in each area at least 4 times in 1947 and 5 times in 1948.

Cruising counts only were taken of singing males in several areas. These areas were of known size and thoroughly covered on each count. Two to 6 counts were made on each area; the largest number of each species observed on any count was taken as the population of that species. This follows Palmgren's (1930) procedure except that no corrections were made for smaller values often obtained with fewer than 4 or 5 counts. Ten comparable censuses obtained by spot-map and cruising procedures in 5 different types of vegetation, although not in the same area the same year, showed only a slight tendency for population size estimates to be lower with the cruising procedure.

Species occurring in different plots of the same vegetation type have been combined and their population sizes averaged (Table 2). Persons wishing the precise location, more complete description of the vegetation and data on the bird population of each sample plot should consult the doctorate thesis of the junior author (Fawver 1950) filed in the University of Illinois Library, Urbana.

Data.—Coefficients of species similarity (S_s) were calculated with the Sørenson equation (Able and Noon 1976):

$$S_s = 2C/(A + B)\cdot 100$$

where C represented number of species common to the 2 communities and A and B total number of species in each community. Multiplying by 100 transfers coefficients into percentages. In these comparisons, species were included with less than 0.5 pairs/40 ha (shown by + marks in Table 2). Larger-sized sampling areas would doubtless have permitted quantification of their densities. Percentages higher than 50 indicate that the 2 communities have more species alike than different.

The above equation does not evaluate the difference in abundance (number of pairs) of a species when it occurs in both communities. Coefficients of population similarity (S_p) were obtained by:

$$S_p = 1.0 - \frac{\Sigma(p_a - p_b)}{P_a + P_b}$$

where p_a is the population of a species in community a and p_b in community b and P_a and P_b are total populations of all species in communities a and b, respectively (Odum 1950). In this calculation the plus sign in Table 2 was taken as zero population.

The Shannon-Weiner species diversity index ($H' = \Sigma p \log_e p$) and equitability index ($J' = H'/H'_{max}$) were calculated for the birds in each plant community where p is the proportion each species population is of the whole and H'_{max}, the maximum possible diversity for the given population size and number of species, is the logarithm of the number of species (Pielou 1966, Sheldon 1969).

Mean number of pairs per species (p/s) and median population of each species were also determined. Skewness (g_1) in the distribution of population sizes among species in a community was calculated with the equation (Zar 1974):

$$g_1 = \frac{(x - \bar{x})^3}{(n - 1)(n - 2)(sd)^3/n}$$

where $x_1 = p/s$ for a species, $\bar{x}$ is the mean p/s, n is number of species, and sd is standard deviation. Testing for statistical significance was performed using Table D25 of Zar (1974).

TABLE 1

CENSUS AREAS AND BIRD CENSUSING METHODS

Plant community and location	Size (ha)	Spot-mapping		Cruising counts	
		1947	1948	1947	1948
Pine-oak forest					
Mature, 6.4 km NW of Gatlinburg	12.0	√	√		
Seral, opposite Park Headquarters	10.2	√	√		
Seral, 1.6 km farther south	6.0		√		
Cove forest					
Porters Creek	7.2		√		
Porters Creek	9.2			5	
Ramsey Prong	12.8				5
Ramsey Prong	6.8	√			3
Ramsey Prong	6.0		√		
Hemlock-deciduous forest					
Roaring Fork	10.0		√		
Roaring Fork	8.0				2
Brushy Mountain	11.6	√			4
Chestnut oak (chestnut) forest					
Bullhead Trail	7.6	√			6
Greenbrier Pinnacle Trail	9.0		√		
Red oak (chestnut) forest					
Greenbrier Pinnacle Trail	7.5				3
Thomas Divide, N.C.	10.0				2
Thomas Divide, N.C.	7.2				2
Pine heath					
Bullhead Trail	12.0	√	√		
Greenbrier Pinnacle Trail	10.0				3
Gray beech forest					
Double Springs Gap	7.6	√			
West of Siler's Bald	8.0		√		
Spruce-fir forest					
Climax, between Newfound Gap and Clingmans Dome	11.6	√	√		
Fraser fir, Clingmans Dome	6.8				2
Early seral, Mount Buckley	6.6	√			3
Mid-seral, Forney Ridge	5.6				3
Late seral, north of Andrews Bald	7.7				3
Heath bald					
Bullhead Trail	4.0				2
Brushy Mountain	10.0			2	

CENSUS AREAS

Pine-oak forest and sere.—The mature forest was an open stand of trees with a shrub layer of *Kalmia* and other Ericaceae. The ground was covered with a dry litter of pine and broad leaves. Two samples of a seral stage leading to the above forest contained both deciduous and pine trees, 1.8–6 m high, scattered through shrubs and open areas. Shrubs were predominantly greenbrier (*Smilax* spp.), smooth sumac (*Rhus glabra*) and briers (*Rubus* spp.). A luxurious growth of herbs covered most of the ground.

Cove forest.—All 5 areas censused were in the Greenbrier section of the Park. In 2 areas along Porters Creek, trees were widely spaced but made a deciduous canopy 25–45 m, occasionally 60 m, above the ground. Great rhododendron (*Rhododendron maximum*) made dense tangled thickets along the stream and herbs were luxuriant. The larger area had been censused by Aldrich and Goodrum (1946) the previous year. The 3 areas along Ramsey Prong are listed in ascending elevations. The lowest area had previously been cut over but had regained a closed canopy. The shrub layer in the highest area included sevenbark (*Hydrangea arborescens*) prominently, as well as rhododendron.

Mixed hemlock-deciduous forest.—Although eastern hemlock occurred prominently in the cove forest, it was the principal dominant in 3 areas censused. Hemlock attained diameters over 1 m and heights of 30 m. Beech formed an understory at low elevations and sweet (*Betula lenta*) and yellow (*B. allegheniensis*) birches at high elevations. Rhododendron and sevenbark were the principal shrubs. Herbs were much reduced compared with the cove forest, and the ground was covered with a thick layer of dry leaf litter.

Chestnut oak (chestnut) forest.—Trees in this forest rarely exceeded 0.5 m diameter and were usually only 6–18 m tall. Ericaceous shrubs were dense, especially at high elevations.

Red oak (chestnut) forest.—No tree counts were taken in this forest, but northern red oak was most prominent. The tree canopy was more closed than in the chestnut oak forest because of fewer dead chestnut trees and the shrub stratum was greatly reduced.

Pine heath.—Pines were widely spaced and only 6–12 m high. The shrub stratum was dense. The herb stratum was greatly reduced and contained bracken fern (*Pteridium* sp.) and some creeping vines.

Gray beech forest.—Beech (*Fagus grandifolia*) here is probably a different variety than occurs at low elevations (Camp 1950). Trees were generally 8–12 m tall, widely spaced and with intervening space covered with grasses, sedges and shrubs.

Spruce-fir forest and sere.—The climax forest contained dense tangles of mountain rose bay (*Rhododendron catawbiense*) and the ground was covered everywhere with thick spongy moss, low herbs and ferns. Numerous fallen trees were covered with mosses and lichens. At the highest elevation on Clingmans Dome, the forest consisted principally of Fraser fir (*Abies fraseri*) and included a few mountain ash (*Sorbus americana*) with the ground covered with thick mosses and *Oxalis*. Trees were numerous but only 12–15 m high.

A recently burned over area was well covered (90%) with shrubby vegetation, 0.6–1.5 m high, composed of fire cherry (*Prunus pennsylvanicus*), red maple (*Acer rubrum*), blackberry (*Rubus canadensis*), sevenbark, red-berried elder (*Sambucus pubens*) and several species of Ericaceae. Dead stubs of spruce and fir were scattered. The herb layer was dense and covered 70% of the ground. A second area, burned over earlier, had a dense stand of fire cherry, 1.8–3 m high. The area with most advanced vegetation, 3–6 m high, had serviceberry (*Amelanchier*), fire cherry, yellow birch and a few small spruce.

A heath bald along Bullhead Trail was covered mostly with mountain laurel (*Kalmia latifolia*) but contained some fire cherry and sourwood (*Oxydendrum arboreum*). The vegetation was dense and about 3 m high. Another heath bald on Brushy Mountain contained chiefly mountain rose bay 1–2 m high.

BIRD POPULATIONS

The data on species populations (Table 2) are listed in taxonomic order and the plant communities in which they were found. The plant communities are arranged as to whether they are seral or mature (climax), according to zones of altitude, and in horizontal gradients from north-facing slopes, coves, or gaps around the mountains to south-facing slopes.

Succession.—The shrubby seral stage at low elevations had a high percentage of restricted species and hence low S_s and S_p compared with either pine-oak or cove forest (Table 3). It likewise had little similarity with shrubby seral stages at high elevations. In contrast, the shrubby seral stages at high elevations had an avifauna with considerable similarity to that of the spruce-fir forest. Heath balds consist of very dense shrubby vegetation of uncertain successional status and contained only 3 species, none of them restricted: Gray Catbird (2.5 pairs/40 ha), Black-throated Blue Warbler (19 pairs), Rufous-sided Towhee (11 pairs).

Forest communities.—The forest contains both deciduous and coniferous species, in mixed or relatively pure stands, and with physiognomies varying from tall, luxuriant cove forest to short-statured gray beech "orchard" to open stands of pine heath. Relatively high S_s occurred among bird populations in cove, chestnut oak, red oak and hemlock-deciduous forests (Table 3). Likewise there was similarity between cove forest avifauna (after those species commonly associated with hemlock were eliminated) and pine-oak avifauna. Individual bird species extended widely among these deciduous plant communities although at different population levels.

When bird species commonly associated with deciduous trees were eliminated from the hemlock-deciduous forest, the remaining "hemlock" avifauna was similar to that of the spruce-fir forest. There was considerable similarity also between avifaunas of spruce-fir forest and high seral stages, even though these plant communities are of different vegetation types.

The avifauna of the pine heath was not closely similar to any other avifauna nor did any of its 14 species reach maximum population here. Many of its species occurred commonly in deciduous forests or shrub stages.

The above classification of avifaunas into separate units has been based largely on coefficients of S_s. However, no S_s above 50 has a value of S_p lower than 31, and no S_s below 50 has a value above 20.

Slope exposure (moisture).—North slopes and coves in the mountains are moist and shady, east and west slopes intermediate and south slopes dry and sunny. Correlated with changes in habitat is a continuum of plant

TABLE 2

AVERAGE BIRD POPULATIONS (PAIRS/40 HA) IN DIFFERENT TYPES OF VEGETATION

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
Ruffed Grouse													
Bonasa umbellus	DF			2.3	0.7	+[b]	3.0	+	5.0			5.0	+
Ruby-throated Hummingbird													
Archilochus colubris	FE		3.0	0.5		1.7							+
Common Flicker													
Colaptes auratus	FE	5.0		1.8	1.5	4.7		1.3					
Pileated Woodpecker													
Dryocopus pileatus	DF			0.5	3.0	2.5+							
Hairy Woodpecker													
Dendrocopos villosus	DF			3.0	2.7	1.3+	1.7		2.5	+			3.0
Downy Woodpecker													
Dendrocopos pubescens	DF	+	1.5+	1.1		+	3.3						
Great Crested Flycatcher													
Myiarchus crinitus	DF			0.5		11+	1.7						
Acadian Flycatcher													
Empidonax virescens	DF	+	5.0	2.0	5.0								
Eastern Wood Pewee													
Contopus virens	DF	4.0	1.5			+	1.7						
Blue Jay													
Cyanocitta cristata	FE			+	0.7	3.0+	3.3	1.3					
Black-capped Chickadee													
Parus atricapillus	DF			3.7	6.7	1.7	6.3	3.7			7.0	10.0	1.5
Carolina Chickadee													
Parus carolinensis	SM	3.7	1.0			6.7							

TABLE 2
Continued

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
Tufted Titmouse													
Parus bicolor	DF		1.5+	0.5	+	5.3+							
White-breasted Nuthatch													
Sitta carolinensis	DF			+		+	3.7						
Red-breasted Nuthatch													
Sitta canadensis	BF				11.0			7.3				+	20.0
Brown Creeper													
Certhia familiaris	BF				4.0							5.0	38.0
Winter Wren													
Troglodytes troglodytes	BF			5.3	7.5					3.0	29.0	+	34.0
Carolina Wren													
Thryothorus ludovicianus	SM	1.3	+	2.1	+	+							
Gray Catbird													
Dumetella carolinensis	FE	5.0				+	2.0	2.0	2.5			5.0	
Brown Thrasher													
Toxostoma rufum	FE	4.3											
American Robin													
Turdus migratorius	FE				3.2		1.3		5.0	+	7.0		3.0
Wood Thrush													
Hylocichla mustelina	DF		3.0	29.0	18.0	5.3+	16.0						
Veery													
Catharus fuscescens	BF			0.6	8.7		15.0		28.0	21.0	14.0	26.0	18.0
Blue-gray Gnatcatcher													
Polioptila caerulea	SM		3.0										

TABLE 2
Continued

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
Golden-crowned Kinglet													
Regulus satrapa	BF				2.5							5.0	38.0
White-eyed Vireo													
Vireo griseus	SM	14.0				3.3							
Yellow-throated Vireo													
Vireo flavifrons	DF	+	6.5										
Solitary Vireo													
Vireo solitarius	BF		1.5	25.0	36.0	+	7.7	+	22.0		7.0	5.0	24.0
Red-eyed Vireo													
Vireo olivaceus	DF	6.3	26.0	16.0	1.0	35.0	14.0						
Black-and-white Warbler													
Miniotilta varia	BF		8.5	3.0		13.0	3.0	+					
Worm-eating Warbler													
Helmitheros vermivorus	DF			1.1		10.0							
Golden-winged Warbler													
Vermivora chrysoptera	FE	12.0											
Parula Warbler													
Parula americana	SM		1.5										
Yellow Warbler													
Dendroica petechia	FE	5.3											
Black-throated Blue Warbler													
Dendroica caerulescens	BF			104.0	67.0	15.0	27.0	25.0	+	3.0	7.0	21.0	6.5
Black-throated Green Warbler													
Dendroica virens	BF			8.8	50.0	5.3	1.3						+

TABLE 2

Continued

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
Blackburnian Warbler													
Dendroica fusca	BF			1.0	41.0								
Yellow-throated Warbler													
Dendroica dominica	SM		30.0										
Chestnut-sided Warbler													
Dendroica pennsylvanica	BF					1.7+	19.0	24.0	46.0	141.0	115.0	47.0	2.5
Pine Warbler													
Dendroica pinus	SM		18.0										
Prairie Warbler													
Dendroica discolor	SM	15.0											
Ovenbird													
Seiurus aurocapillus	DF		16.0	15.0	36.0	29.0	28.0	1.3	2.5				
Louisiana Waterthrush													
Seiurus motacilla	DF	1.3		+									
Kentucky Warbler													
Oporornis formosus	SM	3.7		0.5		7.3							
Common Yellowthroat													
Geothlypis trichas	FE	12.0								27.0			
Yellow-breasted Chat													
Icteria virens	FE	24.0				1.7							
Hooded Warbler													
Wilsonia citrina	DF		10.0	1.0		32.0	3.3	4.7					
Canada Warbler													
Wilsonia canadensis	BF			6.3	32.0		5.0		2.5	6.0+	22.0	21.0	

TABLE 2
Continued

Species	Bird community[a]	Pine-oak forest		Cove forest	Hemlock-deciduous forest	Chestnut oak (chestnut) forest	Red oak (chestnut) forest	Pine heath	Gray beech forest	Spruce-fir forest			
		seral	mature							early seral	mid-seral	late seral	climax
American Redstart													
Setophaga ruticilla	DF	1.3	+	+									
Scarlet Tanager													
Piranga olivacea	DF		1.5	9.8	5.0	15.0	6.7	+					
Summer Tanager													
Piranga rubra	SM		1.5										
Cardinal													
Cardinalis cardinalis	SM	3.0	+			1.7							
Rose-breasted Grosbeak													
Pheucticus ludovicianus	DF				2.5	+	1.3		2.5				
Indigo Bunting													
Passerina cyanea	FE	22.0								+			
Rufous-sided Towhee													
Pipilo erythrophthalmus	FE	12.0	+			34.0	5.3	37.0	2.5	66.0	22.0	5.0	
Dark-eyed Junco													
Junco hyemalis	BF			9.7	30.0		23.0		56.0	102.0	58.0	83.0	125.0
Field Sparrow													
Spizella pusilla	FE	17.0								+			

[a] Bird communities: SM, southeastern mixed; DF, deciduous forest; FE, forest-edge; BF, boreal forest.
[b] Population below 0.5 pair/40 ha.

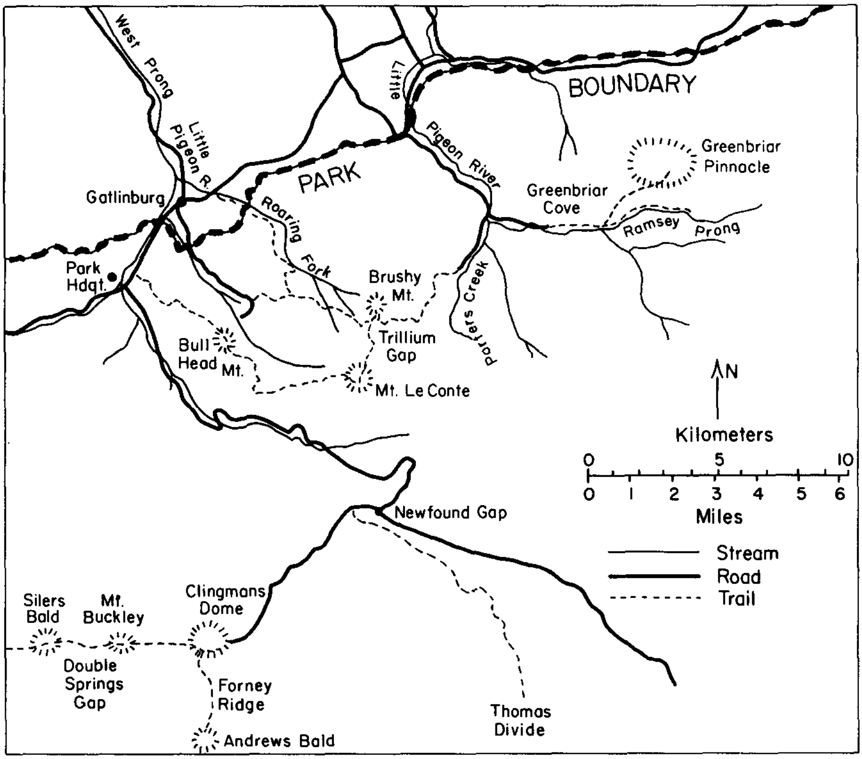

FIG. 2. Map of region in which census areas were located.

communities. At low elevations, there was no observable difference between total bird species and total pairs between cove and hemlock-deciduous forests on north slopes and chestnut oak on intermediate slopes, but fewer species and smaller populations occurred in pine-oak forests on south slopes (Table 4). At higher elevations, there was an observable decrease in both total species and pairs from red oak forests on intermediate slopes to pine heath on exposed south slopes.

Bond (1957), working in southern Wisconsin with a continuum of plant communities in the ecotone between grassland and deciduous forest, found an increase in number of bird species and total populations from moist to intermediate stages and then a decline to the dry end. Individual species varied in their point of greatest abundance along the gradient. Likewise, Smith (1977) observed 3 of the 8 species studied restricted to the moist end of a deciduous forest continuum in the Ozark Mountains of Arkansas and only 1 species extending to the extreme dry end.

TABLE 3
COMPARISON OF SPECIES COMPOSITION AND POPULATIONS BETWEEN COMMUNITIES

	Restricted species					
	1st community		2nd community		Similarity indices	
Communities compared	N	%	N	%	S_s	S_p
Low seral stage: pine-oak forest	13	57	13	57	44	5
Low seral stage: cove forest	8	35	23	74	30	5
Low seral stage: high and early mid-seral stages	19	83	10	71	22	10
High seral stages: spruce-fir forest	5	36	6	40	62	40
Cove forest: chestnut oak forest	8	26	9	28	73	31
Chestnut oak forest: red oak forest	11	34	4	16	74	41
Cove forest: gray beech forest	23	74	5	38	36	20
Gray beech forest: high seral stages	2	15	8	42	69	58
Cove forest: hemlock-deciduous forest	10	32	5	19	74	55
Cove forest: spruce-fir forest	21	68	5	33	22	18
"Hemlock" forest[a]: spruce-fir forest	2	13	2	13	87	34
Pine heath: spruce-fir forest	8	57	9	60	21	9
Pine heath: pine-oak forest	8	57	17	74	32	5
Pine-oak forest: "deciduous cove forest"[b]	10	44	10	44	56	35

[a] "Deciduous forest bird species" eliminated from the hemlock-deciduous forest.

[b] "Hemlock bird species" eliminated.

Elevation.—Increase in altitude or elevation brings lower temperatures, more precipitation including snowfall, shorter growing seasons, greater wind velocities, and more cloudiness and fog (Shanks 1954).

Vertical ranges of the Black-capped and Carolina chickadees overlapped in the chestnut oak (chestnut) forest (Table 5), but the Black-capped was there only in 1947 and the Carolina Chickadee only in 1948. The 2 species have nearly identical territorial requirements, and competitive interrelations of the two are well established (Tanner 1952, Brewer 1963).

The Wood Thrush and Veery overlapped broadly in vertical distribution and in the same census plots. Cavanaugh and Magee (1967) observed that when 1 species was numerous in a mixed coniferous-deciduous forest, the other was less so with the situation reversing in another year, which indicated the possibility of conflict between them. Bent (1949) cited several instances of the Veery and American Robin being driven from their territories by the Wood Thrush, and he observed a Veery driving a Wood Thrush from its territory. Bertin (1977) suggested that in mixed forest

TABLE 4
STATISTICS ON BIRD POPULATIONS IN PLANT COMMUNITIES

						Pairs per species		
Plant community	Elevation (m)	Total species	Total pairs	Species diversity H'	Equitability J'	mean *p/s*	median *p/s*	skewness g_1
Pine-oak forest								
Seral	455–488	23	172+	2.707	0.904	7.5	5.0	0.99
Mature	411–488	23	140+	2.397	0.814	6.1	1.6	1.8
Cove forest	640–1250	31	254+	2.206	0.669	8.2	2.0	4.5
Hemlock-deciduous forest	873–1356	26	376+	2.574	0.810	14.5	5.0	1.4
Chestnut oak (chestnut) forest	817–1074	32	247+	2.706	0.851	7.7	3.2	1.7
Red oak (chestnut) forest	1222–1506	25	204	2.762	0.858	8.2	3.7	1.3
Pine heath	1219–1349	14	108+	1.707	0.741	7.7	1.6	1.7
Gray beech forest	1646–1713	13	177+	1.821	0.733	13.6	2.6	1.5
Spruce-fir forest								
Early seral	1890–1950	12	369+	1.527	0.734	30.8	4.5	1.6
Mid-seral	1798–1920	10	288	1.824	0.792	28.8	18.0	2.2
Late seral	1740–1795	14	328+	1.974	0.794	17.0	5.0	2.2
Climax	1760–1790	15	314+	1.889	0.760	20.9	6.5	2.7

the Veery may segregate into sites with cooler microclimates than those preferred by the Wood Thrush.

Yellow-throated, Red-eyed and Solitary vireos were all present in pine-oak plots and Red-eyed and Solitary vireos occurred in red oak (chestnut) at higher elevations. The Yellow-throated Vireo feeds and nests in both deciduous and pine trees and may be a competitor of the Solitary Vireo in the pine forests of the Piedmont region (Odum 1948). Both Solitary and Red-eyed vireos were abundant in the cove forest but only the Solitary Vireo occurred in the hemlock forest. The Solitary Vireo commonly sang and fed in both deciduous and coniferous trees from 2 m–ca. 12 m above the ground. The Red-eyed Vireo was never observed in coniferous trees and in deciduous trees carried on its activities from 2 m above ground to the tree tops. This agrees in general with observations of the 2 species in mixed forests in New York state (Kendeigh 1945).

The vertical ranges of the 2 nuthatches broadly overlapped but the White-breasted Nuthatch was largely confined to deciduous stands and the Red-breasted Nuthatch to coniferous ones. The ranges of warbler species from the upper and lower elevations did not overlap except for the Hooded and Canada warblers in the cove forest.

Table 5

Vertical Distribution of Congeneric Species in the Great Smoky Mountains

Low elevation species	Highest elevation reached (m)	Congeneric species	High elevation species	Lowest elevation reached (m)	Congeneric species
Carolina Chickadee	817–1045	absent	Black-capped Chickadee	732–802	absent
White-breasted Nuthatch	1415–1506	absent	Red-breasted Nuthatch	873–991	absent
Wood Thrush	1451–1506	present	Veery	899–975	present
White-eyed Vireo	488	absent			
Yellow-throated Vireo	411–488	present	Solitary Vireo	411–488	present
Red-eyed Vireo	1222–1318	present	Solitary Vireo	411–488	present
Yellow Warbler	488	absent			
Prairie Warbler	488	absent			
Yellow-throated Warbler	411–488	absent	Black-throated Blue Warbler	640–820	absent
Pine Warbler	411–488	absent	Black-throated Green Warbler	640–820	absent
			Blackburnian Warbler	732–802	absent
Hooded Warbler	1295–1343	absent	Canada Warbler	899–975	present
Summer Tanager	411–488	absent	Scarlet Tanager	411–488	absent

Summer and Scarlet tanagers both occurred in the pine-oak census plot but in different years. Stupka (1963) states that the 2 species commonly meet at 457–610 m.

DISCUSSION

Local factors.—The predominant factor controlling bird distribution in the Great Smoky Mountains is the relation of bird species to plant communities. The change in moisture gradients from north to south slopes and temperature gradients with elevation are of secondary importance. Plant communities are identified by life forms of their dominant plant species (deciduous tree, coniferous tree, shrub), physiognomy (dense closed forest, open forest, heath), location (cove, bald) and species composition. Each plant community, or at least vegetation type, provides a different environment for birds with respect to microclimate (modification of the macroclimate), plant structure (dimensions, branching, leaf size and arrangement) and food supplies (seeds, nuts, fruit, foliage, insects and other invertebrates). Each bird species has evolved adjustments to these factors but little new information concerning their precise niche requirements and role in the community can be provided beyond those discussed for many of these species by Kendeigh (1945, 1947), MacArthur (1958), James (1971), Anderson and Shugart (1974) and Rabenold (1978).

The difference in bird species composition between seral shrubs and mature pine-oak forest at low elevation appears clearly related to change in life form of the conspicuous plants and the physiognomy of their stands. Forest species with the largest populations are segregated into either deciduous or needle-leaved coniferous vegetation types.

Food resources may be a factor affecting population size. Whittaker (1952) has shown that productivity of foliage insects in the Great Smoky Mountains decreases with slope exposure from moist cove forests to dry oak and pine types and with elevation. Bond (1957) found that foliage insect gleaners decreased and plant feeders increased from moist to dry forests in Wisconsin.

Circumstantial evidence indicated that competition as well as changes in vegetation affected vertical limits of some species in the Great Smoky Mountains. Able and Noon (1976) found no convincing cases of altitudinal competitive exclusion between species in the temperate mountain forests of New York and Vermont. Upper and lower distributional limits of species coincided with ecotones in vegetation. In the tropical forests of New Guinea, Diamond (1973) believed competition to be more important than changes in vegetation in controlling vertical distribution. In the tropical mountains of Peru, Terborgh (1971) ascribed changes in vegetation to account for less than 20% of the altitudinal limits of species, competition for about 33%

and gradually changing physical and other biological conditions for about 50%. Included in this latter category were not only changes in temperature and cloudiness, but also changes in net annual plant productivity, density of insects and importance of epiphytic plants in the vegetation.

Geography.—Avifaunas in similar plant communities at different localities tend to be similar in species composition (S_s) but not identical. Of 301 species recorded in 6 comparisons of localities (Table 6), 62% occurred in both communities, 21% were found in other plant communities in the vicinity, 11% were absent because the locality was beyond their geographic ranges, while 6% were not recorded in the locality. Failure to record a species in a locality within its distributional range may indicate that the sampling area was too small, and this may also be partly responsible for finding species only in other plant communities.

Other factors, however, often affect local occurrence of species. For instance, presence of Red-breasted Nuthatch, Brown Creeper, Winter Wren and Golden-crowned Kinglet in hemlock communities in the Great Smoky Mountains and not on the Heldenberg Plateau of New York may represent an overflow from large populations of these species in nearby spruce-fir communities. In New York state, spruce-fir forests are separated by 25–60 km from the hemlock areas censused. Another local factor is the presence of competing species. In hemlock-deciduous forests on the Highlands Plateau of North Carolina, the Carolina Chickadee replaces the Black-capped Chickadee.

The bird species composition varies, of course, when the plant community is beyond the limit of distribution of the bird species. The Scarlet Tanager was not recorded in the pine-oak community on the Piedmont Plateau of Georgia because it is rare or absent there; the Brown-headed Nuthatch (*Sitta pusilla*) recorded in the Georgia area is rare or absent in the Great Smoky Mountains. Nineteen species found in spruce-fir forests of northern Maine do not extend their ranges south as far as the Great Smoky Mountains. The decrease in species richness in Appalachian spruce-fir forests from north to south is a progressive one (Rabenold 1978).

Coefficients of population similarity, S_p, were not used in these comparisons of avifaunas. They are more sensitive indicators of similarity because they depend not only on the presence or absence of a species as does S_s, but on the replication of identical characteristics of the environment to permit equal sized populations to develop. Populations may also vary locally in sex and age ratios and other properties that would affect realization of comparable population sizes. In our comparisons of avifaunas in different localities, there was an additional complication in that censuses were taken in different years, and population sizes in a locality fluctuate from year to year.

TABLE 6
GEOGRAPHIC COMPARISON OF AVIFAUNAS

				Restricted species at other locality			Pairs/species			
Locality	Distance (km)	Species similarity S_s	Species in common	In other plant communities	Beyond distributional range	Not recorded	Mean p/s	Median p/s	Skewness g_1	Authority
Pine-oak, pine forests										
Great Smoky Mountains	—	—	17	2	1	3	6.1	1.6	1.8	this study
Piedmont Plateau, Georgia	160	67	17	8	1	3	6.9	5.0	3.2	Johnstone and Odum 1956
Chestnut oak, red oak forests										
Great Smoky Mountains	—	—	18	10	3	5	7.7	3.2	1.7	this study
Highlands Plateau, North Carolina	60	67	18	0	0	0	8.9	4.0	1.9	Odum 1950
Hemlock-deciduous forests										
Great Smoky Mountains	—	—	17	1	4	4	14.5	5.0	1.4	this study
Highlands Plateau, North Carolina	60	63	17	11	0	0	10.7	5.0	2.1	Odum 1950
Great Smoky Mountains	—	—	15	8	3	0	14.5	5.0	1.4	this study
Helderberg Plateau, New York	1100	62	15	4	2	1	7.5	4.0	1.8	Kendeigh 1946
Spruce-fir forests										
Great Smoky Mountains	—	—	14	0	0	1	20.9	6.5	2.7	this study
Great Smoky Mountains	25	80	14	5	0	1	14.0	8.0	2.0	Alsop 1969
Greak Smoky Mountains	—	—	13	1	1	0	20.9	6.5	2.7	this study
Aroostock County, Maine	1800	44	13	12	19	0	7.9	10.0	3.2	Stewart and Aldrich 1952

Bird communities, their origins and history.—Hubbard (1971) has a general discussion of the origins of avifaunas in the southern Appalachians but we wish to consider these origins and history from a somewhat different viewpoint. Our analysis above of succession, forest communities, and geography shows considerable similarity in the species composition of avifaunas that occur in plant communities of the same vegetation type, particularly deciduous forest, needle-leaved coniferous forest and shrubby vegetation at low elevations. Each combination of avifaunas in the same vegetation type or bird community shows little similarity to either of the others (Table 3). "Preference" of bird species for particular types of vegetation is indicated by maximum populations being attained in them. Such maximum populations suggest a high degree of anatomical, physiological and behavioral adaptation through association with the vegetation over a long period of geological time. In Table 2, each species is assigned to the bird community to which it most characteristically belongs, although most species have enough flexibility that they occur in small numbers in other communities as well. Much concerning the origin and geological history of each bird community can be learned from the presence of associated plant species in the fossil record of various localities and times, as was traced by Kendeigh (1974).

The uniqueness of the low elevation shrub avifauna is the result of intermingling of bird species belonging to the deciduous forest-edge community (FE) and what we have called the southeastern mixed community (SM). Belonging to this latter are the southern pines and several bird species found in the pine-oak community. This vegetation is derived from the Madro-Tertiary Geoflora originating on the Mexican Plateau, which during the Miocene or earlier extended continuously around the Gulf of Mexico. The southeastern portion and its avifauna became separated when prairie vegetation penetrated to the Gulf of Mexico.

The deciduous forest (DF) and forest-edge (FE) communities are derived from the temperate unit of the Arcto-Tertiary Geoflora that during the Eocene epoch extended from southeastern United States to Alaska (Kendeigh 1974). This forest and its seral stages have been much buffeted by climatic changes during the last 65 million years and are now largely limited to the eastern United States. The mixed mesophytic forest of the southern Appalachian Mountains, best represented here by the cove forest, has been little affected by these changes and may be the oldest forest stand at any locality in temperate North America (Braun 1950).

The gray beech forest, unique to the Appalachian Mountain System, is a segregate from the mixed mesophytic forest (Braun 1950). It is a young forest geologically, and since it is subjected to more climatic stresses than the deciduous forest at lower elevations, only a few bird species from the deciduous forest community have been able to occupy it. Instead, it has become occupied by species from the spruce-fir coniferous forest community.

Seral stages at high elevations became extensive only in recent times as the result of fires and human disturbances. Although a few species have invaded from shrubby seral stages of the lowlands, most of the avifauna is of boreal origin. There are no unique species here, although the Veery and Chestnut-sided Warbler reach peak populations in this vegetation and in the gray beech forest.

The spruce-fir forest (BF) is derived mainly from the boreal unit of the Arcto-Tertiary Geoflora (Kendeigh 1974). In the early Tertiary period, this unit was widely spread over northern North America. During the Pleistocene epoch it became fragmented, with the eastern portion becoming restricted and isolated in the northeastern United States and south through the Appalachian Mountains. During the height of glaciation, the spruce-fir forest in the Great Smoky Mountains probably extended to lower elevations and occupied mountain tops farther south than at present. During the warm dry xerothermic period, beginning some 8000–9000 years ago following the retreat of the last major or Wisconsin glacier, this forest retreated to higher elevations and became eliminated from lower peaks south of Clingmans Dome. During this period the southern distributional limits of many bird species probably retreated northward. The cooler, moister climate of the last 2000–3000 years may have again permitted the spruce-fir forest to expand down the slopes and bird species to extend their ranges southward. The gray beech forest probably originated during these up and down movements of the vegetation (Whittaker 1956).

The eastern hemlock forest lies geographically between boreal and deciduous forests but occurs more often in mixed stands with deciduous trees than with spruce and fir. It was subjected to several contractions and extensions of range during the Pleistocene and Holocene epochs. It differs from the boreal forest in the luxurious development of rhododendron and other shrubs in the Appalachian Mountain System, which together with a more temperate and moist climate presents a somewhat different environment for birds. This has led to a secondary differentiation of its avifauna from that of the spruce-fir forest which is more evident when the 2 forests are some distance apart, as on the Helderberg Plateau of New York, than in the Great Smoky Mountains. Other variations in avifaunas of the boreal forest have been described by Erskine (1977).

The fact that 2 species in hemlock forests of New York and 19 species in spruce-fir forests of Maine were not found as breeding birds in the Great Smoky Mountains may be the result, in part, of these historical shifts in the vegetation. Since the last contraction of their ranges northward, time may not have been sufficient for them to reoccupy southward all favorable breeding areas that have become available. These areas are scattered and require even migratory bird species to jump from one mountain to another for breeding purposes. For example, Golden-crowned Kinglet, Winter Wren, Black-capped Chickadee and Black-throated Green Warbler, although common in the Great Smoky Mountains, were not found in the census areas on the Highlands Plateau of the Blue Ridge Mountains. The Black-throated Green Warbler is of special interest as the Highlands Plateau lies in a hiatus between the ranges of the subspecies in the mountains (*Dendroica v. virens*) and the coastal subspecies (*D. v. waynei*). Odum (1950) has suggested that in dispersal of the species southward, the ranges of the mountain population became split from the coastal population and that the plateau has not yet become occupied by the mountain race.

In addition to slow dispersal rates southward, restriction of species southward may also be in response to unfavorable climate, food resources, or inter-species competition. Rabenold (1978) ignores the probable influence of the post-glacial xerothermic period on bird distribution in the Appalachians and argues that the lower species richness is related to lower food levels during the reproductive season.

Community structure.—The structure of bird communities is commonly analyzed in terms of species richness (s), equitability or eveness of distribution of populations (J') and segregation of species into different niches. The first 2 factors are usually combined into a species diversity index (H'). We are not here concerned with analysis of ecological niches. In our data (Table 4), H' varied positively with s ($r = 0.87$, $P < 0.001$) but J' varied independently of s. We agree with Hurlbert (1971) that the usefulness of H' is limited. There is little advantage in combining the 2 components.

Levels of population size attained by different species in communities or areas is important. Where the distribution of different population sizes follows a normal or Gaussian curve, mean number of pairs per species (p/s) is a reliable estimate. In each of our plant communities, however, the distribution of populations was skewed in that the median population was less than the mean, and the mode, usually poorly defined, was less than the median. The difference (± SD) between the mean and median p/s averaged 65 ± 17% of the mean. The degree to which distribution of populations was skewed (g_1) is indicated in Table 4, all populations being significantly different from symmetrical ($P < 0.05$), although that of the seral stage to pine-oak forest ($g_1 = 0.99$) was borderline.

There is a highly significant negative correlation between g_1 and J' ($r = 0.69$, $P < 0.0025$). A high value of g_1 and a low value of J' both indicate wide scattering of p/s, hence there is no need to use both indices. The distribution of measurements of biological variables commonly adheres to a normal curve, and since g_1 indicates the departure from symmetry it is preferable to J' which indicates departure from equality, which is rare or absent in biological phenomena.

P/s varied negatively with s ($r = 0.69$, $P < 0.025$) and this was related to altitude. At elevations below 1600 m, average s per community was 25 and p/s 8.6; above 1600 m, s was 13 and p/s 22.2. Skewness, g_1, was not statistically correlated with s and varied from 0.99 in the seral shrub stage to 4.5 in the cove forest, both at low elevations (Table 4). If the cove forest is excluded for reasons given beyond, g_1 averaged 1.5 below and 2.0 above 1600 m. At 1800 m elsewhere in the Great Smoky Mountains, s, p/s and g_1 values were intermediate (Table 6, Alsop 1969). In spruce-fir forests occurring at low elevations in Maine, s was higher and p/s lower than in the spruce-fir forest at high elevation in the Great Smoky Mountains, but g_1 was higher (Table 6). At both low and high elevations, g_1 was lower in seral shrubby stages than in forests (Table 4). Able and Noon (1976) state that decreasing s and increasing p/s with elevation seem to be a general rule in forested regions. Other investigators agree that fewer species and greater variability in population size tend to occur in rigorous environments with variable weather and other conditions than in moderate ones (Tramer 1969, Kricher 1972, Rotenberry 1978, Rotenberry et al. 1979).

The considerably skewed distribution of populations in the cove forest ($g_1 = 4.5$) is caused by 1 of the 31 species present, Black-throated Blue Warbler, having 41% of the total number of pairs. This species sings, nests and feeds in rhododendron and other ericaceous shrubs and in the rich herbaceous stratum. *Rhodendron maximum* is a characteristic dominant in the undergrowth of southern Appalachian Mountains but very local or absent from mixed mesophytic forests elsewhere (Braun 1950). The warbler has exploited this special niche and without effective competition from other species, its population has exploded in size. The high g_1 of hemlock-deciduous forests on the Highlands Plateau of North Carolina (Table 6) was also caused by the predominance of this species.

High values of g_1 found in gray beech and high elevation mid- and late seral communities are correlated with exploitation of favorable local niches by the Dark-eyed Junco and Chestnut-sided Warbler. The early seral stage has even larger populations of these 2 species, but g_1 is lower because 3 other species also have large populations so as to give a better balance among the 12 species that occur. The climax spruce-fir forest has several species with large populations, but g_1 is high because the Dark-eyed Junco comprised 40% of the total. Inter-species competition is reduced in these high elevation communities because other potentially competitive boreal species have not extended their ranges this far south.

The high g_1 for pine forests on the Piedmont Plateau of Georgia (Table

6) resulted from the Pine Warbler constituting 25% of the total populations of all 29 species. Pine Warblers nest and feed in long-leaved pines.

In the spruce-fir forest of Maine, the high g_1 resulted from Bay-breasted (*Dendroica castanea*) and Magnolia (*D. magnolia*) warblers making up 30% of total populations even with 44 species present. This may be a temporary unbalance, however, as these species were favored by feeding on the spruce budworm insect infestation then in progress.

Pairs per species (p/s) in hemlock-deciduous and spruce-fir forests of the Great Smoky Mountains are higher and in the chestnut oak and red oak forests lower than at other localities (Table 6). In each comparison, p/s varied inversely with s. It appears that when few species are present the fundamental niches for at least some species may be almost fully occupied so that populations are large. On the other hand, with many species present to provide inter-species competition, realized niches are smaller, hence smaller populations.

SUMMARY

Species composition and population sizes of birds were determined in 12 plant communities of the Great Smoky Mountains during the summers of 1947 and 1948. Plant communities form a mosaic of seral and climax stages that varies with altitude and slope exposure.

Coefficients of species and population similarities indicated that distinct bird communities may be identified, associated with deciduous forest, forest-edge, boreal forest and a southeastern mixed complex. Each type of vegetation with its bird life has had a different geological history that affects its present composition and characteristics. Bird species are classified to the vegetation type to which they appear best adapted as indicated by their attainment of highest populations.

Composition of bird species within particular stands of a vegetation type is influenced by the location of the stand in respect to species' ranges, neighboring avifaunas, annual fluctuations (especially of the less common species), inter-species competition and responses to temperature and possibly moisture as determined by elevation and slope exposure.

The species diversity index (H') varied positively with species richness (s) and was of limited value in comparing bird populations. Distributions of bird population sizes in all plant communities was positively skewed. Skewness (g_1) varied negatively with (J') and is preferred as an index as it indicates degree of departure from a symmetrical distribution rather than from equal population sizes of species.

Increasing elevation was correlated with lower species richness (s), larger number of pairs per species (p/s) and a tendency toward higher g_1, although the latter also varied independently of altitude. Avifaunas with g_1 greater than 2.0 contained one or more species with high abundance resulting from local prevalence of favored vegetation niches and lack of inter-species competition or with temporary super-abundance of a food resource. Values of p/s may be compared when the g_1 of avifaunas are similar. P/s varied negatively with s, indicating that with larger number of species present, inter-species competition caused fundamental niches not to be fully realized, with the consequence that growth of populations for individual species was limited.

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