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BREEDING BIRD POPULATIONS IN RELATION TO CHANGING FOREST STRUCTURE FOLLOWING FIRE EXCLUSION: A 15-YEAR STUDY

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Most studies of avian response to plant succession document bird communities in seral habitats from open field to regional "climax" forest during a period of a few years (Kendeigh 1948, Odum 1950, Johnston and Odum 1956, Shugart and James 1973). Long-term studies of bird communities at one site as the plant community changed in secondary succession are rare (Lanyon 1981, Kendeigh 1982), and other types of succession are seldom considered. A different type of plant succession, from pine to hardwood forest, can occur in the southeastern United States depending on the frequency of fire.

Longleaf pine (*Pinus palustris*) has dominated upland coastal plain forests of the southeastern United States in historic times (Wahlenberg 1946). Fire is a major factor influencing reproduction and maintenance of longleaf pine (Christensen 1981). Fire supresses hardwood growth and removes vegetation thereby exposing bare soil which favors germination of pine seeds. Lightning-started fires formerly burned upland pinewoods over large areas but most burning is now controlled by man.

Frequent fires in pinewoods maintain an open habitat with abundant ground cover of grasses and forbs. The few remaining sections of undisturbed longleaf pine forest which have been burned annually are virtually longleaf monocultures. Along bluffs, ravines, and moist slopes where fire rarely penetrates, American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*) dominate hardwood forests (Delcourt and Delcourt 1977). Beech-magnolia forests with high tree species diversity, subcanopies, and tree-fall gaps, are structurally complex compared to longleaf pine forest. These two forest communities can be thought of as opposite ends of a fire to no-fire continuum in upland areas of the southeastern United States.

Succession to pine forest following agricultural disturbance can be maintained by the presence of frequent fires. Although tree and herbaceous species of oldfield pine forest are different from those found in virgin longleaf pine forest, the abundant ground cover, openness of the habitat, and domination by pines are similar.

We report the results of a 15-year study of the breeding bird community on an 8.6-ha grid of oldfield pineland in northwestern Florida, after fire

FIG. 1. NB66 photographed from the same point in March of 1967 (top) and 1981 (bottom); "a" locates the same tree in each view.

exclusion. Bird census results and vegetation structure of a nearby mature American beech-southern magnolia forest and a relatively undisturbed longleaf pine forest are used as examples of regional old-growth communities in the presence and absence of fire, respectively. The avian communities of these two forests and 15 years of census results on the study plot are compared using rarefaction.

Nomenclature follows Kurz and Godfrey (1962) for trees.

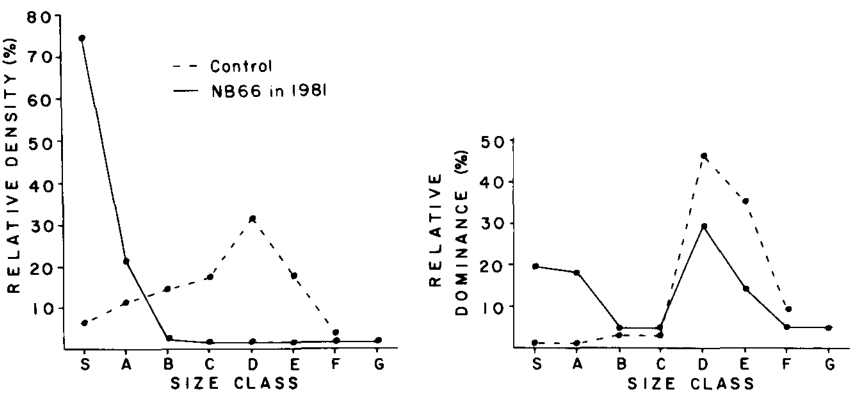


FIG. 2. Tree size class distribution within NB66 and the contiguous annually burned plot (control). Fifteen 0.04-ha circular samples were taken in each habitat.

METHODS

Study site.—In 1966 an 8.6-ha rectangular (360 × 240 m) plot was established on Tall Timbers Research Station, Leon Co., Florida, for long-term studies of plant succession and concommitant changes in bird and mammal populations. The plot was the northern portion of a south-facing slope of annually-burned oldfield pineland, in which loblolly (*Pinus taeda*) and shortleaf (*Pinus echinata*) pine were dominant. Cultivated until about 1865, some portions of the study site continued to be sharecropped until 1935 (Clewell and Komarek, unpubl.). After cessation of cultivation, pines seeded in. "Winter" (February or March) fires burned back hardwoods and shrubs giving the plot an open aspect with scattered trees and a complete ground cover of grasses and forbs. In the 15 years since fire exclusion, sapling hardwoods have grown quickly forming a thick subcanopy about 5 m tall. Photographs of the site were taken from the same perspective in 1967 and 1981 (Fig. 1). All stems >5 cm diameter breast height (DBH) were mapped in 1966 (Clewell and Komarek, unpubl.) and again in 1976 (Tobi 1977). The study plot was last burned in March 1967 and named NB66 (not burned since winter of 1966–1967). Tobi (1977) summarizes background information of the long-term NB66 study.

In 1981 vegetation was sampled within 15, 0.04-ha circular plots (James and Shugart 1970) in a stratified random design within NB66. An additional size class (S, 4–8 cm DBH) was added to the classes of James and Shugart (1970) because saplings are so numerous in NB66. Canopy cover, estimated by ocular-tube sightings, includes hardwood saplings approximately 5 m tall and pine canopy about 30 m tall.

Oldfield pinewoods contiguous with NB66 are still burned annually. Quantitative vegetation samples of these pinewoods, part of the same south-facing slope as NB66, were used to represent the vegetation structure of an annually burned oldfield pine forest. For convenience, we call this the "control" plot. Relative tree species composition (Table 1) and tree size class distribution (Fig. 2) within NB66 and the control plot are compared. Pine-hardwood density and dominance in a mature beech-magnolia forest (Woodyard Hammock) (Engstrom 1982a) and a mature longleaf pine forest (Wade Tract) (Engstrom 1982b) are contrasted to NB66 (Clewell 1981) over time (Fig. 3).

Bird censuses.—Breeding birds were censused on NB66 each spring 1967–1981 by the

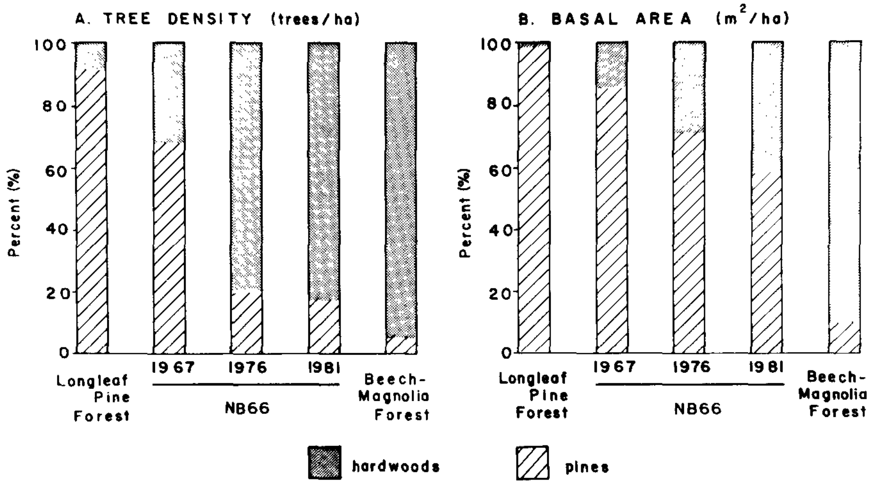


FIG. 3. Pine-hardwood density (A) and dominance (B) in NB66, a mature longleaf pine forest (Wade Tract) and a mature beech-magnolia forest (Woodyard Hammock).

spot-map method (Williams 1936). Each year, 6–11 census trips (median = 10) were made between March and June. Baker censused during 1967–1970, and 1973–1979. Crawford and Baker each completed part of the 1972 census, and Crawford censused in 1971 and during 1979–1981. Bird census results expressed as average number of detections per census trip are plotted over time (Fig. 4); acronyms for bird species (Klimkiewitz and Robbins 1978) are given in Appendix I. Species are listed in order of year of maximum abundance and number of years observed. Numerical data are available upon request. We use average number of detections per trip instead of an estimate of the number of breeding pairs as an index of abundance, not necessarily proof of breeding. For example, Red-cockaded Woodpeckers roosted and nested within NB66 only through 1974, but individuals from a neighboring clan continued to forage in the study area until 1979. We compared average number of detections per trip to an estimate of the number of territorial individuals. In the 1982 census (not included in this paper) Crawford defined individual territories according to the spot-mapping procedure suggested by the International Bird Censusing Committee (Anon. 1970). Compared with spot-mapping, average detections overestimated abundance of three species, underestimated three species, and had equal estimates for the abundance of 20 species. Abundance in terms of mean number of detections per trip is congruous to the number of territorial pairs.

Species detected on <3 trips during any year and species not always detected in morning hours such as Red-tailed Hawk (*Buteo jamaicensis*), Chuck-will's-widow (*Caprimulgus carolinensis*), Great Horned Owl (*Bubo virginianus*), and American Crow (*Corvus brachyrhynchos*) were not included in the species total. Census trips took 1–1.5 h and were conducted in the morning before 09:30. Birds using the plot edge were excluded from censuses. "Visitors," those species having three (in years having seven or fewer visits), four (8–10 visits), and five (11 visits) detections per census year were not included in the annual species totals. This is slightly more conservative than the recommendations of the International Bird Census Committee (Anon. 1970) because of the small area of NB66.

Rarefaction.—Rarefaction is a statistical technique which can be used to compare com-

TABLE 1

RELATIVE COMPOSITION OF TREE SPECIES WITHIN NB66 AFTER 15 YEARS AND THE ADJACENT ANNUALLY BURNED PLOT (CONTROL); 15, 0.04-HA CIRCULAR SAMPLES WERE TAKEN IN EACH AREA

Species	Tree/ha		Relative density (%)		Relative dominance (%)		Frequency (%)	
	NB66	Control	NB66	Control	NB66	Control	NB66	Control
Water oak (*Quercus nigra*)	855	12	41	10	17	2	100	27
Loblolly pine (*Pinus taeda*)	257	23	12	20	28	33	93	40
Laurel oak (*Quercus hemisphaerica*)	179	2	9	1	5	<1	100	7
Sweetgum (*Liquidambar styraciflua*)	179	—	9	—	4	—	67	—
Black cherry (*Prunus serotina*)	138	2	7	1	3	<1	93	7
Flowering dogwood (*Cornus florida*)	115	8	5	7	2	<1	73	13
Shortleaf pine (*Pinus echinata*)	91	16	4	14	29	18	73	33
Sassafras (*Sassafras albidum*)	74	—	4	—	1	—	27	—
Waxmyrtle (*Myrica cerifera*)	63	—	3	—	1	—	53	—
Black tupelo (*Nyssa sylvatica*)	30	—	1	—	1	—	53	—
Pine (dead)	23	8	1	7	1	8	33	20
Post oak (*Quercus stellata*)	21	3	1	3	<1	<1	47	13
Live oak (*Quercus virginiana*)	20	2	1	1	5	<1	47	7
White oak (*Quercus alba*)	13	—	1	—	<1	—	27	—
Plum sp. (*Prunus* sp.)	13	—	1	—	<1	—	27	—
Southern red oak (*Quercus falcata*)	12	13	1	11	<1	4	20	27
Deciduous (dead)	8	—	<1	—	<1	—	20	—
Mockernut hickory (*Carya tomentosa*)	7	—	<1	—	<1	—	13	—
Longleaf pine (*Pinus palustris*)	3	26	<1	23	2	33	13	47
Tree sparkleberry (*Vaccinnium arboreum*)	2	—	<1	—	<1	—	7	—
Total	2103	115						

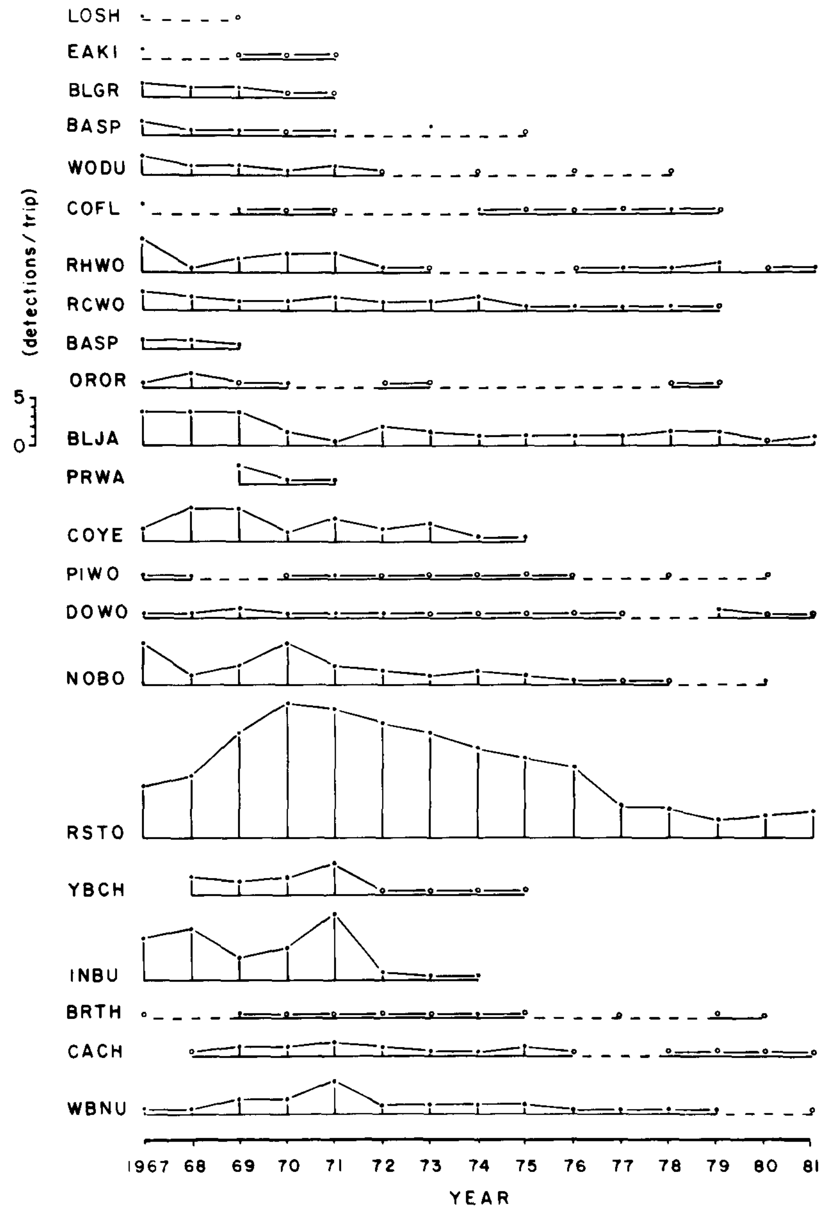
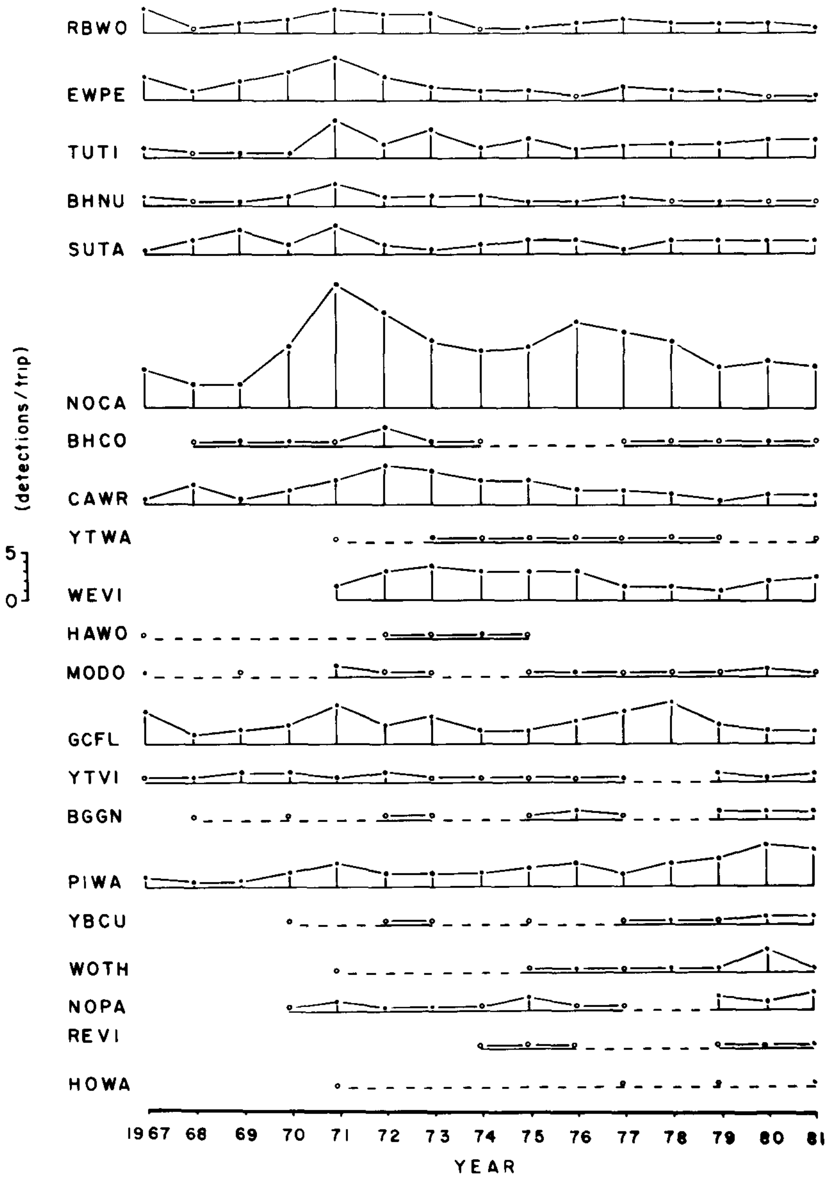


FIG. 4. Patterns of abundance in individual species over the 15-year study period. Abundance is measured in average number of detections per trip rounded to the nearest half. Open points represent "visitors" in which a species was detected only a few times during



the census year (see Methods). Species are arranged according to year of maximum abundance and number of years observed (early maxima and short duration are first in the list; late maxima and short duration are last).

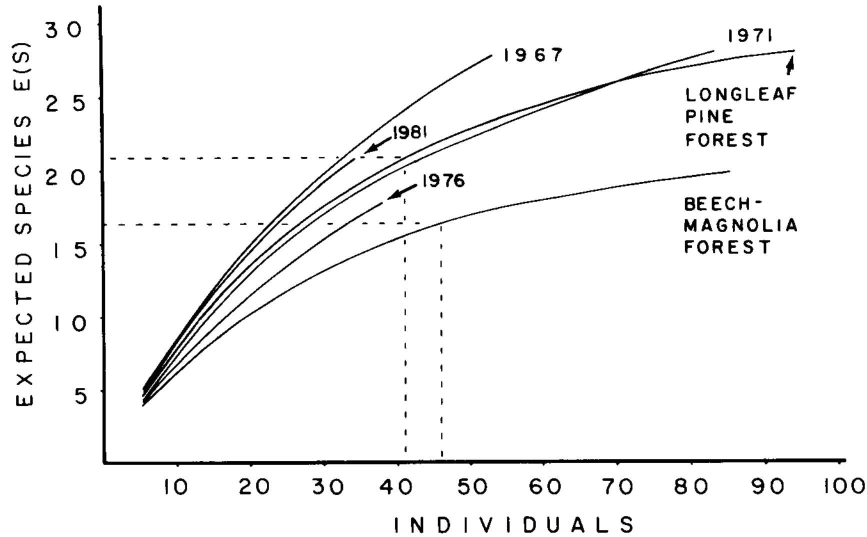


FIG. 5. Rarefaction curves for Breeding Bird Censuses of mature longleaf pine and beech-magnolia forests and selected years of NB66. Dashed lines represent the number of individuals and the expected number of species, E(S), on an 8.6-ha subplot (same size as NB66) of the mature longleaf pine (20-ha plot) and beech-magnolia (15.75-ha plot) forests.

munities with unequal sample sizes (Simberloff 1972, Heck et al. 1975). It is used here to compare number of species expected in different communities given equivalent sample area (James and Wamer 1982). In this case we compare bird species richness of three forests: a 15.75-ha mature beech-magnolia forest (Engstrom 1982a), a 20-ha mature longleaf pine forest (Engstrom 1982b), and NB66. To estimate the number of bird species expected for an 8.6-ha plot (the same size as NB66) within the larger longleaf pine and beech-magnolia forests, we first derive rarefaction curves (Fig. 5). The x-axis is the number of individuals and the y-axis is the expected number of species. End points of the curves represent the actual numbers of species (excluding visitors) and individuals found on the plots from Breeding Bird Censuses. As the sample of individuals decreases (moving toward the origin), the expected number of species declines. Assuming that the number of individuals is proportional to the area, an estimate of the number of species expected for a smaller sample of individuals (and area) than the original sample can be obtained.

RESULTS

Changes in vegetation structure over 15 years were extensive. Fire exclusion allowed sapling hardwoods (primarily water oak [*Quercus nigra*]), previously suppressed by winter fires, to grow rapidly. Comparing vegetation structure of the control plot to NB66 in 1981, canopy cover increased from 43–91% and ground cover decreased from 85–21%. Eight tree species found in NB66 in 1981 did not occur in the control (Table

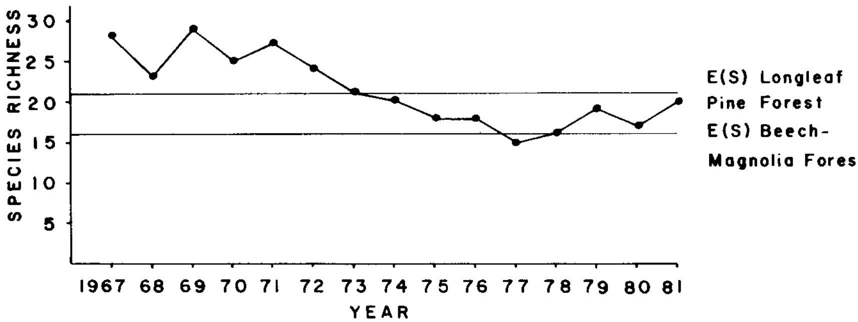


FIG. 6. The number of species within NB66 (excluding "visitors" as defined in Methods) over time compared to the number expected in an 8.6-ha sample of a mature Longleaf Pine forest (Wade Tract) and a mature beech-magnolia forest (Woodyard Hammock).

1). Density of water oaks ranged from 12 stems/ha in the control plot to 855 stems/ha in NB66, clearly showing the magnitude of structural changes occurring over 15 years (Table 1). A shift to greater density and dominance of smaller size classes is evident (Fig. 2). Relative composition of pines and hardwoods within NB66 changed markedly over time as hardwoods have become more abundant (Fig. 3).

Many deciduous trees which appeared on NB66 following fire exclusion had been present as root crowns in the annually burned forest (Tobi 1977). Root crowns send up small saplings every growing season but are burned back in winter. Hardwoods also started from seed in NB66. In February 1981, 28 American holly (*Ilex opaca*) and two southern magnolia seedlings were found within NB66 although neither species was present in 1966. These species are common in the region's mesic hardwood forests.

The bird community changed dramatically in 15 years (Fig. 4). Open habitat species (Eastern Kingbird, Loggerhead Shrike, Blue Grosbeak, and Bachman's Sparrow) disappeared within 5 years after fire exclusion. Prairie Warbler and Yellow-breasted Chat were observed for only a few years after the shrub layer began to develop (years 2–9); other species (Common Yellowthroat, Indigo Bunting, Rufous-sided Towhee, White-eyed Vireo, and Northern Cardinal) reached maximum numbers during the brushy stage (years 3–7) then slowly declined. Rufous-sided Towhee, the most abundant species for the first 8 years was not encountered in 1982. After a subcanopy of saplings developed, species associated with mesic woods (Yellow-billed Cuckoo, Wood Thrush, Red-eyed Vireo, Hooded Warbler and visitors such as Acadian Flycatcher [*Empidonax virescens*] and Kentucky Warbler [*Oporornis formosus*]) appeared in the study plot. Canopy species (Eastern Wood-Pewee, Great Crested Flycatcher, Blue Jay, and

Summer Tanager) seemed least affected by vegetation changes. Although brush encroachment has often been suggested as a cause for colony abandonment, the entire Red-cockaded Woodpecker population of Tall Timbers Research Station started to decline in 1975 (Baker 1983), so its disappearance from NB66 may have been caused by factors other than changes in vegetation structure in the colony area.

Bird species richness of mature longleaf pine forest (20-ha plot), mature beech-magnolia forest (15.75-ha plot), and the 15-year NB66 study (8.6-ha plot), compared by rarefaction, revealed that the Wade Tract contains more bird species than Woodyard Hammock (Fig. 5). In NB66 bird species abundance was greatest during the first 5 years of censusing, declined to a low in 1978, and started to increase until 1981 (Fig. 6).

DISCUSSION

Vegetation structure and species composition in the forests of northern Florida are strongly influenced by fire. Kurz (1944:78), describing vegetation changes in secondary succession following fire exclusion, emphasized the rapid sprouting of water and laurel oaks into a "phalanx of young trees" and the subsequent loss of "the undergrowth of jumbled forbs, grasses, sprouting woody plants, and interwoven vines."

The transition from an open, fire-dominated forest to a closed-canopy deciduous forest is a gradual process. Blaisdell et al. (1973) suggested that in north Florida, beech-magnolia forest will emerge in upland areas if they are not burned and are near seed sources. Although mechanisms of plant succession are complex and most generalizations must be qualified (McIntosh 1980), it is noteworthy that southern magnolia and American holly seedlings are established in NB66 as predicted (Blaisdell et al. 1973).

Wade Tract and Woodyard Hammock may be considered opposite ends of a fire/no-fire continuum, while NB66 is a community in structural transition. Tree density and species abundance are low in mature, fire-maintained pine forests compared to mesic hardwood forests (Engstrom 1982a, b). For example, in the Wade Tract, 92% of the trees are longleaf pine, whereas in Woodyard Hammock, 28 species of trees occur in addition to the dominants, American beech and southern magnolia. NB66 was an oldfield pine forest before fire exclusion, not a relatively undisturbed longleaf pine community like the Wade Tract. It was not as uniform as the Wade Tract because of past agricultural use; however, general structural characteristics of abundant ground cover, sparse canopy cover, and dominance of pines were similar.

Some studies of bird communities in relation to plant succession have shown that bird species richness increases with forest age (Johnston and Odum 1956, Shugart and James 1973). Our study is different in that we started with a mature pine forest maintained by fire and have followed bird community changes to an early stage of a mixed pine-hardwood forest. Bond (1957) analyzed bird communities in Wisconsin in numerous wooded sites along a moisture gradient. He concluded that bird species occur in a pattern of community-types along the xeric-mesic gradient but the responses of individual species merge to changing habitat conditions in a continuum of communities. Abundance of bird species in NB66 also changed individualistically in relation to habitat structure (Fig. 4). James and Wamer (1982) compared avian species richness and vegetation characteristics of Breeding Bird Censuses reported in "American Birds." Greatest bird species richness occurred in habitats having intermediate tree species richness and canopy height. Low bird density and species richness occurred in habitats with low tree species richness, low canopy height, and high density of small trees. Lowest bird species richness within NB66 over the study period was 8–11 years after fire exclusion when oaks formed a low, dense layer beneath the pine canopy (Fig. 5). An important component of regional open-pinewoods bird communities is the ground-nesting and foraging guild which is affected adversely by decreases in grass and herbaceous cover following fire exclusion.

Coastal plain uplands in the southeastern United States were dominated historically by longleaf pine forest, whereas beech-magnolia forest was restricted to areas protected from fire (Delcourt and Delcourt 1977). Bird species richness is greater in the structurally simple longleaf pine forest than in the species rich and more structurally complex beech-magnolia forest (Figs. 5, 6). This argues against the hypothesis of greater bird species diversity with increased vertical foliage layering (MacArthur and MacArthur 1961). Greater bird species richness of the longleaf pine forest compared to the beech-magnolia forest is possibly related to the greater area of pinewoods compared to hardwoods. Palynological samples have indicated that pines have been dominant in the southeastern coastal plain over the past 5000 years (Watts 1971). More bird species could have adapted to the most common habitat, longleaf pine forest, in spite of its structural simplicity. Small plot size, greater patchiness, and more sources of food are possible reasons why more bird species occurred in NB66 than in the Wade Tract.

Of the 11 bird species observed every year of the study in NB66 (Red-bellied Woodpecker, Eastern Wood-Pewee, Great Crested Flycatcher, Blue Jay, Tufted Titmouse, Brown-headed Nuthatch, Carolina Wren, Pine Warbler, Summer Tanager, Northern Cardinal, and Rufous-sided Towhee), four species (Eastern Wood-Pewee, Brown-headed Nuthatch, Pine Warbler, and Rufous-sided Towhee) which occur regularly on the Wade Tract do not occur in Woodyard Hammock. These species may be the next to leave NB66 permanently as the proportion of deciduous canopy increases.

Even though the pines will persist in NB66 for many years, the bird community changed significantly in the first 15 years after fire exclusion. Species nesting in ground cover quickly left the area, while birds using the high pine canopy for foraging and nesting remain in the study plot despite the hardwood growth. Species associated with mesic conditions such as Red-eyed Vireo, Wood Thrush, and Hooded Warbler are becoming increasingly common.

SUMMARY

For 15 years after fire exclusion in 1966, annual breeding bird censuses were conducted on an 8.6-ha plot of oldfield pine forest in northern Florida. Changes in vegetation structure were assessed using data from plant succession studies and by taking 0.04-ha circular samples within the study area 15 years after fire exclusion and in a contiguous annually burned oldfield forest. Using rarefaction, a statistical technique, annual bird species totals for this study are compared to bird species richness in nearby old-growth longleaf pine and mature beech-magnolia forests.

Changes in the bird community and vegetation structure were dramatic. Only 11 of 43 bird species were encountered every year of the study. Most finches and brush nesting species no longer occur on the study area while several species associated with mesic conditions have increased in abundance.

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APPENDIX

SCIENTIFIC NAMES OF BIRDS AND ACRONYMS

Wood Duck (*Aix sponsa*)	WODU
Northern Bobwhite (*Colinus virginianus*)	NOBO
Mourning Dove (*Zenaida macroura*)	MODO
Yellow-billed Cuckoo (*Coccyzus americanus*)	YBCU
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	RHWO
Red-bellied Woodpecker (*M. carolinus*)	RBWO
Downy Woodpecker (*Picoides pubescens*)	DOWO
Hairy Woodpecker (*P. villosus*)	HAWO
Red-cockaded Woodpecker (*P. borealis*)	RCWO
Northern Flicker (*Colaptes auratus*)	NOFL
Pileated Woodpecker (*Dryocopus pileatus*)	PIWO
Eastern Wood-Pewee (*Contopus virens*)	EWPE
Great Crested Flycatcher (*Myiarchus crinitus*)	GCFL
Eastern Kingbird (*Tyrannus tyrannus*)	EAKI
Blue Jay (*Cyanocitta cristata*)	BLJA
Carolina Chickadee (*Parus carolinensis*)	CACH
Tufted Titmouse (*P. bicolor*)	TUTI
White-breasted Nuthatch (*Sitta carolinensis*)	WBNU
Brown-headed Nuthatch (*S. pusilla*)	BHNU
Carolina Wren (*Thryothorus ludovicianus*)	CAWR
Blue-gray Gnatcatcher (*Polioptila caerulea*)	BGGN
Wood Thrush (*Hylocichla mustelina*)	WOTH
Brown Thrasher (*Toxostoma rufum*)	BRTH
Loggerhead Shrike (*Lanius ludovicianus*)	LOSH
White-eyed Vireo (*Vireo griseus*)	WEVI
Yellow-throated Vireo (*V. flavifrons*)	YTVI
Red-eyed Vireo (*V. olivaceus*)	REVI
Northern Parula (*Parula americana*)	NOPA
Yellow-throated Warbler (*Dendroica dominica*)	YTWA
Pine Warbler (*D. pinus*)	PIWA
Prairie Warbler (*D. discolor*)	PRWA
Common Yellowthroat (*Geothlypis trichas*)	COYE
Hooded Warbler (*Wilsonia citrina*)	HOWA
Yellow-breasted Chat (*Icteria virens*)	YBCH
Summer Tanager (*Piranga rubra*)	SUTA
Northern Cardinal (*Cardinalis cardinalis*)	NOCA
Blue Grosbeak (*Guiraca caerulea*)	BLGR
Indigo Bunting (*Passerina cyanea*)	INBU
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	RSTO
Bachman's Sparrow (*Aimophila aestivalis*)	BASP
Field Sparrow (*Spizella pusilla*)	FISP
Brown-headed Cowbird (*Molothrus ater*)	BHCO
Orchard Oriole (*Icterus spurius*)	OROR