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Forest Size and Avian Diversity in New Jersey Woodlots with Some Land Use Implications

Richard T.T. Forman, Anne E. Galli, and Charles F. Leck

Departments of Botany and Zoology, Rutgers University,
New Brunswick, New Jersey 08903, USA

Summary. The effect of forest size on avian diversity was studied in oak forest patches in rural New Jersey. Number of bird species continued to increase significantly in old oak woods up through 40 ha. This was due to the progressive addition of carnivorous species with increasing minimum forest size requirements. One large woodlot had more species than the same area subdivided into smaller woodlots. To maintain maximum regional diversity more than three large forests are required. Primary land use priority should be to protect large forests. Second priority should be to maintain a high density of small woodlots.

Introduction

The number of species on an island is influenced by the island's size, internal environmental heterogeneity, age, and distance from a species source (MacArthur and Wilson, 1967). Studies in a diversity of archipelagos support this island biogeographic theory (Koopman, 1958; Johnson et al., 1968; Diamond, 1969, 1973; Wilson and Simberloff, 1969; Simberloff and Wilson, 1970; Wilson, 1969). The theory appears to apply also to patches or islands in a terrestrial matrix (Whittaker, 1960; Vuilleumier, 1970; Brown, 1971; Simpson, 1974; Terborgh, 1973, 1974, 1975; Opler, 1974). In most studies the relative importances of several factors affecting species number are determined. Island size is generally found at or near the top as a predictor of species number, and found to be linearly correlated with species number on log-log axes, though often with considerable variation. Interactions between island characteristics as variables, plus the variation present in the island size vs species number correlations, suggest the value of studying island size in the absence of other variables. Certain terrestrial situations, where the matrix between islands is not a barrier to species dispersal, are advantageous for a test of size effects alone.

Though the importance of size as an independent factor affecting diversity, and the means by which size alone might limit diversity on islands, are critical points of biogeographic theory (Terborgh, 1973; MacArthur and Wilson, 1967; Forman, 1964), they are seldom considered in relation to land management. The application of island biogeographic theory to the terrestrial landscape offers a scientific basis for land use decisions on the value of forest ecosystems of different sizes (Terborgh, 1974, 1975; Sullivan and Shaffer, 1975).

Galli et al. (1976) found that in old oak woodlots bird species number increased up through at least 24 ha in size. Foliage height diversity did not change significantly with increasing size, and the increase in species number was considered due to increasing area without increasing environmental heterogeneity. The species increase reflected a changing proportion of forest interior to forest edge birds along the size gradient. The objective of this paper is to further evaluate the importance of area, and how it may operate, in determining avian diversity of forest patches in the landscape, and to indicate certain consequent land-use priorities for maintaining high regional species diversity.

Methods

Thirty forest islands (woodlots) were selected, representing 10 sizes: 0.01, 0.2, 0.8, 1.2, 2.0, 3.0, 4.0, 7.5, 10, and 24 ha. The 10 sizes were replicated in each of three adjacent geographic sections of the red shale Piedmont. Two of the sections were censused three times and the other section twice, making a total of eight bird censuses for each forest size. Birds were sampled from 0630 to 0900 during breeding season June 5 to August 8, 1972, by walking marked parallel lines 30 m apart throughout each forest (Emlen, 1971; Galli et al., 1976).

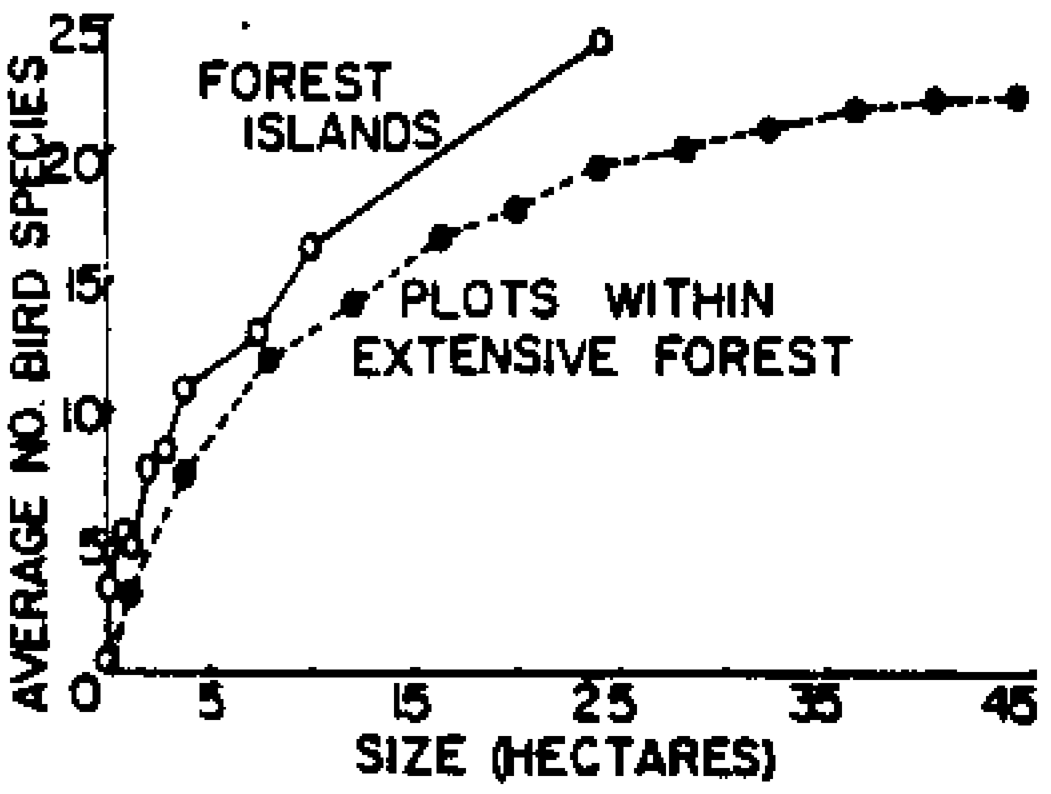
The red shale Piedmont is approximately 25 km in diameter, and because of the convoluted perimeter of the Piedmont, no island is more than 8 km from a species source, an extensive forest. Criteria for forest selection were: minimal internal environmental heterogeneity, Penn soils, slope < 10°, no streams, distant from housing developments and air pollution sources, relatively isodiametric in shape, mature oaks (*Quercus alba*, *Q. velutina* and *Q. borealis*) dominate the canopy, dogwood *Cornus florida* in understory, *Viburnum acerifolium* in shrub layer, and no major human disturbance evident. There are exceptions for some of the criteria but we believe their effects are negligible. Several factors, including large canopy trees (40–100 cm dbh), a distinct mature forest edge, and the presence of many islands on early twentieth century soils maps, permit the assumptions that the islands have not been clear-cut for approximately a century (and perhaps never), that they have not changed in size for at least several decades, and that their species are in equilibrium with the surrounding environment. Detailed descriptions of the woodlots are given in Galli (1974), Forman and Elfstrom (1975), and Elfstrom (1976).

In order to determine the species-area relationship within an extensive mature oak forest, a 44-ha plot was chosen nearby on the Piedmont. This was similar in forest structure but on a differing soil type (Galli, 1974; Galli et al., 1976). The plot was sampled once using the same census methods.

All identified birds were included in the censuses, except those flying above the forest, and most were assumed to be breeding in the forests (Galli, 1974), because they are known nesting summer residents throughout the area (Swinebroad, 1962; Leck, 1971, 1975). Scientific names of birds are given in Galli et al. (1976).

Though numerous indices of species diversity have been used in ecological literature, we use it in its simplest sense of species number. Other common indices, which synthesize both species number and the relative abundance of species, correlate well with species number as an index of avian diversity during the breeding season on the Piedmont of New Jersey (Kricher, 1972). Tramer (1969) found this also to be true for avian communities in a wide variety of habitats.

1



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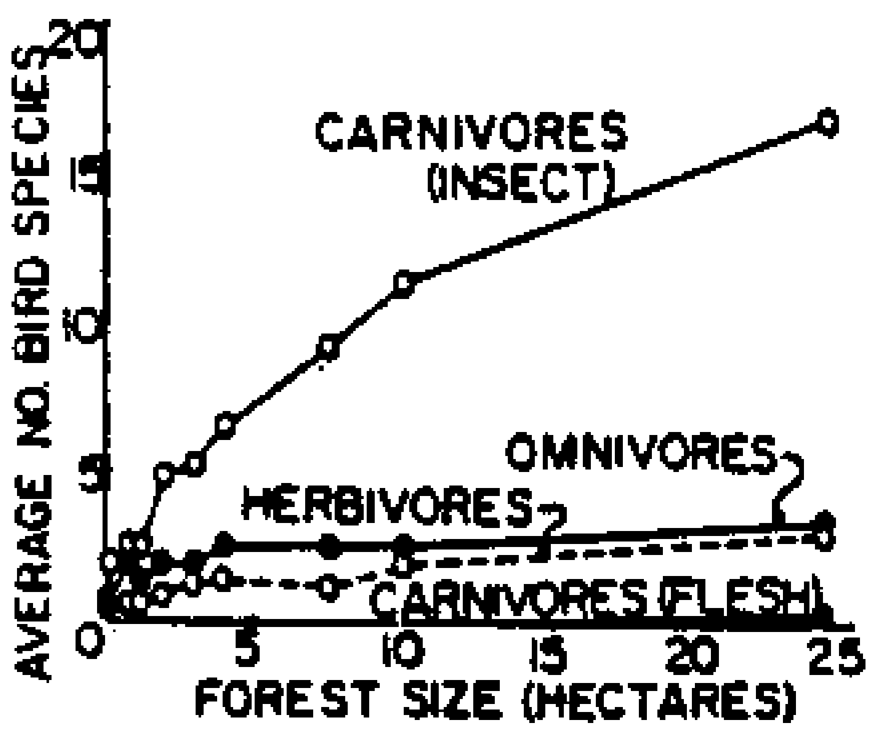

Fig. 1. Forest size and number of bird species. Each point for the forest islands is based on eight breeding-season censuses. Each point for the extensive forest is the average number of bird species in ten plots, selected randomly in a censused 44 ha portion of an extensive forest. $LSD_{0.05}$ confidence interval for forest islands is 6.1

Fig. 2. Forest size and avian diversity by feeding type. Each point is based on eight breeding season censuses. $LSD_{0.05}$ confidence intervals are: 2.0 carnivores (insect), 0.8 omnivores, 1.0 herbivores

Results and Discussion

Forest Size and Avian Diversity

In the forest islands, number of species was still increasing sharply at 24 ha, the largest size (Fig. 1). A species-area curve in the 44-ha plot within a nearby extensive forest showed that species number was also increasing sharply at 24 ha (Fig. 1), and diversity continued to increase significantly up through 40 ha.

The 40 ha point on the curve, the so-called minimum area point (Goodall, 1952; Cain and Castro, 1959; Greig-Smith, 1964; Vestal and Heermans, 1945; Vestal, 1949), is objectively defined here as the point where a 5% increase in species with a doubling in forest size is reached. The fact that the slope is steeper at 24 ha in the curve for forest islands than for the extensive forest (Fig. 1) suggests that 40 ha is a conservative estimate for the size of woods through which species number increases significantly. Sampled areas well above 44 ha are needed to further refine the 40 ha estimate.

A comparison of the curves in Figure 1 also reveals a progressive divergence as size increases. Though the number of species in the lower curve is an approximately constant percent of that in the upper curve, the actual number of species above the species-area curve was greater in large islands than in small islands. Thus, in addition to the major diversity increase due to the greater area of large islands, the number of species which could be attributed to the island nature of the woodlots increased with area.

A major characteristic of islands, absent within the extensive forest, is the edge portion of the forest (Wales, 1972; Bull, 1964; Johnston, 1947). The curve for forest islands is higher due to more species which primarily inhabit the forest edge. For example, at 24 ha, forest edge species comprise 30% of the forest island and 23% of the extensive forest bird species. The gray catbird, rufous-sided towhee and common flicker were common edge species of the 24 ha islands but were rare or uncommon in the 44 ha area within the extensive forest.

In evaluating how forest size might affect number of bird species. we found that the increase in diversity above approximately 1.5 to 2 ha was due almost entirely to an increase in insect-eating carnivores (Fig. 2). Herbivores and omnivores increased negligibly above the small island sizes, and flesh-eating (vertebrate-eating) carnivores were present only in the largest islands.

We examined the 46 bird species encountered to determine whether any, especially the insect-feeders, were limited to a particular forest size, or whether increasing forest size leads to a random species enrichment. Thirteen species were found over the entire spectrum of forest sizes above 0.01 ha, and are considered size independent. The 13 species were: house wren, starling, common grackle, catbird, American robin, rufous-sided towhee, common flicker, tufted titmouse, indigo bunting, song sparrow, mourning dove, northern oriole, and common crow (common names from Check-list of North American Birds, 1957; The Auk, 1973).

Eighteen other species, however, were limited to a particular range of forest sizes (Table 1). Of the remaining species, eleven were rare in the samples (numbers given are frequency of occurrence out of eighty censuses): eastern phoebe (1), Swainson's thrush (1), eastern bluebird (2), field sparrow (2), ruffed grouse (2), eastern kingbird (2), vireo species (1), American woodcock (1), chestnut-sided warbler (1), house sparrow (1), and yellow warbler (1). Four species were uncommon with size dependence uncertain: red-winged blackbird (5), rose-breasted grosbeak (8), blue-winged warbler (4), and ring-necked pheasant (3).

Thus, over half the common and uncommon species are considered size-dependent. In all cases the range is from the largest island down to a specific size (Table 1). Each of the size-dependent species appears to have its own minimum area, with the minimum areas ranging from 0.8 to 11 ha. All (Table 1) except the blue jay and cardinal are categorized as carnivores, and of these only the flesh-eating red-shouldered hawk is not an insect-feeder.

We therefore conclude that the increase in bird species diversity from 2 to 40 ha (Fig. 1) is due to the progressive encountering of the differing minimum areas (Table 1) of carnivorous species, primarily insect-feeders. This is consistent with the increase in feeding-territory size requirements of birds along a diet gradient from herbivores to arthropod predators to vertebrate predators (Schoener, 1968; Lack, 1968).

There is probably no single mechanism which determines the minimum areas of the species in Table 1. The species density of an island, measured as average number of bird species in 0.2 ha plots throughout each forest, is high (1.4–3.3) in the smallest islands, but constant from 1 ha up (1.1), and the ratio of forest edge to forest interior changes along the size gradient. All the insect-feeders in Table 1, except the brown thrasher, live in the forest interior. Some, such as the hairy woodpecker and the black-capped chickadee, may be limited by the number of standing dead trees available for nest sites. Others, such as the red-bellied woodpecker and scarlet tanager, require a large territory

Table 1. Birds limited to a particular range of forest sizes. Eight censuses for each forest size were taken. The table gives the numbers of censuses in which a species was recorded

Species	Forest size (ha)									
	0.01	0.2	0.8	1.2	2	3	4	7.5	10	24
Blue Jay	0	0	5	5	6	8	8	8	8	8
Great Crested Flycatcher	0	0	1	1	2	2	2	3	6	7
Cardinal	0	0	2	0	1	2	3	1	3	5
Wood Thrush	0	0	2	0	2	2	4	7	8	8
Red-eyed Vireo	0	0	1	0	0	2	1	2	3	4
Brown Thrasher	0	0	1	0	0	0	2	2	3	6
Downy Woodpecker	0	0	0	4	4	4	3	6	5	8
Eastern Wood Pewee	0	0	0	0	3	7	4	6	6	8
White-breasted Nuthatch	0	0	0	0	2	1	2	2	4	7
Hairy Woodpecker	0	0	0	0	1	1	1	1	2	6
Black-capped Chickadee	0	0	0	0	1	1	0	3	3	7
Red-bellied Woodpecker	0	0	0	0	0	2	0	4	2	7
Scarlet Tanager	0	0	0	0	0	1	0	0	1	5
Yellow-billed Cuckoo	0	0	0	0	0	0	1	2	0	3
Ovenbird	0	0	0	0	0	0	3	6	6	7
Black-and-White Warbler	0	0	0	0	0	0	0	1	1	2
Black-billed Cuckoo	0	0	0	0	0	0	0	1	0	2
Red-shouldered Hawk	0	0	0	0	0	0	0	0	2	2

for acquiring their specific insect foods. The large red-shouldered hawk may require larger forests in order to obtain sufficient food (mice and snakes).

Predictability is high for species number (Figs. 1 and 2 with attendant confidence intervals), but lower and size-dependent for species composition (Table 1). The presence of many species in large woods (e.g. blue jay, wood thrush and downy woodpecker in 24 ha) and the absence of many species in small woods (e.g. eastern wood pewee, ovenbird and red-bellied woodpecker in 0.8 ha) are predictable with reasonable confidence (Table 1). But in small and medium sized islands, low predictability of species composition is emphasized by the abundance of low bird frequencies of 1 to 6 (Table 1).

When avian diversity is plotted against the number of islands of a particular size, the curve shows a significant increase up through three islands (Fig. 3), the maximum number sampled. This is true for all sizes and may be expected for 40 ha islands also. The curve results from the fact that species composition differs significantly among islands of a given size. The larger the island size the greater the number of species gained between the first and third islands (Fig. 3), which could be predicted from the greater increase in area. However, the gain in species from the first to third islands relative to the number of species in the first island is lowest for large islands (Fig. 3). This indicates that the minimum area point, or more appropriately the minimum number-of-islands point, is lowest for large islands. The minimum island combination required to include all 46 species encountered in this study was two 24 ha, one 11 ha, one 1.2 ha and one 0.2 ha islands.

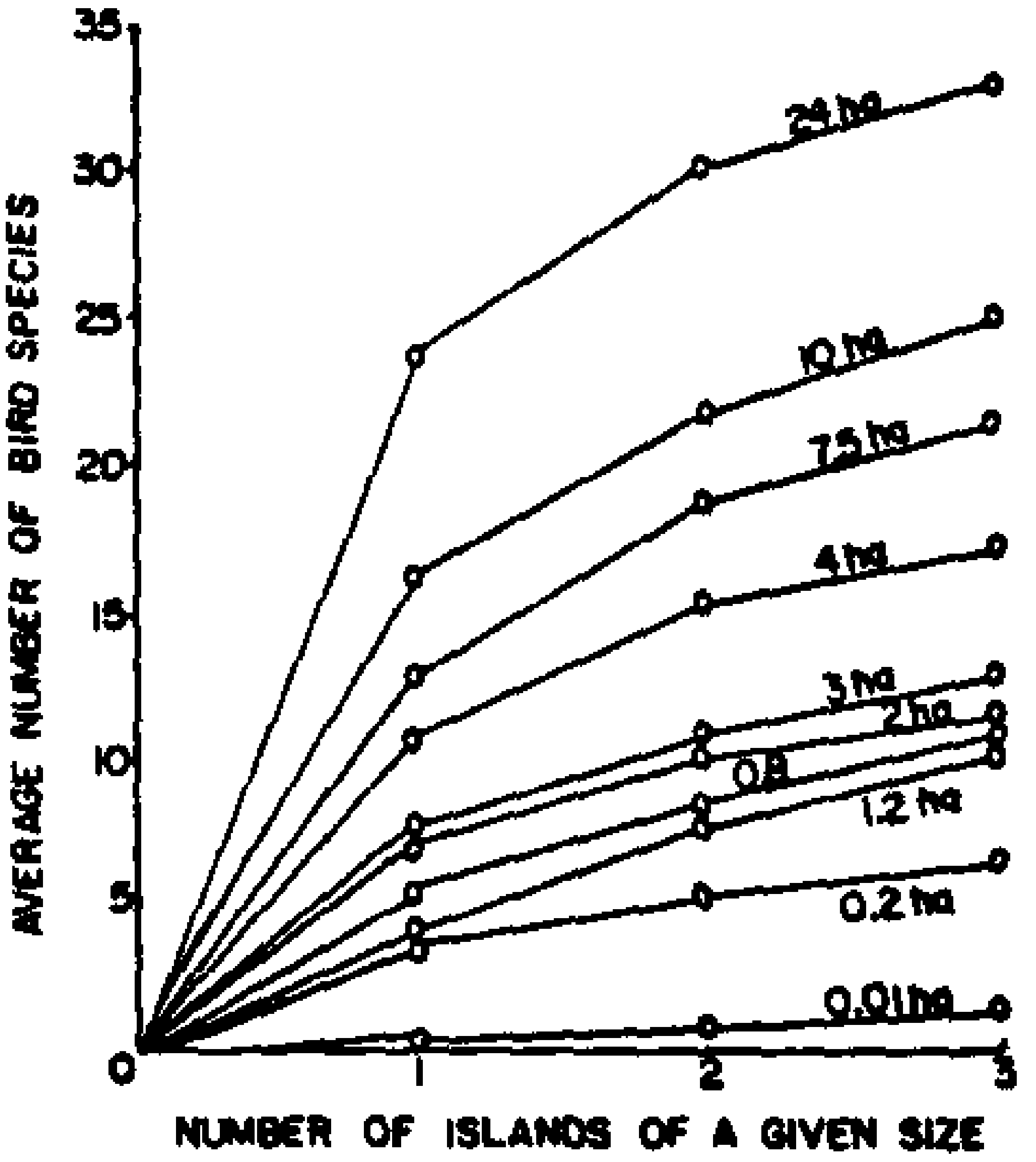

Fig. 3. Number of islands and avian diversity. Each curve represents the average of six curves: two time censuses × three orderings of the three islands of a particular size (i.e. northern island, central island, southern island; central, southern, northern; southern, northern, central)

Figure 3 also permits a comparison of the number of species in a particular island with the number of species in the same total area, but subdivided into smaller islands. Larger islands contained more species than an equal area of smaller islands. For example, a single 24 ha island would contain slightly more species than two 12 ha islands and more than three 8 ha islands, or a single 4 ha island would contain more species than two 2 ha islands and still more than three 1.3 ha islands. This negative correlation pattern between diversity and number of islands disappeared in small to medium sized islands where there was considerable variation, and the slope relating diversity to number of island subunits was negative, positive or zero. Thus, for larger islands above 3 ha there are more species in a single island than in the same area subdivided into two or three equal-sized islands.

Land-Use Implications

The relationship of avian diversity (Fig. 1) and composition (Table 1) with forest size can be applied readily to land use planning. To maintain maximum regional species diversity top priority should be placed on identifying and protecting large forests, rather than protecting an equal area of small forests. In the New Jersey Piedmont the most valuable forests would be larger than 40 ha. Thirty-five percent of the species encountered in the forest islands were found only in forests of at least 3 ha, and 22% were only in forests of at least 8 ha. Additionally, since large forests are the most scarce, most of these species are the rare and uncommon upland species of the region. Since almost all of these species are predatory, their presence may produce a significant stabilizing effect on other trophic levels of the ecosystem (Paine, 1966, 1971; Slobodkin, 1964; Harper, 1969; Janzen, 1970; May, 1973).

We conclude that protecting large ecosystems will protect rare species, will maintain biotic diversity in a region, and may aid in limiting insect pest outbreaks. The data are consistent with Terborgh's thesis (1974, 1975) that extremely large parks are needed to minimize species extinctions.

Little is known of the number or density of islands needed to maintain regional diversity. Five woods, including three large ones, were required to encounter all species in this study in an area of approximately 500 km^2. Three woods were inadequate to reach the minimum number-of-islands point for a particular forest size. We conclude that more than three large woods are required in this 500 km^2 New Jersey Piedmont area to maintain maximum regional diversity of upland forest birds.

Small woods are valuable for different reasons, including the previously mentioned high density of bird species, and the importance of many woodlots as stepping stones or rest stops for species dispersal between forests. The latter will decrease extinctions of species in woodlots and facilitate rapid recolonization following extinctions. Therefore a second land use priority is the maintenance of numerous small woods.

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