RESEARCH ARTICLE

Does Bird Community Composition Vary along a Disturbance Gradient in Northeast Iowa, USA, Forests?

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ABSTRACT: Most previous studies of bird-habitat relationships in midwestern U.S. forests have excluded recently disturbed habitats from consideration. We investigated whether the composition of a forest avifauna varies along a disturbance gradient ranging from mature, infrequently disturbed forests to successional, frequently disturbed forests impacted by logging and pasturing practices. We evaluated the degree of disturbance of 44 forests in northeast Iowa, USA (including mature and recently disturbed forests), using an additive, multicriteria index ranging in value from 20 (mature; infrequently disturbed) to 0 (successional; highly disturbed). We conducted forest bird censuses at these study sites using point counts in 1995 and 1996. Then, we used stepwise regression analyses to test for relationships between the abundance (mean number of birds detected per census point at each site) and species richness (mean number of bird species detected per census point at each site) of birds and the index. For these analyses, birds were divided into subsets by migratory status, nest substrate, and conservation categories. The disturbance index predicted the abundance of 2 out of 10 bird groups; permanent residents were more abundant in frequently disturbed forests, and area-sensitive bird species were more abundant in infrequently disturbed forests. The index predicted the species richness of 7 out of 10 bird groups. Short-distance migrants, permanent residents, and ground nesters were more diverse in frequently disturbed, successional forests, while neotropical migrants, tree nesters, species of high management concern, and area-sensitive birds had higher species richness in mature, infrequently disturbed forests. These results suggest that mature forest vegetation is important habitat for uncommon and rare bird species in northeast Iowa.

Varía la Composición de la Comunidad de Pájaros en Bosque a lo largo de un Gradiente de Disturbio en el Noreste de Iowa, USA?

RESUMEN: La mayoría de los estudios de relación entre pájaros y hábitats en bosques en el centro oeste de USA han excluido la consideración de hábitats recientemente modificados. Investigamos si la composición de la avifauna del bosque varía a lo largo de un gradiente de disturbio en un rango desde bosque maduro, levemente modificado a bosque sucesional, frecuentemente perturbado, impactado por la extracción madedera y las prácticas de pastoreo. Evaluamos el grado de disturbio de 44 bosques en el noreste de Iowa, USA (incluyendo bosques maduros y recientemente perturbado), usando un índice aditivo multicriterio, con valores desde 20 (maduro, levemente modificado) a 0 (sucesional, altamente perturbado). Realizamos censos de pájaros en bosques en los sitios de estudio usando conteos en puntos durante 1995 y 1996. Luego usamos análisis de regresión stepwise para testear la relación entre la abundancia (número medio de pájaros detectados por punto de censo en cada sitio) y la riqueza de especies de pájaros (número medio de especies de pájaros por punto de censo en cada sitio) y el índice. Para estos análisis, los pájaros fueron dividido en dos grupos dependiendo de su característica migratoria, substrato del nido, y categoría de conservación. El índice de disturbio predijo la abundancia de 2 de 10 grupos de pájaros; los residentes permanentes fueron más abundantes en bosques frecuentemente perturbados, y las especies de pájaros sensibles fueron más abundantes en los lugares levemente perturbados. El índice predijo una riqueza de especies de 7 sobre 10 grupos de pájaros. Los pájaros que migran distancias cortas, los residentes permanentes, y los que nidifican en el suelo fueron más diversos en bosques sucesionales frecuentemente perturbados, mientras que los que migran al neotrópico, que nidifican en árboles, especies de alta prioridad de manejo, y sensibles tuvieron mayor riqueza específica en bosque maduros, levemente perturbados. Estos resultados sugieren que bosques con alta calidad de vegetación son hábitats importantes para las especies de pájaros poco comunes y raras en el noreste de Iowa.

Index terms: birds, disturbance, forest, habitat relationships, northeast Iowa

INTRODUCTION

Several classic studies (Ambuel and Temple 1983, Blake and Karr 1987) have demonstrated that bird community structure in midwestern USA forests is related to both vegetation and landscape characteristics. Recently disturbed (logged, pastured) forests, however, were excluded from these studies. We argue that these forests are relevant in studies of avian habitat relationships because many resident bird species, especially neotropical migrants, are habitat specialists (Sherry and Holmes 1995) with narrow habitat preferences (successional forests, mature forests, etc.). Furthermore, successional habitats, whether naturally occurring or caused by human activity, often comprise the majority of forest cover in midwestern landscapes (such as northeast Iowa) and are preferentially used by many bird species in the eastern United States (Brawn et al. 2001, Thompson and DeGraaf 2001)

Recent attention has focused on the effects of specific silvicultural practices (e.g., clearcutting, selective cutting) on bird community structure in eastern deciduous and mixed-deciduous forests (Thompson et al. 1995, 1996; Annand and Thompson 1997; Robinson and Robinson 1999; Gram et al. 2001); however, we know of almost no published research documenting the effects of pasturing on bird communities in eastern deciduous forests. Logging and pasturing usually modify forest structural characteristics and alter patterns of plant species dominance in one or more forest strata (Webb et al. 1977, Thompson et al. 1995). Habitat structural characteristics and plant species composition are both well known to influence habitat selection (MacArthur and MacArthur 1961, Cody 1981) and foraging behavior (Holmes and Robinson 1981, Wiens and Rotenberry 1981, Robinson and Holmes 1984, Gabbe et al. 2002) of birds; thus, there is little doubt that forest management affects bird community structure in the Midwest.

A variety of methods have been employed to investigate the effects of forest management on forest bird communities (Thompson et al. 2000). One approach is to randomly assign forest management treatments of interest (e.g., clearcut, selective cut, no cutting) to mature forests that have not undergone recent disturbance. Then, at some date after the silvicultural treatments have been imposed on the experimental units (i.e., forest tracts), the researchers assess the effects of each treatment by comparing bird community attributes (e.g., abundance, species richness) among treatments. This experimental approach, employed in the current Missouri Ozark Forest Ecosystem Project (MOFEP) in Missouri (Gram et al. 2001), has the advantage of both randomization and replication. Another approach is to select forest stands for study that have already received the silvicultural treatment of interest (e.g., clearcut, shelterwood, group selection, single-tree selection, mature forest). As above, the effects of the various silvicultural treatments are inferred by comparing bird community attributes among treatments (Annand and Thompson 1997).

In this investigation, we address the effect of forest management on bird communities from a different perspective. Rather than focus on the effects of specific forest management practices on bird community patterns, we asked whether bird community attributes (abundance, species richness) vary predictably along a gradient of disturbance in forest vegetation. Specifically, we developed a quantitative method to measure the degree to which a given forest resembles that same forest (maturity, structural diversity, tree species dominance patterns) in the absence of recent (50 to 75 y) major anthropogenic disturbance (timber harvest, pasturing, etc.). Our method (Norris and Farrar 2001) is an additive, multicriteria system (Smith and Theberge 1986, 1987) that relies upon the scoring of six criteria from vegetation survey data, collected in 0.10-ha circular plots, which are summed to yield an index of disturbance (D) for each survey plot ranging in value from 0 to 20. The mean of these D values yields an overall index of disturbance ($\bar{D}$) for each forest site. This enabled us to answer our specific research question: Are the abundance and species richness of forest birds (subsetted into management assemblages) predictable given the degree of recent disturbance and total area of a forest?

The use of indices to evaluate bird habitat is not unprecedented (see Gotmark et al. 1986, Anselin et al. 1989). There are several reasons why we used this approach to evaluate habitat use by birds in northeast Iowa forests. First, the majority of forests in this region are privately owned and have been subjected to a wide number of human impacts making it difficult, if not impossible, to categorize a given forest as "clear cut," "selectively cut," "pastured," etc. Second, protected forests (i.e., those withheld from timber harvest and pasturing for many years) in northeast Iowa are scarce, and it is natural for wildlife managers and foresters to ask to what extent these forests are utilized by breeding birds relative to less pristine forests.

STUDY AREA

Field work for this study took place in Allamakee, Clayton, Delaware, Dubuque, Fayette, and Winneshiek Counties in northeast Iowa. This corner of Iowa was predominantly forested (59% forest cover) in the middle of the last century (Anderson 1995). Logging and conversion of forested lands to agricultural purposes have reduced this historic forest cover to a patchwork of forest remnants (current forest cover = 19%). Forests in northeast Iowa belong to the Central Hardwoods (Braun 1964) and have been described by Cahayla-Wynne and Glenn-Lewin (1978). The typical canopy dominants of forests on ridgetops and sloping terrain in this region are oaks (*Quercus alba* L., *Q. ellipsoidalis* E.J. Hill, *Q. macrocarpa* Michx. and *Q. rubra* L.), sugar maple (*A. saccharum* Marsh.), and American basswood (*Tilia americana* L.). In floodplain forests, black walnut (*Juglans nigra* L.), hackberry (*Celtis occidentalis* L.), and elms (*Ulmus Americana* L., *U. rubra* Muhl.) are the usual canopy dominants.

A small number of northeast Iowa forests (state preserves, state parks, forest reserves) have been protected for many years and have closed canopies, well differentiated canopy and subcanopy layers, diffuse shrub layers, and high native plant diversity (Norris and Farrar 2001). However, the majority of forests in northeast Iowa have been logged and/or grazed within the past two decades. Such forests are characterized by reduced overstory stratification and shrubby understories dominated by prickly shrub species uncharacteristic of mature forests, including gooseberry (*Ribes missouriense* Nutt. ex T. & G.), prickly ash (*Zanthoxylum americanum* P. Miller), blackberry (*Rubus allegheniensis* Porter ex Bailey), and black raspberry (*Rubus occidentalis* L.).

METHODS

Field Work

Forest Site Selection

We selected 44 forest sites ranging in area from 32 to 486 ha in northeast Iowa for inclusion in this study. Among these were 17 public properties encompassing several state parks and forest preserves and many wildlife management areas. Among the 27 privately owned sites were forests that had been recently logged and/or grazed as well as others set aside in forest reserve programs. Study sites were not selected from the Mississippi River floodplain because the avifauna of this ecosystem has already been extensively studied (Knutson et al. 1996, Knutson and Klaas 1997).

Few forests in northeast Iowa are "patches" in the strict sense (i.e., isolated on all sides from other timber) but rather are connected to other forests by at least a narrow corridor of trees. Thus, our study sites were not isolated "patches" in the sense of Hanski and Simberloff (1997). The majority of our study sites, however, were surrounded by cropfields or open pasture along the majority of their borders (80% or more).

We used a stratified random sampling scheme to allocate bird census points to each study site in proportion to area. We marked the center of each bird census point with two parallel bands of white paint and pink flagging on a tree, and placed them at least 50 m from the forest edge so that the entire point (50 m radius) would be within the forest. Census points were situated at least 250 m apart to minimize the possibility of double counting individual birds during a census (Ralph et al. 1993). Our smallest site (32 ha) had two census points and the largest site (486 ha) had twelve such points. Bird census points were thus located on a variety of topographic positions, including upland habitats (ridgetops, slopes, ravines), lowland floodplains and narrow wooded creek bottoms.

Bird Census Protocol

We conducted bird censuses between May 30 and July 15 in both 1995 and 1996. All field technicians working on this project received 2 wk of training in bird song recognition immediately prior to conducting these censuses. We followed the protocol established by Ralph et al. (1993) for conducting bird censuses, which always took place on calm, rainless mornings from sunrise to 1000. Bird censuses were conducted at all 189 bird census points three times each season at approximately 2-wk intervals, with replicate censuses at each point conducted by different observers to minimize observer bias. Each point count was 10 min in duration. We recorded all birds detected during the census as occurring either inside or outside a 50-m-radius circle centered on the marked tree.

Vegetation Survey Protocol

We used standard releve methods (Mueller-Dombois and Ellenberg 1974) to survey the woody vegetation at each study site. We established numerous 0.10-ha circular plots in each forest site (independent of the bird points). These vegetation survey plots were allocated in proportion to forest area such that one 0.10-ha plot was established for every 20 ha of forest area, plus two additional plots (to increase the number of plots in small forests). Prior to survey, we marked all survey plots on a topographic map of each forest to represent all available topographic aspects (e.g., ridge, slope, bottomland).

Our survey methodology assumes that woody vegetation (excluding vines) in northeast Iowa commonly occurs in three layers: a canopy (all trees with canopy exposed to the sky), a subcanopy (all trees greater than 2 m in height and underneath the canopy or in a canopy gap), and a shrub layer (all woody vegetation between 0.5 m and 2 m in height). At each survey plot, we visually estimated and recorded the total cover provided by woody species (excluding vines) in each of these layers. Then, we recorded the component woody species occurring in these three layers within broad cover classes. We also estimated and recorded the total cover by shrubs that indicate severe recent disturbance in a forest (e.g., *Ribes missouriense*, *Rubus occidentalis*, *Zanthoxylum americanum*). Finally, we recorded the diameter at breast height (dbh) of the four largest trees within each survey plot: one tree in each of the four cardinal directions. Our survey form can be viewed and downloaded by following the link to Forest Sampling Methods, Rapid Assessment Method at the internet address http://www.public.iastate.edu/~bot356/homepage.html.

Data Summarization

Characterization of Forest Bird Communities

We conducted separate analyses for total birds as well as for "management assemblages" determined by migratory class (neotropical migrants, permanent residents, short-distance migrants), nest substrate (cavity, ground, shrub, tree), level of management concern, and area sensitivity. The assignment of birds to the migratory and nest substrate assemblages is based on assignments given in Best et al. (1996). Birds grouped together as "high management concern" species are neotropical migrants with high values ($\geq$ 3.0) for a conservation priority index (PIF = Partners in Flight Index) developed by the U.S. Fish and Wildlife Service (Thompson et al. 1993). This index ranges from 1 (low concern) to 5 (high concern); scores for each species are based on means of seven criteria values. Birds grouped together as "area sensitive" are those demonstrated in the majority of other studies to prefer large forest tracts (Best et al. 1996). All raptors, nightjars, late spring vagrants, and flyovers were omitted from these analyses.

We calculated an abundance index for birds in each management assemblage (separately for 1995, 1996) by first calculating the total number of bird observations (inside a 50-m-radius circle) per census point, then calculating the mean number of detections per census point (across temporal replicates) at each site. Similarly, we determined the species richness of birds in each management assemblage (separately for 1995, 1996) by first calculating the total number of bird species detected per census point (no distance restriction), then calculating the mean number of bird species detected per census point (across temporal replicates) for each site.

Disturbance Index

Norris and Farrar (2001) developed a method for evaluating the degree of disturbance (frequency, intensity) of forest vegetation on a scale of 0 to 20. This method relies upon the summation of scores obtained from six criteria (Tree Size, Tree Structure, Shrub Structure, Canopy Dominance, Subcanopy Dominance, Shrub Dominance) at each survey plot. The rules for assignment of points are explicit and are calibrated with respect to survey data that we obtained in northeast Iowa forest preserves and state parks. Forests in these protected areas are mature and have been relatively unaffected by human impacts (logging, cattle grazing) for at least 50 y. A brief description of these six evaluation criteria appears below.

The "Tree Size" (4 pts) criterion is based on tree girth; forests with large trees receive higher scores than those with small trees. The "Tree Structure" (3 pts) criterion is based on degree of development and differentiation of canopy and subcanopy layers in a forest; maximum points are awarded when canopy and subcanopy layers are both present and clearly delineated. In contrast, maximum points are awarded for the "Shrub Structure" (3 pts) criterion when the shrub layer is diffuse (1% to 10% total cover) because this is the condition observed in protected forests. As for the "Canopy Dominance" (4 pts), "Subcanopy Dominance" (2 pts), and "Shrub Dominance" (4 pts) criteria, maximum points are awarded when the dominant tree and shrub species, respectively, are those known to be dominant in the appropriate forest layer in northeast Iowa state preserves.

The scores from all six criteria are summed to yield a disturbance index (D) for each 0.10-ha survey plot; the index ranges in value from 0 (most frequent/severe anthropogenic disturbance) to 20 (least frequent/severe anthropogenic disturbance). We obtained a measure of the overall disturbance ($\bar{D}$) at each study site by computing the mean D value from all vegetation survey plots within the given site.

The above method for measuring degree of disturbance is described more thoroughly in Norris and Farrar (2001).

Characterization of Forest Area

The boundaries of our forest sites almost always corresponded to private ownership boundaries. In many cases, these boundaries corresponded to transitions between forest and nonforest habitat; in some cases, they did not. For this reason, we measured the total forest area within a 1-km extension of forest site boundaries (rather than inside the political boundaries of the site) for use in later regression analyses. To do this, we first created an arc coverage (GIS) of site boundaries from 7.5 series USGS quadrangles. From this site coverage, we created a 1-km buffer coverage, which we subsequently used to clip a land-use raster coverage classified from recent (1992) 30-m resolution Thematic Mapper (TM) satellite imagery. Finally, we calculated the amount of total forest area within 1 km of site boundaries (A) using FRAGSTATS software (McGarigal and Marks 1994).

Analysis of Influence of Vegetation/Area/Year on Avian Abundance and Species Richness

Our original intention was to test for relationships between bird community attributes (avian abundance and species richness), and overall forest disturbance ($\bar{D}$) and the criteria (Tree Size, Tree Structure, Shrub Structure, Canopy Dominance, Subcanopy Dominance, Shrub Dominance) used to construct ($\bar{D}$). Prior to conducting regression analyses, we subjected the values obtained for the six individual criteria (mean values for each study site) to principal components analysis (PCA) to eliminate collinearity. PCA is a technique for forming new variables that are linear combinations of the original variables. The new variables obtained from PCA, which are interpreted via examination of the eigenvectors associated with the original variables, are uncorrelated (Sharma 1996). We used the first three principal components (PCA1, PCA2, PCA3) as independent variables in subsequent regression analyses; their interpretation is presented in the Results. Given high correlation (r = 0.98, P = 0.99) between PCA1 and our original disturbance index ($\bar{D}$), we decided to use PCA1 as a proxy for our disturbance index, rather than testing for relationships between bird community attributes and $\bar{D}$ directly.

In addition to the above variables that summarize vegetation characteristics for each site, we included site area (AREA) as an independent variable because it has been found to influence abundance and species richness of forest birds elsewhere in the Midwest (Ambuel and Temple 1981, Blake and Karr 1987, Hayden et al. 1987). We calculated Pearson correlation coefficients (r) between AREA and the above vegetation variables (PCA1, PCA2, PCA3) prior to its inclusion in the set of independent variables (α=0.05). Likewise, we included the variable YEAR in our set of independent variables because avian abundance and species richness can vary annually (Schooley 1994).

Ultimately, we used stepwise regression with the MAXR selection method to test for relationships of avian attributes (abundance and species richness) with vegetation variables (PCA1, PCA2, PCA3), site area (AREA), and year (YEAR). In stepwise regression, independent variables are entered into a regression equation one at a time following a predetermined selection criterion. The MAXR selection procedure finds the one-variable regression with the highest r^2, then finds the two-variable regression equation with the highest r^2, and so on (Cody and Smith 1997). We used α = 0.05 as our cutoff for statistical significance in the above analyses.

RESULTS

Bird Community Composition

A list of all birds detected (inside the 50-m-radius census circle) at least 10 times during fieldwork over the 2 y appears in Table 1. We present the total number of detections (inside the 50-m-radius circle) for each bird species as well as its migratory status, preferred nest substrate, level of management concern, and degree of area sensitivity as given in Best et al. (1996), Thompson et al. (1993), and Harrison (1975).

Table 1. Bird species detected during point counts in 44 study sites in northeast Iowa forests (1995–1996). N = number of observations (inside a 50-m-radius circle) during both years. Life history characteristics, conservation status, and area sensitivity are as given in Best et al. (1996). Birds detected fewer than ten times are not listed. Nomenclature follows American Ornithologists' Union (1998).

Species	N	Migratory Status[a]	Nest Substrate[b]	Food Substrate[c]	PIF Prioritizations[d]	Area Sensitivity[e]
Brown-headed cowbird (*Molothrus ater* Boddaert)	628	sho	—	g	—	(+)
Blue-gray gnatcatcher (*Polioptila caerulea* L.)	556	neo	t	t	2.43	++
Eastern wood-pewee (*Contopus virens* L.)	484	neo	t	a	3.29	+
Red-eyed vireo (*Vireo olivaceus* L.)	482	neo	t	t	2.14	+
American redstart (*Setophaga ruticilla* L.)	373	neo	s	s	2.86	+
House wren (*Troglodytes aedon* Vieillot)	317	neo	c	s	1.57	(?)
Ovenbird (*Seiurus aurocapillus* L.)	311	neo	g	g	3.14	++
Indigo bunting (*Passerina cyanea* L.)	292	neo	s	s	2.86	(-)
White-breasted nuthatch (*Sitta carolinensis* Latham.)	285	per	c	b	—	+
Northern cardinal (*Cardinalis cardinalis* L.)	255	per	s	g	—	(-)
Great crested flycatcher (*Myiarchus crinitus* L.)	250	neo	c	a	3.29	+
Blue jay (*Cyanocitta cristata* L.)	242	per	t	g	—	(+)
Gray catbird (*Dumetella carolinensis* L.)	233	neo	s	g	2.86	(-)
Black-capped chickadee (*Poecile atricapillus* L.)	205	per	c	s	—	(+)
Red-bellied woodpecker (*Melanerpes carolinus* L.)	183	per	c	b	—	+
Hairy/downy woodpecker (*Picoides villosus* L. /*Picoides pubescens* L.)	165	per,per	c, c	b, b	—, —	+, +
Rose-breasted grosbeak (*Pheucticus ludovicianus* L.)	163	neo	s	t	3.14	+
Yellow-throated vireo (*Vireo flavifrons* Vieillot)	163	neo	t	t	3.00	+
Scarlet tanager (*Piranga olivacea* Gmelin)	153	neo	t	t	3.00	++
American goldfinch (*Carduelis tristis* L.)	142	sho	s	s	—	(?)
American robin (*Turdus migratorius* L.)	141	sho	t	g	—	(-)
Acadian flycatcher (*Empidonax virescens* Vieillot)	129	neo	t	a	3.43	++
Eastern towhee (*Pipilio erythrophthalmus* L.)	112	sho	g	g	—	-
Baltimore oriole (*Icterus galbula* L.)	102	neo	t	t	2.86	(+)
Tufted titmouse (*Baeolophus bicolor* L.)	97	per	c	s	—	+
Wood thrush (*Hylocichla mustelina* Gmelin)	73	neo	s	g	3.57	++
American crow (*Corvus brachyrhynchos* Brehm.)	70	per	t	g	—	(+)
Chipping sparrow (*Spizella passerina* Bechstein)	69	neo	s	g	1.86	(-)
Red-winged blackbird (*Agelaius phoeniceus* L.)	48	sho	g	g	—	(-)
Common yellowthroat (*Geothlypis trichas* L.)	47	neo	g	s	2.29	(?)
Yellow warbler (*Dendroica petechia* L.)	47	neo	s	s	1.57	(+)
Yellow-bellied sapsucker (*Sphyrapicus varius* L.)	37	sho	c	b	—	+
Cerulean warbler (*Dendroica cerulea* Wilson)	36	neo	t	t	4.29	++
Ruby-throated hummingbird (*Archilochus colubris* L.)	36	neo	t	f	2.57	(+)
Song sparrow (*Melospiza melodia* Wilson)	35	sho	s	s	—	(?)
Blue-winged warbler (*Vermivora pinus* L.)	33	neo	g	s	3.57	?
Red-headed woodpecker (*Melanerpes erythrocephalus* L.)	32	sho	c	a	—	(+)
Pileated woodpecker (*Dryocopus pileatus* L.)	31	per	c	b	—	+

continued

Table 1, *continued*

Species	N	Migratory Status[a]	Nest Substrate[b]	Food Substrate[c]	PIF Prioritizations[d]	Area Sensitivity[e]
Common grackle (*Quiscalus quiscula* L.)	27	sho	t	g	—	0
Least flycatcher (*Empidonax minimus* Baird and Baird)	25	neo	t	a	2.71	++
Field sparrow (*Spizella pusilla* Wilson)	23	sho	g	g	—	(+)
Warbling vireo (*Vireo gilvus* Vieillot)	23	neo	t	t	2.57	+
Yellow-billed cuckoo (*Coccyzus americanus* L.)	22	neo	s	s	3.29	+
Cedar waxwing (*Bombycilla cedrorum* Vieillot)	21	sho	t	a	—	*
Eastern phoebe (*Sayornis phoebe* Latham)	21	sho	b	a	—	+
Northern flicker (*Colaptes auratus* L.)	19	sho	c	g	—	(+)
Louisiana waterthrush (*Seiurus motacilla* Vieillot)	17	neo	b	sh	3.00	++
Veery (*Catharus fuscescens* Stephens)	17	neo	g	g	3.29	++
Brown thrasher (*Toxostoma rufum* L.)	12	sho	s	g	—	(?)
Chestnut sided warbler (*Dendroica pensylvanica* L.)	12	neo	s	*	3.57	?
Mourning Dove (*Zenaida macroura* L.)	11	sho	t	g	—	(?)

[a] Migratory Status: neo = neotropical; per = permanent resident; sho = short-distance migrant.

[b] Nest Substrate: c = cavity; g = ground; s = shrub; t = tree; b = streambanks; bu = man-made structures.

[c] Food Substrate: a = air; b = bark; f = flowers; g = ground; s = shrub; sh = shore; t = tree.

[d] PIF (Partners in Flight) Prioritizations: Values range from 1 to 5. See text for more details.

[e] Area Sensitivity: ++ = consistently positive area sensitive; + = primarily positive area sensitivity but some studies detected none; (+) = primarily no area sensitivity but some studies detected positive area sensitivity; 0 = consistently no area sensitivity; (-) = primarily no area sensitivity but some studies detected negative area sensitivity; - = primarily negative area sensitivity but some studies detected none; (?) = area sensitivity unknown because of contradictory results; ? = area sensitivity unknown because it has not been studied

A complete list of all bird species encountered during fieldwork for this study appears in Hemesath and Norris (1998).

Principal Components Analysis of Evaluation Criteria

Three components derived from principal components analysis were sufficient to account for 74% of the total variance of the six original criteria used to construct the natural quality index (Table 2). The first component, PCA1 (37% of total variance), is a surrogate for our original disturbance index, $\bar{D}$, because all six criteria have high positive loadings in the associated eigenvector.

Table 2. Eigenvectors for principal components derived from criteria used to evaluate natural quality of forest vegetation. Variables are described in the Methods.

Evaluation Criteria	Principal Components		
	PCA1	PCA2	PCA3
TREE SIZE	.33	.52	.01
TREE STRUCTURE	.22	.65	-.28
SHRUB STRUCTURE	.39	-.54	-.36
CANOPY DOMINANCE	.38	-.04	.80
SUBCANOPY DOMINANCE	.49	-.08	.19
SHRUB DOMINANCE	.56	-.08	-.35
Eigenvalue	2.2	1.4	.87
Variance Explained (%)	37	23	14
Cumulative Variance Explained (%)	37	60	75

The second component, PCA2 (23% of total variance), is a proxy for forest structure because high loadings on Tree Size and Tree Structure contrast with high negative loadings for Shrub Structure. Forests with high values for PCA2 would have large trees, a closed canopy, and the shrub layer deviating from that typically encountered in protected forests (i.e., diffuse) by being either absent or profuse.

The third component, PCA3 (14% of total variance), summarizes both structural and floristic information. It contrasts Canopy Dominance (large positive loading) with three other variables: Tree Structure, Shrub Structure, and Shrub Dominance (large negative loadings). Forests with high values for PCA3 would have canopy tree species typical for the terrain (e.g., oak species and sugar maple in upland topography) but with canopies unclosed. In such forests, extensive shrub layers would occur in canopy gaps and be dominated by shrub species not typically dominant in the shrub layers of protected forests (e.g., Missouri gooseberry, prickly ash).

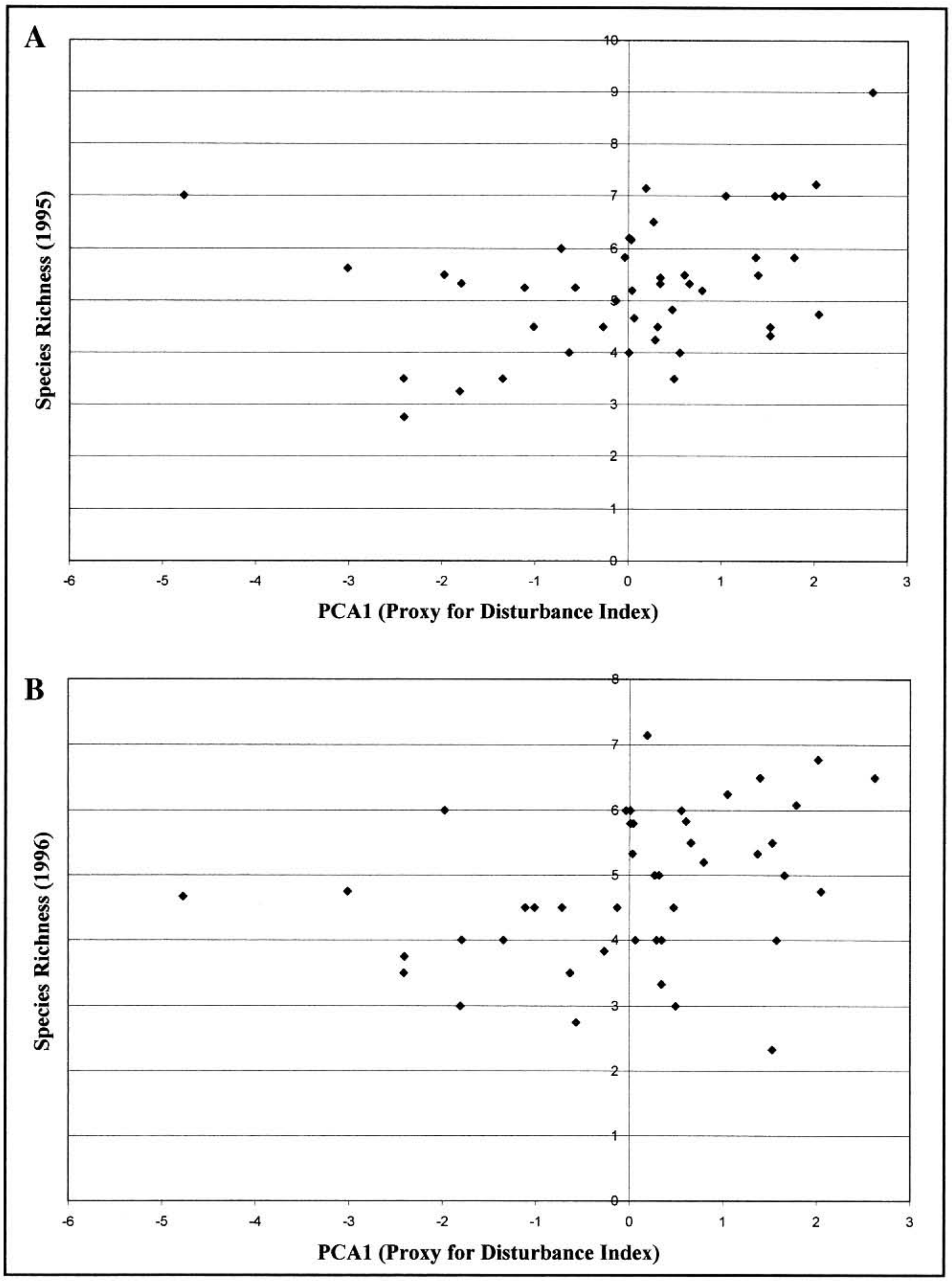

Figure 1. Relationship between species richness (mean number of species detected per bird census point in a site) of Partners in Flight bird species of high management concern and PCA1 (proxy for disturbance index) in northeast Iowa, USA, forests. High values of PCA1 correspond to infrequently disturbed, mature forests. Low values of PCA1 correspond to heavily disturbed, successional forests. A) 1995 data. B) 1996 data.

PCA1, PCA2, and PCA3 are uncorrelated due to the nature of principal components analysis. There was little evidence of correlation between forest area (A) and PCA1 (r = 0.15, P = 0.33), PCA2 (r = 0.10, P = 0.50), or PCA3 (r = -0.029, P = 0.85). Therefore, subsequent stepwise regression analyses were not hampered by problems of collinearity among independent variables.

Influence of Disturbance Regime on Avian Abundance and Species Richness

We found significant relationships between PCA1 (our disturbance index proxy) and the abundance of only two bird groups. Permanent residents were more abundant in highly disturbed forests (i.e., low values of PCA1), while area-sensitive birds tended to be more abundant in relatively undisturbed forests (i.e., high values of PCA1) (Table 3). On the other hand, PCA1 was a good predictor of species richness for 7 out of 10 bird groups (Table 4). Short-distance migrants, permanent residents, and ground nesters had higher species richness in highly disturbed forests, while neotropical migrants, tree nesters, PIF birds of high management concern, and area-sensitive species were more diverse in infrequently disturbed forests. Figure 1 is a graphical representation of the relationship between species richness of PIF birds of high management concern and our disturbance index proxy (PCA1).

We detected no relationship between variable PCA2 ("structure") and either the abundance or species richness of any bird group (Tables 3, 4). Likewise, PCA3 ("structure and floristics") had very little predictive value. It was not related to the species richness of any bird group, and was related to the abundance of only two

Table 3. Stepwise regression analysis (MAXR selection) of avian abundance on forest area (AREA), vegetation variables (PCA1, PCA2, PCA3), and year (YEAR). Abundance was determined as the mean number of detections (inside a 50-m-radius circle) per census point at each site. AREA is the total amount of forest (ha) within a 1-km extension of the political boundaries of each site. PCA1 is a "disturbance index"; PCA2 represents "structure"; PCA3 represents "structure and floristics" (see text for more complete descriptions of these variables). TOT = total birds; NEO = neotropical migrants; SHO = short-distance migrants; PER = permanent residents; TRE = tree nesters; CAV = cavity nesters; GRO = ground nesters; SHR = shrub nesters; PIF = Partners in Flight birds of high management concern; ARS = area sensitive birds. r^2 = proportion of total variance explained by the regression model; β = regression coefficient; SE = standard error of b. a = 0.05; significant relationships are in boldface.

		AREA			PCA1			PCA2			PCA3			YEAR		
	r^2	β	SE	*P* > F	β	SE	*P* > F	β	SE	*P* > F	β	SE	*P* > F	β	SE	*P* > F
TOT	0.27	-0.0032	0.0020	0.12	-0.049	0.370	0.90	-0.078	0.46	0.87	-0.47	0.59	0.43	-0.55	0.11	**<0.0001**
NEO	0.22	-0.0017	0.0015	0.26	0.41	0.27	0.13	0.17	0.34	0.62	-0.035	0.428	0.94	-0.35	0.08	**<0.0001**
SHO	0.032	-0.00010	0.00067	0.88	-0.12	0.12	0.35	-0.027	0.15	0.86	-0.25	0.19	0.19	-0.0014	0.0356	0.97
PER	0.29	-0.0014	0.0008	0.09	-0.35	0.15	**0.02**	-0.23	0.19	0.22	-0.19	0.24	0.43	-0.20	0.04	**<0.0001**
TRE	0.19	-0.00010	0.00092	0.91	0.31	0.17	0.07	-0.037	0.207	0.86	-0.12	0.26	0.64	-0.19	0.05	**0.0002**
CAV	0.29	-0.0025	0.0008	**0.004**	-0.23	0.15	0.13	-0.18	0.19	0.33	-0.43	0.24	0.07	-0.18	0.04	**0.0001**
GRO	0.25	0.0015	0.0004	**<0.0001**	-0.083	0.065	0.20	0.14	0.08	0.09	0.21	0.10	**0.05**	-0.018	0.019	0.34
SHR	0.10	-0.0020	0.0010	**0.05**	-0.026	0.179	0.88	-0.056	0.222	0.80	0.0084	0.2824	0.98	-0.11	0.051	**0.03**
PIF	0.31	0.0011	0.0007	0.099	0.23	0.12	0.06	0.26	0.15	0.10	0.53	0.19	**0.008**	-0.16	0.04	**< 0.0001**
ARS	0.33	0.00048	0.00121	0.69	0.51	0.22	**0.02**	0.30	0.27	0.28	0.12	0.35	0.74	-0.37	0.06	**<0.0001**

groups: ground nesters (+) and PIF birds of high management concern (+) (Tables 3 and 4).

Forest area (AREA) influenced the abundance and species richness of selected bird groups. The abundance of cavity nesters and shrub nesters was higher in small forests, while the abundance of ground nesters was higher in larger forests (Table 3). Neotropical migrants, ground nesters, PIF species of high management concern, and area-sensitive birds tended to have higher species richness in large forest tracts (Table 4).

Finally, both avian abundance and species richness showed strong variation over the two years of this study. The abundances of eight bird groups and species richness' of five bird groups declined from 1995 to 1996 (Tables 3 and 4).

DISCUSSION

It is not surprising that the species richness (mean number of birds detected per census point at each site) of total birds was not related to our proxy for the disturbance index (PCA1) in northeast Iowa (Table 4). Obviously, "total birds" consists of both generalists and specialists; *en masse*, one would expect to encounter these in a wide range of forest types that span the spectrum of forest quality. On the other hand, the negative relationship between this variable and the species richness of short-distance migrants and permanent residents (Table 4) suggests that the majority of these birds frequent successional forests, which are abundant in northeast Iowa. Likewise, Blake and Karr (1987) found that the species richness of permanent residents and short-distance migrants in Illinois woodlots was related to the presence of shrubby vegetation.

We also infer from our analyses that ground nesters have higher species richness in frequently disturbed forests (Table 4). It is likely that these birds prefer to build their nests in such forests because these tend to have shrubby understories for potential nest concealment. The Eastern towhee (*Pipilio erythropthalmus* L.), for instance, typically places its nest on or near ground under

Table 4. Stepwise regression analysis (MAXR selection) of avian species richness on forest area (AREA), vegetation variables (PCA1, PCA2, PCA3), and year (YEAR). Species richness was determined as the mean number of species detections (no distance restrictions) per census point at each site. AREA is the total amount of forest (ha) within a 1-km extension of the political boundaries of each site. PCA1 is a "disturbance index"; PCA2 represents "structure"; PCA3 represents "structure and floristics" (see text for more complete descriptions of these variables). TOT = total birds; NEO = neotropical migrants; SHO = short-distance migrants; PER = permanent residents; TRE = tree nesters; CAV = cavity nesters; GRO = ground nesters; SHR = shrub nesters; PIF = Partners in Flight birds of high management concern; ARS = area sensitive birds. r^2 = proportion of total variance explained by the regression model; β = regression coefficient; SE = standard error of b. a = 0.05; significant relationships are in boldface.

		AREA			PCA1			PCA2			PCA3			YEAR		
	r^2	β	SE	*P* > F	β	SE	*P* > F	β	SE	*P* > F	β	SE	*P* > F	β	SE	*P* > F
TOT	0.27	-0.0032	0.0020	0.12	-0.049	0.370	0.90	-0.078	0.46	0.87	-0.47	0.59	0.43	-0.55	0.11	**<0.0001**
TOT	0.11	0.0019	0.0010	0.06	-0.26	0.18	0.17	0.10	0.23	0.65	0.0064	0.29	0.98	-0.11	0.054	**0.04**
NEO	0.18	0.0015	0.0007	**0.04**	0.32	0.13	**0.01**	0.13	0.16	0.43	0.078	0.20	0.70	-0.081	0.038	**0.03**
SHO	0.17	0.0006	0.00054	0.25	-0.38	0.098	**0.0002**	0.042	0.12	0.73	0.12	0.15	0.44	0.015	0.028	0.61
PER	0.16	-0.0001	0.0004	0.79	-0.20	0.076	**0.01**	-0.079	0.095	0.41	-0.20	0.12	0.11	-0.046	0.022	**0.04**
TRE	0.13	0.0004	0.00045	0.36	0.16	0.082	**0.05**	-0.069	0.102	0.51	-0.23	0.13	0.08	-0.046	0.024	0.06
CAV	0.090	-0.0003	0.00049	0.54	-0.16	0.09	0.08	-0.081	0.101	0.46	-0.14	0.14	0.32	-0.040	0.026	0.12
GRO	0.21	0.00079	0.00029	**0.007**	-0.17	0.05	**0.001**	0.10	0.07	0.11	0.093	0.082	0.26	-0.011	0.015	0.48
SHR	0.053	0.00076	0.00048	0.12	-0.11	0.09	0.23	0.039	0.109	0.72	0.13	0.14	0.36	-0.0061	0.0254	0.81
PIF	0.27	0.0013	0.0004	**0.003**	0.23	0.08	**0.005**	0.16	0.10	0.10	0.14	0.13	0.27	-0.046	0.023	**0.05**
ARS	0.24	0.0018	0.0007	**0.01**	0.26	0.13	**0.04**	0.20	0.16	0.20	0.0010	0.20	0.96	-0.12	0.04	**0.002**

or in small bushes (Harrison, 1975).

Our finding that neotropical migrants, tree nesters, PIF species of high management concern, and area-sensitive birds are most diverse in infrequently disturbed forests (Table 4) suggests that mature forest vegetation in northeast Iowa, though scarce, is important wildlife habitat. These bird species may have evolved preferences for particular foliage structural attributes and/or woody plant species available in mature forests but not in successional habitat. For instance, Holmes and Robinson (1981) showed that the occurrence of some bird species in northern hardwood forests is linked to preferences for particular tree species that provide abundant food resources and/or unique structural attributes that differentially influence foraging behavior. Likewise, May (1982) found that specialist feeding guilds were more prevalent in older forests than in younger forests in Virginia. May attributed this pattern to the addition of several insectivorous guilds in late successional stages. Similar phenomena may explain why some or many of the birds in the above groups are attracted to mature, infrequently disturbed forests in northeast Iowa.

Our disturbance index proxy (PCA1) was less successful in predicting patterns of avian abundance. We detected significant relationships between PCA1 and the abundances of only two bird groups: permanent residents (-) and area-sensitive species (+). An obvious question that arises when one inspects our results is why the abundances of neotropical migrants, tree nesters, PIF species, and area-sensitive birds do not vary predictably with PCA1, given that this index does predict patterns of variation in species richness of these bird groups. A possible explanation is that one member of all these bird groups, the eastern wood-pewee (*Contopus virens* L.), was the third most frequently detected birds in this study (Table 1). The high abundance of eastern wood pewee in northeast Iowa forests may indicate that it is a habitat generalist (as was reported for this species by Bond [1957] for upland forests in southern Wisconsin). Alternatively, eastern wood-pewees may actually prefer mature, infrequently disturbed forests, but as niches in such forests are occupied by adult pewees, young birds may be pushed into less desirable (i.e., more frequently disturbed) forests (L. Powell, School of Natural Resource Sciences, University of Nebraska, pers. com.). As such, the apparent noncorrelation between the abundances of the above bird groups and our disturbance index may actually reflect the ubiquity and sheer numbers of eastern wood-pewees.

The other two variables that summarize vegetation, PCA2 and PCA3, did not explain much variation in avian abundance or species richness. Only PCA3 ("structure and floristics") had any explanatory power: it was related to ground nester (+) and PIF bird (+) abundance, respectively (Table 3). Forests with high values of PCA3 may be interpreted as having the expected canopy dominants (e.g., oak and sugar maple on upland topography) in an unclosed canopy; extensive shrub (Missouri gooseberry, prickly ash) layers would occur on the forest floor within these canopy gaps. Such a forest would attract ground nesters for reasons mentioned above, i.e., nest concealment. As for PIF birds, some birds in this group, such as the rose-breasted grosbeak (*Pheucticus ludovicianus* L.), Acadian flycatcher (*Empidonax virescens* Vieillot), and wood thrush (*Hylocichla mustelina* Gmelin), may be attracted to such forests because they utilize shrub vegetation for either nest or food substrate (Table 1).

Is the "Disturbance Index" Meaningful?

As we have constructed it, the original index of disturbance ($\bar{D}$) summarizes the overall condition of a forest with respect to tree size, foliage distribution, and dominance patterns exhibited by woody plant species in canopy, subcanopy and shrub layers. Individual birds are known to use a variety of cues when selecting habitat (structure, plant species, topography, etc.), but it is uncertain whether these cues interact independently, hierarchically, or synergistically (Cody 1985). Of course, habitat isn't actively selected by a "bird community," but it is interesting nevertheless to ask whether the factors that influence bird community composition operate independently or interactively. In our analyses (Table 4), our proxy for this disturbance index (PCA1) predicted patterns of variability in the species richness of 7 (out of 10) bird groups; in contrast, neither PCA2 nor PCA3 had any predictive value for this bird community attribute. Thus, our composite index, which incorporates many aspects of forest vegetation, may be better at explaining local patterns of bird species richness than a single or small number of vegetation attributes. Hence, this index provides a tool to conservationists charged with managing forests for maximum diversity of desirable bird species.

Management Recommendations

In our study, we determined that forests at both ends of a disturbance gradient provide habitat for birds in northeast Iowa. Frequently disturbed (successional) forests occupy one end of this gradient, and are especially attractive to many permanent resident, short-distance migrant, and ground-nesting bird species in northeast Iowa (Table 4). Thus, the role of successional forests must be acknowledged in any regional plan to manage northeast Iowa forests for bird conservation. However, given the current preponderance of successional forests in northeast Iowa, we do not see them as being the primary focus of such a plan.

We also determined that neotropical migrants, tree nesters, PIF birds of high management concern, and area-sensitive birds tend to be more diverse in mature, infrequently disturbed forests that have been long withheld from recent logging and pasturing (Table 4, Figure 1). We believe that maintenance of suitable habitat for utilization by these bird species is a reasonable and desirable goal for management of northeast Iowa forests at this time. To accomplish this, we recommend that existing mature forests be protected from human impacts and suggest that other, mid-successional forests be allowed to recover and thus provide habitat for future generations of these habitat specialists.

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