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# Bird Communities and Habitat as Ecological Indicators of Forest Condition in Regional Monitoring

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**Abstract:** *Ecological indicators for long-term monitoring programs are needed to detect and assess changing environmental conditions. We developed and tested community-level environmental indicators for monitoring forest bird populations and associated habitat. We surveyed 197 sampling plots in loblolly-shortleaf pine forests, spanning an area from Georgia to Virginia (U.S.A.) and representing a gradient in levels of anthropogenic disturbance. Ninety of these plots were randomly selected from a sampling grid, permitting quantitative assessment of cumulative distribution functions for bird community and habitat parameters. Species were independently classified into habitat assemblages indicating birds typical of disturbed habitat (e.g., shrubland, forest edge) and undisturbed habitat (mature forest). Relative abundances of these assemblages were used to form a bird community index—similar to the index of biotic integrity applied to aquatic systems—showing the effects of habitat disturbance on forest bird communities. Bird communities on the majority of the sample area (52–75%, 90% confidence interval) were dominated by disturbance-tolerant species. Sites dominated by mature-forest species were comparatively uncommon. Habitat assemblages appeared to be particularly useful tools for environmental monitoring; individual species abundance was positively correlated with assemblage species richness, and assemblage members showed consistent responses to variations in disturbance level. To a lesser extent, component species of nesting guilds showed this pattern of cohesive responses, but those of foraging guilds did not. We also developed a habitat index based on habitat variables that predicted bird community index values. Habitat and bird community indices were strongly correlated in an independent validation dataset, suggesting that the habitat index can provide a reliable predictor of bird community status. The two indices may be used in combination, with the bird community index providing a direct measure of the status of the bird community and the habitat index providing a basis on which to separate changes in the bird community into local habitat effects versus other factors (e.g., landscape level effects, changes on wintering grounds).*

Comunidades de Aves y Hábitat Como Indicadores Ecológicos de la Condición del Bosque en Monitoreos Regionales

**Resumen:** *Se necesitan indicadores ecológicos para programas de monitoreo a largo plazo para detectar y evaluar condiciones ambientales cambiantes. Desarrollamos y evaluamos indicadores ambientales a nivel de comunidad para monitorear poblaciones de aves en bosques, así como en el hábitat asociado. Evaluamos 197 cuadrantes de muestreo en bosques de pino, abarcando un área de Georgia a Virginia (E.U.A.) y representando un gradiente en niveles de perturbación antropogénica. Noventa de estos cuadrantes fueron seleccionados al azar, permitiendo una evaluación cuantitativa de funciones acumulativas de distribución de aves y parámetros de hábitat. Las especies fueron clasificadas independientemente en ensamblajes de hábitat indicando aves típicas de hábitat perturbado (por ejemplo, bordes arbustivos del bosque) y hábitat no perturbado (bosque maduro). Las abundancias relativas de estos ensamblajes fueron utilizadas como un índice*

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*de comunidad de aves similar al índice de integridad biótica aplicado a sistemas acuáticos, mostrando efectos de la perturbación del hábitat en las comunidades de aves del bosque. En la mayor parte del área muestreada (52–75%, 90% intervalo de confianza) las comunidades de aves estuvieron dominadas por especies tolerantes a la perturbación. Los sitios dominados por especies de bosque maduro fueron comparativamente poco comunes. Los ensamblajes del hábitat aparentemente son herramientas especialmente útiles para el monitoreo ambiental; la abundancia de especies individuales estuvo positivamente correlacionada con la riqueza de especies de los ensamblajes y los miembros del ensamblaje mostraron respuestas consistentes a la variación en el nivel de perturbación. En menor grado, las especies que conforman los gremios de aves que anidan mostraron este patrón de respuestas cohesivas, no así los gremios que forrajean. También desarrollamos un índice de hábitat basado en las variables del hábitat que predijeron los valores de los índices de la comunidad de aves. El hábitat y los índices de la comunidad de aves estuvieron fuertemente correlacionados en un juego de datos de validación independiente, sugiriendo que el índice de hábitat puede proveer una predicción confiable del estado de la comunidad de aves. Los dos índices pueden ser utilizados en combinación; el índice de comunidad de aves puede proporcionar una medición directa del estado de la comunidad de aves y el índice del hábitat puede proporcionar las bases para separar cambios en la comunidad de aves debidos a efectos locales de hábitat de los debidos a otros factores (por ejemplo, efectos a nivel de paisaje, cambios en áreas de hibernación).*

## Introduction

Determination of the extent to which ecological systems are experiencing anthropogenic disturbance and change in structure and function is critical for the long-term conservation of biotic diversity in the face of changing landscapes and land use. The ability to assess status and trends in the condition of ecological systems over broad geographic regions can allow identification of existing or developing problems prior to a crisis. Yet the complex and diverse nature of ecological systems necessitates the use and appropriate validation of some restricted set of indicators of biological condition to allow efficient monitoring of a broad range of systems. Species have been proposed as environmental indicators under an assumption that the responses of individual species are representative of the responses of other species within a habitat or community (e.g., the National Forest Management Act; U.S. Code of Federal Regulations 1985 (36 CFR Chapter II 219.19:64)). This indicator species concept has been criticized, however, because individual species do not necessarily reflect trends in other co-occurring species (Morrison 1986; Landres et al. 1988). Indeed, co-occurring species typically differ in habitat requirements and life histories (Martin & Li 1992; Martin 1993, 1995) and can respond independently to environmental variation (e.g., James et al. 1984), so individual species are questionable indicators of community responses.

On the other hand, individual species may function as indicators of a restricted component of the community, such as the abundance of other members of the same guild (Severinghaus 1981), defined as collections of species that exploit the same class of environmental resources in a similar way (Root 1967). Yet this approach still assumes that all species within a guild respond simi-

larly to environmental changes. Depending on guild definition, the occurrence of individual species within a guild may give little information about overall guild abundance or diversity, because of the different environmental requirements of individual species. Thus, species that make up the ground-nesting guild, for example, can differ markedly between or even within habitat types, whereas overall guild abundance and diversity may not differ because of species substitutions.

To a lesser extent these difficulties also exist when the overall abundance of a guild, rather than individual species, is used as the indicator (Verner 1984). Large increases in one or two species can mask the decline or loss of others in the same guild (Mannan et al. 1984). Consistency of population responses among species in a guild is thus important for the guild's utility as an indicator. Guilds can be useful for evaluating the collective responses of multiple species to changes in resources or ecological conditions that define the guild (Block et al. 1995). Thus, the definition of a guild ultimately is critical to its effectiveness as an indicator of the environmental issue of concern.

For these purposes species can be categorized into functional groups based on criteria that traditionally define guilds (e.g., foraging strategies or nesting substrates; Root 1967; Willson 1974; Karr 1980; Martin 1981; Szaro 1986). Other criteria such as habitat preference can also be useful for defining functional groups (Finch 1991), although functional groups based on habitat (hereafter, habitat assemblages) are not guilds as defined by Root (1967) because they do not reflect partitioning of a specific ecological resource. (We define habitat in the narrow sense of vegetation structure rather than as the full array of physical, chemical, and biological factors in the environment.) We compared functional groups based on foraging, nesting, and habitat preferences as indica-

tors for monitoring disturbance to forest bird communities. We assessed the consistency of population responses among members of a functional group and the association between group species richness and forest disturbance. We examined habitat assemblages because anthropogenic disturbance of forests often results in the loss of species requiring undisturbed or late-successional conditions and invasion by species typical of earlier successional stages (e.g., Mannan & Meslow 1984). Discovering and monitoring such replacement patterns are particularly important because species that depend on large blocks of mature forest (i.e., forest interior species) may be especially susceptible to population problems from fragmentation and loss of forests (Robbins et al. 1989).

Habitat assemblages can be defined according to successional habitat preferences, thus reflecting this disturbance gradient (e.g., Croonquist & Brooks 1991). Szaro (1986) also found that "response guilds" reflecting avian habitat use had notably higher correlations with the abundance of their component species than did guilds defined by foraging substrate. Habitat assemblages have the advantage of allowing direct evaluation of community responses to the modification of vegetation structure by land-management practices. But individual habitat assemblages still can indicate only the particular resource condition defining them, so multiple habitat assemblages should be considered for evaluating entire communities.

The approach of combining several metrics to measure ecological condition was originally used to develop an index of biotic integrity for aquatic systems (Karr 1981; 1991; Karr et al. 1987). This method measures biotic integrity using various metrics—trophic levels, species richness, disease prevalence, abundance of pollution-tolerant taxa—of an assemblage of fishes, benthic invertebrates, or other taxa. The index of biotic integrity assesses how closely the species composition of a local fish community matches that of reference watersheds with minimal human influence, thus indicating community changes brought about by anthropogenic disturbance. The combination of several metrics improves the robustness of the index by reducing the effects of variation in individual parameters. The index of biotic integrity may thus be more appropriate than indices reflecting species diversity alone for assessment of ecological status for management purposes (Angermeier & Karr 1994).

The index of biotic integrity has been applied primarily to aquatic systems, but the concept is also applicable to terrestrial systems such as bird communities (Bradford et al. 1998). The types of metrics used in aquatic systems may be inappropriate in terrestrial systems, however, in which trophic patterns may not differ greatly across disturbance types and the health of individual animals is difficult to assess. Habitat assemblages are likely to integrate multiple effects of disturbance on a bird community, including changes in foraging and nesting substrates and

scale-dependent fragmentation effects. Therefore, we developed and tested an index that characterized forest bird communities on a gradient from disturbed to mature forest over a broad geographic region. Because birds are the focus of existing large monitoring programs such as the Breeding Bird Survey (Price et al. 1995), avian indices calculated at appropriate scales could ultimately be used in conjunction with the extensive data sets collected by these programs. We surveyed birds directly and measured bird habitat as a complementary approach because each provides important independent information that could be combined in an ongoing monitoring program to differentiate between population changes attributable to local habitat alteration and changes due to other factors.

## Methods

### Study Area

We conducted our study in conjunction with the Forest Health Monitoring (FHM) component of the Environmental Monitoring and Assessment Program (EMAP), administered jointly by the U.S. Forest Service and Environmental Protection Agency. The EMAP has planned a nation-wide network of long-term environmental monitoring plots selected from a regular, triangular grid of 40-km<sup>2</sup> hexagons with a spacing of 27.1 km between hexagon centers. One sampling site is located within each EMAP hexagon. In Virginia and Georgia, sites are located on the U.S. Forest Service's Forest Inventory and Analysis systematic photo grid, at the photo point nearest to the hexagon center. Sites in North Carolina and South Carolina are located on a random, systematic 1-km grid at the grid point nearest to the hexagon center. If a site is forested (including clearcuts and forest edges) and contains a stand over 0.40 ha in size and over 36.6 m wide, it is selected for monitoring as a long-term FHM plot. The FHM plots thus constitute a random sample of the forest habitat within a region. To monitor long-term trends in indicator values over large biogeographic sampling regions, FHM plans to revisit these plots every 4 years, surveying a systematic subsample of one-quarter of the grid points each year. Palmer et al. (1991), Alexander and Barnard (1992), and Lewis and Conkling (1994) provide details of the sampling scheme.

Our work was conducted as part of an FHM pilot study in the southeastern loblolly-shortleaf pine ecotype during 1992 and 1993 (Lewis & Conkling 1994). Survey plots were distributed across the coastal plain and Piedmont of Georgia, South Carolina, North Carolina, and Virginia. The plots we used were divided into two types, "on-frame" and "off-frame" plots. On-frame plots were long-term FHM plots located on the EMAP grid (thus separated by >20 km). Over 2 years of the

4-year rotation, we surveyed the 90 on-frame plots (47 in 1992, 43 in 1993) that included stands dominated by loblolly pine (*Pinus taeda*) or shortleaf pine (*P. echinata*). Except for South Carolina, which we did not sample during 1992 because plot coordinates were unavailable, the plots constituted a random, representative sample of loblolly-shortleaf pine forests within the region sampled. On-frame plots were used to quantify regional patterns and provide independent data to evaluate the accuracy of habitat models developed from the off-frame plots. The off-frame plots were selected to evenly represent a complete disturbance gradient, from mature forest to recently clearcut sites, for development of models. Site-level disturbances included clearcutting, selective cutting, burning, broadleaf understory removal, strip mining, and urban development. The most highly disturbed areas were typically recent clearcuts with high shrub density and few canopy trees. The off-frame plots were distributed through the same geographic area and forest types described above. Off-frame plots were separated from on-frame plots by a minimum of 200 m and usually by 1 km or more. Off-frame sites were always at least 2 km away from the nearest other off-frame site. Off-frame site locations were otherwise selected arbitrarily. We surveyed 107 off-frame plots, 66 in 1992 and 41 in 1993.

### Bird and Vegetation Surveys

We surveyed our plots from mid-May to early July of 1992 and 1993. One 20-minute point count was conducted at the center of each plot, and all bird species seen or heard were recorded. Surveys were completed before 1100 hours, under calm weather conditions. Only birds detected within a 50-m fixed radius plot were used in the analysis, so survey data can be effectively compared to local habitat measurements (Petit et al. 1995a). Observers (three in 1992, two in 1993) were trained and tested in simultaneous surveys prior to each season to minimize bias and confirm consistency. Each observer surveyed plots across the full disturbance gradient.

Repeated visits to a plot were not logistically feasible because of the need to maximize the number of plots and adequately sample a wide geographic area. By our fixed-radius method, a 20-minute count period allows detection of a number of species equivalent to two 6-minute counts on separate days (Petit et al. 1995a). Our long count period thus allowed us to detect more species per plot, representing the local bird community more completely than a shorter survey, without the logistical difficulties of repeated visits. Ultimately, we were most interested in determining the species composition at sampling plots because our index depended on examining species for presence or absence rather than for density; thus, the possibility of double-counting individuals during the count period does not affect our analysis.

We collected local vegetation data within four circular subplots (5-m radius) on each bird-sampling plot. The first vegetation subplot was located at the plot center, and the other three were located 33 m away at compass bearings of 0, 120, and 240 degrees. Within each subplot the number of deciduous and coniferous stems was recorded in seven categories of diameter at 1.4 m height (A, 0–1.0 cm; B, 1.1–2.5 cm; C, 2.6–8.0 cm; D, 8.1–15.0 cm; E, 15.1–23.0 cm; F, 23.1–30.0 cm; and G, >30.0 cm). Basal areas of all coniferous and deciduous stems of size class C and larger were combined to give a measure of total tree basal area ( $m^2/ha$ ). The mean height of canopy trees within each subplot was estimated separately for deciduous and coniferous trees by use of a range-finder. At two predetermined locations within each subplot, we measured a vertical vegetation profile by scoring whether a graduated 10-m vertical pole (approximately 2.5 cm diameter) touched coniferous or deciduous vegetation within each of the 10 1-m increments. We measured percent canopy cover using densiometers at a height of 1.2 m, taking readings in the four cardinal directions from the center of each subplot. Each vegetation parameter was averaged across the four subplots to characterize the habitat within the 50-m radius survey plot.

During the 1992 season, each survey plot was subjectively rated for disturbance level on the following scale: 1, undisturbed mature forest >40 years old with closed canopy (usually >80%) and plot center >200 m from major forest edge; 2, mature (or occasionally 20- to 30-year-old) forest with closed canopy and signs of human intervention (foot trails, major edge 100–200 m away, etc.); 3, forest usually 10–20 years old with mostly closed canopy (>50%) but clear recent disturbance (selective logging, partial understory removal, edge within 50 m); 4, clearcuts 4–10 years old or occasionally mature stands with partial (approximately 50% canopy) and recent disturbance (logging, major understory removal, camping area, edge within 50 m); and 5, clearcuts <3 years old with little or no canopy or extensively developed sites. Observers practiced estimating disturbance level on over 20 training plots and encountered little or no disagreement in estimates.

### Data Analysis

We classified bird species of the southeastern United States into four habitat assemblages (Appendix) grouped as disturbance-sensitive species (mature forest assemblage), disturbance-tolerant species (shrubland and forest-edge assemblages), and neutral species (habitat generalist assemblage). Habitat assemblage classifications were based on habitat association data from the literature (e.g., Sprunt & Chamberlain 1947; Johnston & Odum 1956; Burleigh 1958; Meyers & Johnson 1978; Hamel et al. 1982; Robbins et al. 1989). To avoid circularity of inference, we did not use our survey data for this classification.

Members of the mature-forest assemblage are sensitive to forest disturbance and are rarely found in early-successional or fragmented forests, indicating a sensitivity to forest patch size (Robbins et al. 1989). In this assemblage we included species typical of mature subclimax pine forests as well as birds typical of climax deciduous forest. This assemblage is thus characteristic of mature continuous forests without discriminating between pine and hardwood dominance. Disturbance-tolerant species were divided into two distinct habitat assemblages: shrubland birds, characteristic of brushy habitat and early-successional clearcuts, and birds of forest-edge habitats, characteristic of suburbs, agricultural land, and fragmented forests. Species that could not be unambiguously classified in one of the habitat assemblages were assigned to a neutral "habitat generalist" assemblage. Most of these species use intermediate habitats or are broad generalists that occur in a variety of habitats. We found appropriate group assignments to be ambiguous for 10 species, so we also assigned all of these species to alternative habitat assemblages (Appendix) to examine the sensitivity of our analyses to these assumptions. In addition, based primarily on information from Ehrlich et al. (1988), each species was classified by diet, foraging guild, and nesting guild. Scientific names of species and assignments to functional groups are summarized in the Appendix.

Our analysis of these data was based on the presence or absence of species rather than on the number of individuals detected. (Use of abundance-based indices in preliminary analyses did not improve the predictive power of models because most plots had only one or two individuals per species, and higher abundance was not linked to habitat characteristics.) We counted the number of mature-forest (MF), shrubland (SL), and forest-edge (FE) species observed on each plot. We developed a bird-community index to express variation in forest bird communities associated with habitat disturbance, calculated according to the a priori formula  $\ln(\text{MF} + 1) - \ln(\text{SL} + \text{FE} + 1)$ . This formula contrasted disturbance-sensitive (mature forest) species against disturbance-tolerant (shrubland and forest-edge) species and did not include generalist species. Positive values for the bird-community index thus indicated bird communities dominated by disturbance-sensitive, mature-forest species, whereas negative values indicated communities dominated by disturbance-tolerant species typical of landscapes altered by human use. Our use of a log-ratio between the assemblages rather than unmodified counts of one assemblage was intended to reduce potential bias from weather and observer skill (both disturbance-sensitive and disturbance-tolerant species are expected to be most detectable with optimum weather and skilled observers), and to reduce the skewness of the distribution.

To test the assumption that individual species within a functional group generally reflect the responses of other

members of the same group, we examined each foraging and nesting guild and habitat assemblage, calculating correlation coefficients between the presence or absence of each individual species and the number of other species present from the same functional group (on-frame and off-frame data pooled;  $n = 197$  plots). Single-species groups were excluded because correlations between species and group were undefined. Independent assortment of species within a group would yield a distribution of correlations centered approximately on zero. Conversely, predominantly positive correlations within a group would indicate that it was internally cohesive with similar population responses among its constituent species. Use of a simple  $t$  test of whether the mean of such a correlation distribution is significantly greater than zero is inappropriate because correlation coefficients for different species within a functional group are not independent; in the extreme case, for two-species groups the correlations for both species are necessarily equal. Therefore, for each functional group we used a Monte Carlo simulation program (10,000 replicates) to empirically determine the distribution of mean correlations for a null model (assuming that all species in the group were distributed randomly and independently over 197 plots, with each species occupying the same number of plots as actually observed in our study). We then compared the observed mean correlation for the functional group to the simulated distribution of mean correlations to calculate a one-tailed  $p$  value indicating the probability of obtaining a mean correlation value as large or larger than the observed value given the null hypothesis of independently occurring species.

To assess whether vegetation parameters could be used appropriately as a measure of forest disturbance, we calculated intercorrelations among subjective disturbance level, canopy cover, and tree basal area, pooling all on-frame and off-frame data. Pearson correlations were used to compare canopy cover to basal area ( $n = 197$ ); Spearman rank correlations ( $r_s$ ) were used for disturbance-level comparisons ( $n = 113$ ).

To examine responses of individual species to disturbance, we used logistic regression to predict the probability of occurrence for each species relative to canopy cover as a measure of disturbance. All on-frame and off-frame data were used ( $n = 197$ ), and canopy cover was removed from the equation if it was not significant at  $p < 0.05$ .

To test whether species richness of a guild or assemblage was correlated with forest disturbance, we grouped bird species observed on each plot into diet types, foraging guilds, nesting guilds, and habitat assemblages. We calculated correlations between the species richness of each functional group (number of species per plot) and two indices of disturbance effects on local vegetation (canopy cover and tree basal area). Correlations with these disturbance measures were also calculated for the bird-community index and total species richness.

In future surveys we hope to separate variation in bird-community composition associated with local habitat dis-

turbance from variation associated with other factors (changes on wintering grounds, nonlocal effects of forest fragmentation, etc.) to help identify causes of trends or spatial variation in bird-community composition. Therefore we used data from bird surveys and vegetation measurements on the off-frame plots to develop a habitat index as a predictor of the bird-community index. We initially reduced the large pool of vegetation variables by summing groups of comparable variables that were strongly intercorrelated ( $r > 0.50$ ), yielding 14 variables (Table 1). These variables were entered into a principal components analysis to identify orthogonal principal components. Using off-frame data, the principal components were entered into multiple regression analysis as predictors of the bird-community index. Positive values for formula output (the habitat index) indicate relatively undisturbed mature forest, whereas negative values indicate young or highly disturbed stands. As a comparison to assess the predictive power of this multivariate method, we also used simple regression to predict the bird-community index from canopy cover and from tree basal area.

We evaluated the predictive accuracy of the habitat index with independent data by comparing bird-community index and habitat index values in the on-frame plots. We evaluated how closely the indices reflected forest disturbance by calculating their correlation with subjective disturbance level (using Spearman rank correlation), canopy cover, and tree basal area in the on-frame plots.

On-frame plots were also used to determine the distribution of both index values across the sampling region. We used cumulative distribution function (CDF) plots to show the cumulative proportion of the sample population (y-axis), with index values less than or equal to the values shown on the x-axis. We calculated the CDF plots and confidence intervals using a maximum likelihood-estimation computer program (CDFGEN7) developed by Rob Binns and David Cassell of the Forest Health Monitoring program. On-frame data from 1992 (47 plots) and 1993 (43 plots) were pooled for

this analysis. Because on-frame plots in South Carolina were not surveyed during 1992, the six South Carolina plots that were surveyed during 1993 were weighted double for CDF analysis to compensate appropriately for the lower sampling intensity in that state (D. Cassell, personal communication).

## Results

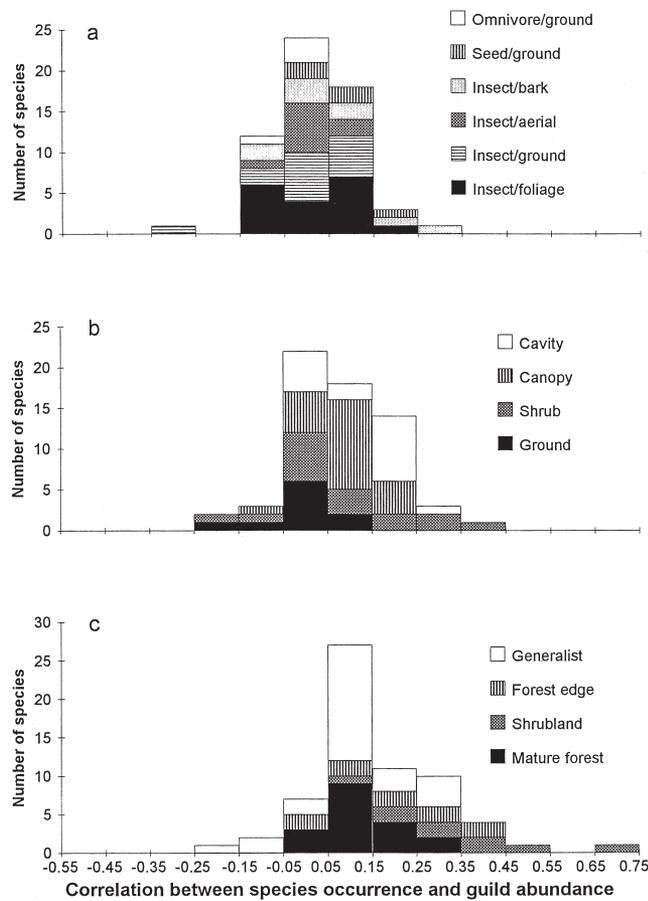
### Consistency of Variation within Functional Groups

The mean correlation between individual species and the number of other species of the same functional group was not significantly greater than zero ( $p > 0.05$  in all cases) for any of the foraging guilds (Fig. 1a). Responses were more consistent for nesting guilds (Fig. 1b). Mean correlations were significantly greater than 0 for shrub nesters (mean  $r = 0.08$ ;  $p < 0.001$ ), canopy nesters (mean  $r = 0.08$ ;  $p < 0.001$ ), and cavity nesters (mean  $r = 0.12$ ;  $p < 0.001$ ), although they were not significantly positive for ground nesters. The strongest positive correlations, however, were exhibited within the habitat assemblages (Fig. 1c); all four of the habitat assemblages had strongly positive within-group correlations ( $p < 0.001$ ), indicating that they tended to be internally cohesive as groups of species with similar population responses to the range of environmental variation that we sampled. In fact, the forest-edge assemblage (mean  $r = 0.19$ ) and mature-forest assemblage (mean  $r = 0.13$ ) each included only one species that was negatively correlated with the species richness of other assemblage members (House Finch and Hairy Woodpecker, respectively). The shrubland assemblage (mean  $r = 0.33$ ) had no negatively correlated species. Even the species in the habitat generalist assemblage had predominantly positive correlations with species richness of other assemblage members (mean  $r = 0.09$ ). Individual correlations between species and groups were significant at  $p < 0.0008$  ( $\alpha = 0.05$ , Bonferroni-adjusted for multiple comparisons),

**Table 1.** Interpretation of major axes from principal components analysis of 14 vegetation variables\* for off-frame plots ( $n = 107$ ).

Axis	Cumulative percent variance explained	Interpretation of positive axis values
PC1	26.9	mature deciduous: many deciduous trees (size D-E and F-G), few small conifers (sizes A-C), high deciduous canopy cover, high deciduous foliage density 4-10 m in height, and low coniferous foliage density 0-4 m in height
PC2	45.4	mature coniferous with deciduous understory: many conifers (sizes A-C and D-E) and small deciduous stems (sizes A-C), high coniferous canopy cover, high coniferous foliage density 4-10 m in height and high deciduous foliage density 1-4 m in height
PC3	61.6	sapling regeneration: many small deciduous stems and conifers (sizes A-C), high coniferous and deciduous foliage density 0-1 m in height, low coniferous canopy cover, low abundance of conifers (sizes D-E and F-G)
PC4	70.0	deciduous undergrowth: high deciduous foliage density 0-1 m in height, many small deciduous stems (sizes A-C)

\*Deciduous and coniferous stem densities in size classes A-C (0-8 cm), D-E (8-23 cm), and F-G (>23 cm); deciduous and coniferous canopy cover; and deciduous and coniferous vertical foliage profile from 0-1, 1-4, and 4-10 m above ground level. Description includes all variable loadings  $> 0.40$  or  $< -0.40$  from principal components analysis.

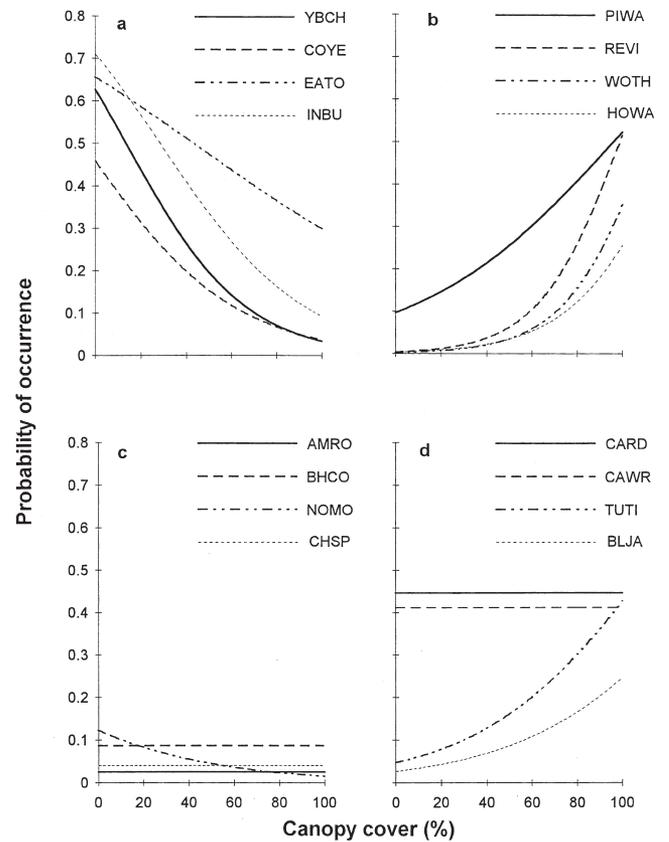


**Figure 1.** Correlations between presence or absence of individual bird species and the number of other bird species present from the same functional group for every individual species. Each datum shown in the histograms represents a species-group correlation coefficient for a single species. The three grouping criteria (Table 2) are plotted on separate histograms: (a) diet and foraging guilds, (b) nesting guilds, (c) habitat assemblages. Plots with predominantly positive correlations indicate functional groups that are internally cohesive with similar population responses in their constituent species. Single-species groups are excluded. On-frame and off-frame data (plots on and off sampling grid) are pooled ( $n = 197$ ).

where  $|r| > 0.23$ ; the distribution of significant correlations across functional groups (Fig. 1) generally followed patterns similar to those noted above. Sensitivity analysis with the alternative grouping of habitat assemblages altered mean correlations only slightly, without changing the significance levels noted above.

### Consistency of Species Responses to Disturbance within Functional Groups

We examined the probability of occurrence of individual species with respect to canopy cover to examine the



**Figure 2.** Probability of occurrence versus canopy cover for the four most abundant species in each of four habitat assemblages: (a) shrubland, (b) mature forest, (c) forest edge, (d) generalist. Probabilities are calculated from stepwise logistic regression of species presence or absence versus canopy cover. Species codes in key are defined in the Appendix.

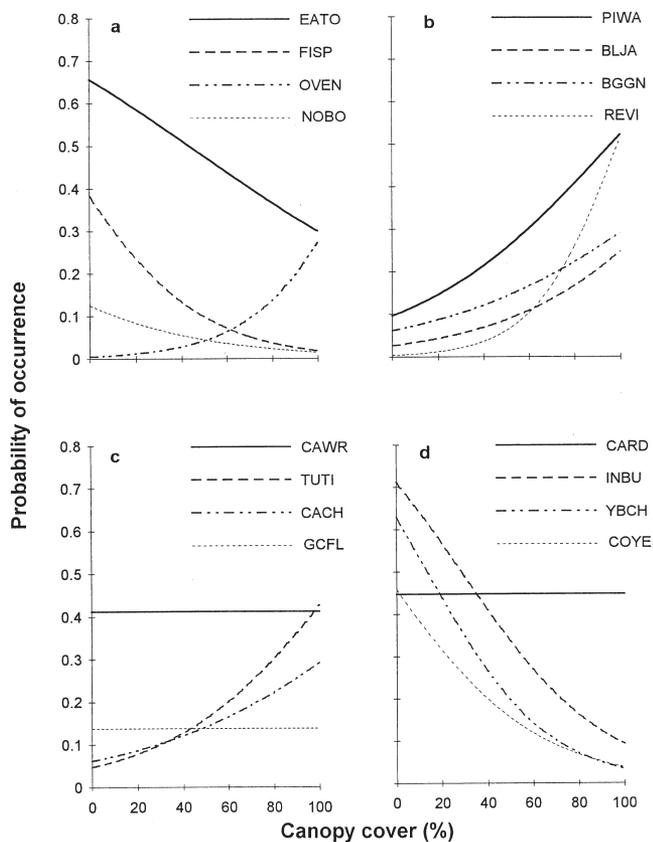
responses of individual species to disturbance. Our assumption that canopy cover and tree basal area can roughly characterize forest disturbance was supported by the strongly significant correlations ( $p < 0.001$ ,  $n = 113$ ) of subjective disturbance level with canopy cover ( $r_s = -0.83$ ) and tree basal area ( $r_s = -0.86$ ).

Examination of the four most commonly occurring species in each of the four habitat assemblages showed that all four species in the shrubland assemblage decreased with increasing canopy cover, and all four species in the mature forest assemblage increased with canopy cover (Fig. 2). The forest-edge assemblage showed no consistent response, probably because forest-edge species responded primarily to landscape-scale rather than local habitat disturbance. The habitat generalist assemblage also showed no consistent trend. Similar plots for nesting guilds (Fig. 3) and foraging guilds (Fig. 4) showed that they were typically composed of species with differing responses to canopy cover; these guilds often included species that significantly increased, significantly decreased, and had no significant

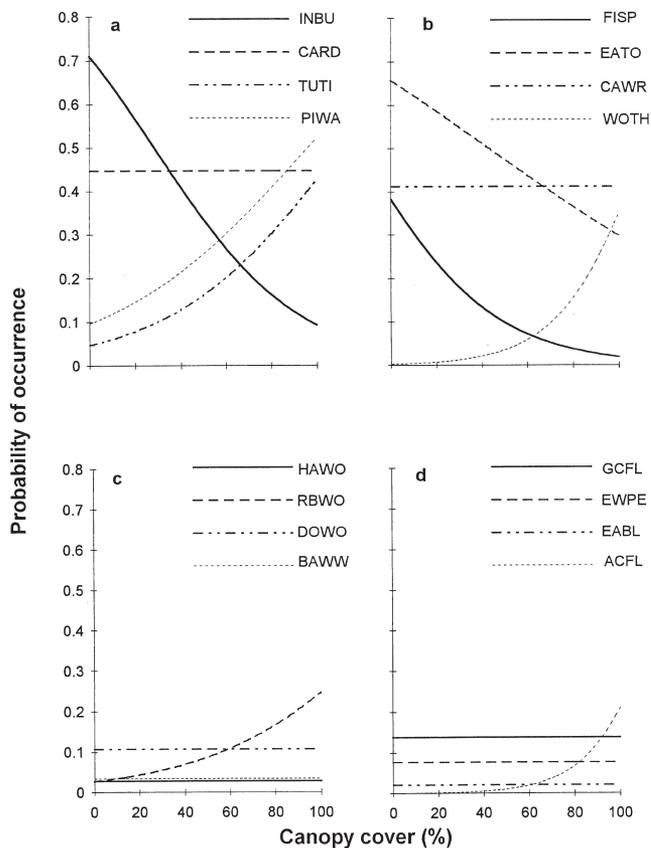
trend across the gradient. Of the four nesting guilds and four foraging guilds examined, only the canopy-nesting guild had consistent directional responses in its four most abundant species. The shrubland and mature-forest habitat assemblages thus showed a response of bird communities to forest disturbance more consistently than most nesting and foraging guilds.

**Correlations of Functional Groups with Disturbance Measures**

Canopy cover and tree basal area were strongly intercorrelated ( $r = 0.78, p < 0.001$ ). As a result, functional groups showed similar correlations with each of these measures of disturbance (Table 2). Diet type and foraging guilds generally had weak correlations with canopy cover and tree basal area; granivores and bark-foraging insectivores had the strongest responses among these functional groups (Table 2). Nesting guilds showed stronger correlations, particularly the shrub-nesting and canopy-nesting guilds, which may have responded to differences in nest-



*Figure 3. Probability of occurrence versus canopy cover for the four most abundant species in each of four nesting guilds: (a) ground-nesting, (b) canopy-nesting, (c) cavity-nesting, (d) shrub-nesting. Probabilities are calculated from stepwise logistic regression of species presence or absence versus canopy cover. Species codes in key are defined in the Appendix.*



*Figure 4. Probability of occurrence versus canopy cover for the four most abundant species in each of four foraging guilds: (a) foliage-gleaning insectivores, (b) ground-foraging insectivores, (c) bark-foraging insectivores, (d) aerial-foraging insectivores. Probabilities are calculated from stepwise logistic regression of species presence or absence versus canopy cover. Species codes in key defined in Appendix.*

site availability caused by disturbance. Nonetheless, the strongest correlations with measures of disturbance were shown by habitat assemblages (Table 2). The shrubland and mature-forest habitat assemblages were the most strongly correlated with the two disturbance indices. The forest-edge assemblage had weaker correlations with disturbance indices, and a combination of shrubland and forest-edge species to represent disturbance-tolerant species gave correlations similar to the shrubland assemblage alone. Habitat generalists showed lower correlations than the shrubland and mature-forest assemblages, as expected. Ultimately, a bird-community index produced by combining shrubland, forest-edge, and mature-forest assemblages showed stronger correlations with canopy cover and tree basal area than did any of the individual assemblages. In contrast, overall community diversity (measured by total species richness) was not significantly correlated with disturbance metrics.

**Table 2.** Correlation coefficients relating the bird-community index and species richness in selected functional groups to canopy cover and tree basal area.<sup>a</sup>

Functional group classification	Correlation <sup>b</sup>	
	canopy cover	tree basal area
<b>Diet</b>		
Omnivores	+0.22**	+0.10
Granivores/herbivores	-0.22**	-0.26***
Insectivores	+0.10	+0.10
Nectarivores	-0.01	+0.10
Carnivores	+0.11	+0.14
<b>Foraging guild</b>		
Ground-foraging insectivores	-0.06	-0.03
Bark-foraging insectivores	+0.28**	+0.27**
Foliage-foraging insectivores	+0.08	+0.02
Aerial-foraging insectivores	+0.04	+0.13
Ground-foraging granivores	-0.22*	-0.27***
Foliage-foraging granivores	-0.04	-0.02
Ground-foraging omnivores	+0.05	+0.06
Foliage-foraging omnivores	+0.25**	+0.13
<b>Nesting guild</b>		
Ground nesters	-0.22**	-0.25**
Shrub nesters	-0.38***	-0.47***
Canopy (tree branch) nesters	+0.42***	+0.43***
Cavity nesters	+0.29***	+0.31***
<b>Habitat assemblage</b>		
Shrubland species	-0.54***	-0.55***
Forest edge species	-0.13	-0.05
Generalist species	+0.26**	+0.20*
Mature forest species	+0.59***	+0.61***
Disturbance tolerant species (shrubland & forest edge)	-0.55***	-0.53***
Bird community index <sup>c</sup>	+0.68***	+0.67***
Total species richness	+0.08	+0.10

<sup>a</sup>Significance levels are Bonferroni adjusted for number of comparisons by guild (five food types, eight foraging guilds, four nesting guilds, five habitat assemblages).

<sup>b</sup>Probability: \* $p < 0.05$ ; \*\* $p < 0.001$ ; \*\*\* $p < 0.001$ .

<sup>c</sup>Bird-community index =  $\ln(\text{mature forest} + 1) - \ln(\text{shrubland} + \text{forest edge} + 1)$ . On-frame and off-frame data are pooled for this analysis ( $n = 197$ ).

### Analysis of Bird Community Index and Habitat Index

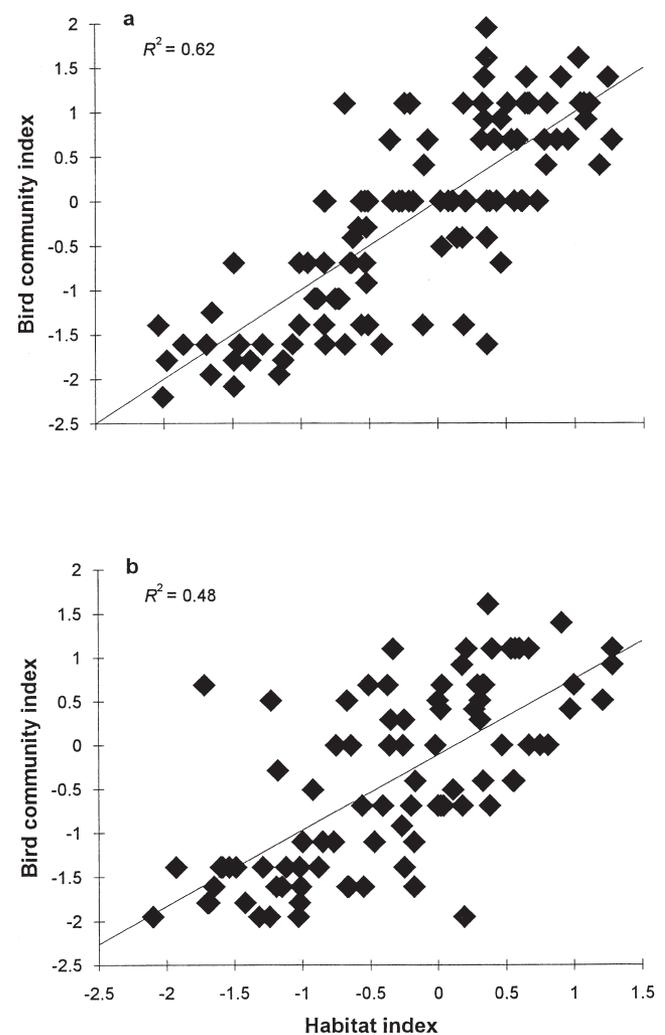
Principal components analysis of vegetation data yielded four principal component axes cumulatively describing 70% of the variance in the data (Table 1). A habitat index based on off-frame data was calculated from a regression formula including all four of the principal component axes:

$$\text{HI} = -0.253 + 0.716(\text{PC1}) + 0.137(\text{PC2}) - 0.347(\text{PC3}) - 0.200(\text{PC4}).$$

The resulting index accounted for 62% of the variation in the bird community index on off-frame plots (Fig. 5a). (By contrast, canopy cover or tree basal area individually explained only 42% of variation in the bird-community index in simple regression analysis.) To test the ability of the habitat index to predict the bird-community index for independent data, the correlation of these two indi-

ces was examined for on-frame data (Fig. 5b). The correlation coefficient ( $r = 0.69$ ,  $p < 0.001$ ) indicates that the habitat index generally predicts the bird-community index. Not surprisingly, the habitat index also was more strongly correlated with habitat-based disturbance measures, such as canopy cover and tree basal area, than was the bird-community index (Fig. 6). Similarly, the habitat index was more strongly correlated with subjective disturbance level ( $r_s = -0.78$ ,  $p < 0.001$ ) than was the bird-community index ( $r_s = -0.73$ ,  $p < 0.001$ ).

The specific habitat assemblages that dominated bird communities on our plots (Appendix) included habitat generalists such as Cardinal and Carolina Wren and shrubland birds such as Indigo Bunting and Eastern Towhee. Forest species such as Pine Warblers, Acadian Flycatch-



**Figure 5.** Habitat index versus bird-community index values, modified from Martin et al. (1994): (a) off-frame data (outside sampling grid) used for model development ( $n = 107$ ) and (b) independent on-frame data (on sampling grid) used to test model ( $n = 90$ ).

ers, and Red-eyed Vireos were much less common. The forest-edge assemblage typical of towns and highly fragmented habitat—cowbirds, mockingbirds, robins—was also comparatively uncommon in the sample. These results suggest that bird communities in much of the area we sampled were substantially affected by disturbance.

Cumulative probability distributions for varying values of the bird-community index and habitat index can be used to assess the frequency of different community-disturbance levels on a regional scale. Within our sample, these cumulative probability distributions for the index values can be examined without bias from site selection because our on-frame plots were selected randomly from loblolly-shortleaf pine forests throughout the study region, and differences in sampling intensity are appropriately weighted in the analysis. (Neither bird-community index nor habitat index values differed significantly between 1992 and 1993 within the area sampled in both years, suggesting that combining data for the 2 years is appropriate.) This distribution is graphically represented with cumulative distribution function (CDF) plots for each index, including upper and lower

bounds for a 90% confidence interval (Fig. 7). Sites dominated by disturbance-tolerant birds and disturbed habitat are common in the region. If a cutpoint between undisturbed and disturbed bird communities is defined by a bird-community index of zero, representing equal numbers of disturbance-tolerant and disturbance-sensitive species, then 52–75% (90% c.i.) of the loblolly-shortleaf pine forests in the study region indicate disturbed bird communities (Fig. 7a). For the habitat index, a similar calculation indicates that 49–71% of the sampled area can be classified as disturbed habitat (Fig. 7b). This approach also allows cutpoints to be established at levels other than zero, depending on local or regional habitat-management goals.

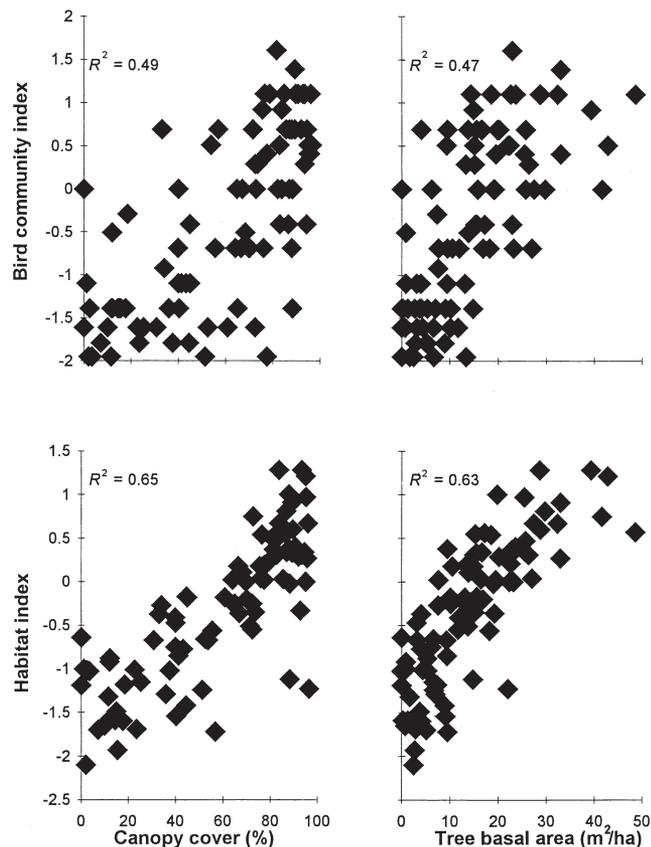


Figure 6. Bird-community index and habitat index versus canopy cover and tree basal area ( $n = 90$ ) for on-frame plots ( $p < 0.001$  for all correlations).

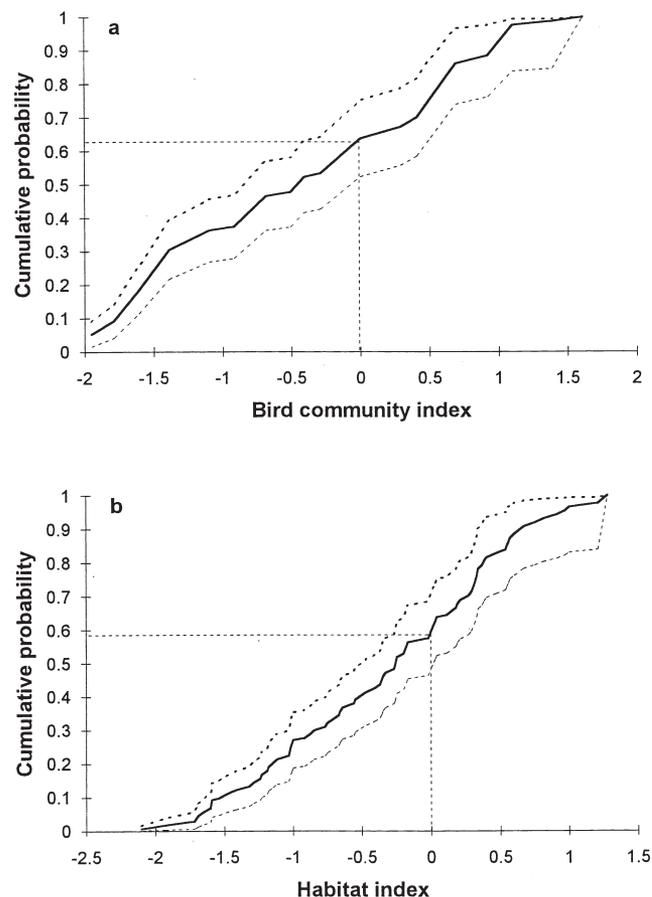


Figure 7. Cumulative distribution functions for bird community and habitat index values in southeastern loblolly-shortleaf pine forests ( $n = 90$  on-frame plots), modified from Martin et al. (1994): (a) bird-community index and (b) habitat index. Solid line indicates the percentage of the sampled region (y-axis) with index values at or below those shown on the x-axis (sample cutpoint at zero shown). Dashed line indicates 90% confidence interval.

## Discussion

The bird-community and habitat indices, like the index of biotic integrity (Karr 1981; 1991; Karr et al. 1987; Angermeier & Karr 1994), each give a deliberately simplified picture of ecological composition by condensing diverse systems into a single index reflecting the degree of disturbance. Thus, the indices represent only a small subset of available information. The bird-community index, for example, does not show the particular responses of individual species to habitat variation. The bird-community index, however, was developed to provide a broad-based indicator of the extent to which a bird-community has been affected by forest disturbance, rather than to describe use of habitat by individual bird species. Species-specific information is not lost and can still be used to interpret index values. The dimension of disturbance reflected by our indices constitutes an important aspect of ecological condition relative to conservation of biotic diversity and ecological resources (Angermeier & Karr 1994).

The bird-community index will detect avifaunal responses to major anthropogenic disturbance—clearcutting and fragmentation through conversion of forest to agricultural and residential uses. These factors clearly affected the avifauna in our sampling area. Indeed, because the on-frame sample excludes nonforested plots, the region as a whole is almost certainly dominated by disturbance-tolerant species—particularly the forest-edge assemblage—to a greater extent than represented here. Southeastern forest landscapes in more natural conditions (Sharitz et al. 1992), however, would also be characterized by periodic disturbance, whether such conditions are defined as the pre-Columbian state, which included agricultural clearing and burning by Native Americans, or as a hypothetical state without human influence, which would still be affected by windthrow and lightning-ignited fires. Such a landscape would include early-successional patches with bird-community and habitat index values lower than those of mature forest and would probably be dominated by some mixture of climax hardwood forests and mature but relatively open forests of subclimax pine. Although an index of biotic integrity (Karr 1991) should measure biological condition by reference to a landscape-scale natural state, the appropriate reference state is not always clearly understood or easily selected.

Yet, given current levels of anthropogenic disturbance it appears that old-growth stands and unfragmented forests would be substantially underrepresented in our study area relative to the pre-Columbian or human-free reference states, whereas early-successional and fragmented forest would be similarly overrepresented. The region's forest extent declined due to massive agricultural clearing and timber harvest in the nineteenth and early twentieth centuries, which was later partially re-

versed by abandonment of farms. Urban expansion and short-rotation logging, however, continue to cause fragmentation and loss of mature forest (Sharitz et al. 1992). In this context, the bird community and habitat indices are useful for monitoring the relative availability of mature-forest and disturbed habitat and the resulting consequences for associated bird communities.

By comparison to the habitat assemblages used in the bird-community index, traditional guilds—based on foraging, diet, or nesting substrate—are more ambiguous in their implications for conservation goals because it is unclear how to prioritize them. For example, should we manage for ground-foragers over aerial insectivores or shrub-nesters over cavity-nesters? Most guilds, as well as total species richness, also showed relatively weak responses to habitat disturbance, whereas species within shrubland and mature-forest habitat assemblages typically had more consistent and stronger responses to habitat variation (Table 2; Fig. 2). Because anthropogenic habitat modification is a major and widespread stressor throughout the study region, habitat assemblages are a logical tool for monitoring its effects on bird communities. Moreover, habitat assemblages become particularly powerful indicators of disturbance to natural systems when multiple assemblages are combined through the bird-community index because a broad range of species is included. Nonetheless, guilds may be worth considering in concert with the bird-community index to help detect problems associated with particular resources. A consistent response in particular guilds might provide important insight into general changes in resource availability, such as nesting snags or declines in insect abundance, or other stressors such as pesticides that may affect specific guilds (Welsh 1987; DesGranges et al. 1987).

The bird-community index should not be used uncritically as a guide to management or without regard to the status of individual species. Declines in individual species can be masked by general guild trends (Mannan et al. 1984). The greater cohesiveness of habitat assemblages lessens this problem but does not eliminate it. Trends in threatened or endangered species can supersede concerns for broadly defined community indices. The status of individual species of concern can be addressed through separate analyses, however.

Birds, or any other highly mobile organisms, may fail to be reliable indicators of the local resource conditions being monitored because populations could be affected by habitat conditions on other parts of the year-round range of migratory species (Temple & Wiens 1989). The habitat index, developed as a predictor of the bird-community index, can be used as an independent measure of local habitat disturbance affecting the bird community. Moreover, habitat index values can be generated with vegetation data collected by relatively inexperienced field technicians, so some information about

likely bird-community composition can be gained from vegetation measurements even if bird censuses are not feasible. Yet the bird community index can also be applied to existing broad-scale bird surveys such as the Breeding Bird Survey or Christmas Bird Count to detect trends in the relative abundance of disturbance-sensitive and disturbance-tolerant species, whereas broad-scale habitat databases suitable for calculating habitat index values do not currently exist. Both the bird community and habitat indices can provide important information.

Examining potential influences on environmental indicators is an important aspect of monitoring programs (Koskimies 1989). In this context, the habitat index may prove particularly useful for interpreting the possible causes of variation and trends in the bird-community index. Deviations from the line of equality between the bird-community index and the habitat index could reflect factors external to the local site. In particular, negative deviations indicate sites where the bird community appears more strongly disturbed than expected from local vegetation structure, possibly reflecting broader-scale, landscape-level factors such as forest patch size or regional forest cover that can affect community composition (Robbins et al. 1989; Petit et al. 1995*b*). Landscape effects could be analyzed in conjunction with the habitat index and might significantly improve its predictive power. Also, an increase over time in the proportion of negative deviations could be detected with long-term surveys. If such an effect were caused by decreasing long-term trends in the bird-community index (due to decreasing frequency of mature forest species) but not the habitat index, it could suggest that migratory forest birds are being affected by changes on their migration routes or wintering grounds rather than by local habitat on the breeding grounds.

Finally, the cumulative distribution function of the bird-community and habitat indices (Fig. 7) provides a strong tool for evaluating these indices of forest condition on a regional scale and, over the long term, evaluating trends in the indices. The systematic method used for selection of plots under the EMAP protocol allows cumulative distribution functions to show the distributions of index values across a study region without bias from site selection. Although potential sample sizes for EMAP bird censuses are small compared to a broad-based volunteer monitoring project such as the Breeding Bird Survey, the unbiased sampling design of EMAP gives an important statistical advantage. Nonetheless, our bird-community index can be readily adapted to larger databases such as the Breeding Bird Survey to evaluate broad-scale patterns and trends in bird-community status. If the index is not restricted to a single dimension, our approach could be generalized to assess bird communities of different habitat types (grassland, wetlands, etc.) by use of multiple habitat assemblages.

In short, the approach we outline here makes it possible to monitor the regional effects of changing land use and habitat structure on indices of forest disturbance (habitat index) and disturbance to the breeding-bird community (bird community index). A comparison of the trends in these two indices could be useful in determining whether population changes are related to local habitat effects or extraneous factors such as landscape-scale processes or changes in wintering habitat.

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**Appendix 1**

Names, abbreviated codes, membership in guilds and habitat assemblages, and abundance for bird species detected on on-frame (*n* = 90) and off-frame<sup>a</sup> (*n* = 107) plots.<sup>b</sup>

Species name	Code	Diet/foraging substrate	Nesting substrate	Number of plots occupied	
				on-frame	off-frame
Mature-forest assemblage (late-successional forests)					
Pine Warbler ( <i>Dendroica pinus</i> )	PIWA	insect/foilage	canopy	25	38
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	REVI	insect/foilage	canopy	19	18
Red-bellied Woodpecker ( <i>Melanerpes carolinus</i> )	RBWO	insect/bark	cavity	10	15
Wood Thrush ( <i>Hylocichla mustelina</i> )	WOTH	insect/ground	shrub	12	11
Ovenbird ( <i>Seiurus aurocapillus</i> )	OVEN	insect/ground	ground	9	11
Hooded Warbler ( <i>Wilsonia citrina</i> )	HOWA	insect/foilage	shrub	12	6
Acadian Flycatcher ( <i>Empidonax virescens</i> )	ACFL	insect/aerial	canopy	4	7
Scarlet Tanager ( <i>Piranga olivacea</i> )	SCTA	insect/foilage	canopy	2	6
Northern Parula ( <i>Parula americana</i> )	NOPA	insect/foilage	canopy	1	7
Black-and-white Warbler ( <i>Mniotilta varia</i> )	BAWW	insect/ bark	ground	5	1
Hairy Woodpecker ( <i>Picoides villosus</i> )	HAWO	insect/bark	cavity	4	2
Brown-headed Nuthatch ( <i>Sitta pusilla</i> )	BHNU	insect/bark	cavity	3	2
Pileated Woodpecker ( <i>Dryocopus pileatus</i> )	PIWO	insect/bark	cavity	2	2
Yellow-throated Warbler ( <i>Dendroica dominica</i> )	YTWA	insect/bark	canopy	1	2
Prothonotary Warbler ( <i>Protonotaria citrea</i> )	PROW	insect/bark	cavity	0	2
Swainson's Warbler ( <i>Limnothlypis swainsonii</i> ) <sup>c</sup>	SWWA	insect/ground	shrub	1	1
Kentucky Warbler ( <i>Oporornis formosus</i> )	KEWA	insect/ground	ground	0	2
Louisiana Waterthrush ( <i>Seiurus motacilla</i> )	LOWA	insect/ground	ground	0	1
Shrubland assemblage (early-successional clearcuts)					
Eastern Towhee ( <i>Pipilo erythrophthalmus</i> )	EATO	insect/ground	ground	44	43
Indigo Bunting ( <i>Passerina cyanea</i> )	INBU	insect/foilage	shrub	36	24
Yellow-breasted Chat ( <i>Icteria virens</i> )	YBCH	insect/foilage	shrub	20	20
Common Yellowthroat ( <i>Geothlypis trichas</i> )	COYE	insect/foilage	shrub	16	15
White-eyed Vireo ( <i>Vireo griseus</i> )	WEVI	insect/foilage	shrub	16	13
Prairie Warbler ( <i>Dendroica discolor</i> )	PRAW	insect/foilage	shrub	12	15
Field Sparrow ( <i>Spizella pusilla</i> )	FISP	insect/ground	ground	10	12
Blue Grosbeak ( <i>Guiraca caerulea</i> )	BLGR	seeds/ground	shrub	3	10
Gray Catbird ( <i>Dumetella carolinensis</i> ) <sup>d</sup>	GRCA	insect/ground	shrub	5	2
Forest-edge assemblage (fragmented landscapes)					
Brown-headed Cowbird ( <i>Molothrus ater</i> )	BHCO	insect/ground	parasite	5	12
Northern Mockingbird ( <i>Mimus polyglottos</i> ) <sup>c</sup>	NOMO	insect/ground	shrub	7	2
Chipping Sparrow ( <i>Spizella passerina</i> ) <sup>c</sup>	CHSP	insect/ground	shrub	6	2
American Robin ( <i>Turdus migratorius</i> )	AMRO	insect/ground	canopy	3	2
Eastern Bluebird ( <i>Sialia sialis</i> )	EABL	insect/aerial	cavity	2	2
Common Grackle ( <i>Quiscalus quiscula</i> )	COGR	omnivore/ground	canopy	1	3
Eastern Kingbird ( <i>Tyrannus tyrannus</i> )	EAKI	insect/aerial	canopy	2	1
Red-headed Woodpecker ( <i>Melanerpes erythrocephalus</i> )	RHWO	insect/aerial	cavity	2	0
Orchard Oriole ( <i>Icterus spurius</i> )	OROR	insect/foilage	canopy	1	1
House Finch ( <i>Carpodacus mexicanus</i> )	HOFI	seed/ground	canopy	1	0
Habitat generalist assemblage					
Cardinal ( <i>Cardinalis cardinalis</i> )	CARD	insect/foilage	shrub	44	44
Carolina Wren ( <i>Thryothorus ludovicianus</i> )	CAWR	insect/ground	cavity	41	40
Tufted Titmouse ( <i>Baeolophus bicolor</i> ) <sup>e</sup>	TUTI	insect/foilage	cavity	21	24
Blue-gray Gnatcatcher ( <i>Poliptila caerulea</i> )	BGGN	insect/foilage	canopy	15	23
Carolina Chickadee ( <i>Poecile carolinensis</i> )	CACH	insect/foilage	cavity	15	20
Blue Jay ( <i>Cyanocitta cristata</i> )	BLJA	omnivore/foilage	canopy	16	16
Great Crested Flycatcher ( <i>Myiarchus crinitus</i> )	GCFL	insect/aerial	cavity	9	18
Summer Tanager ( <i>Piranga rubra</i> )	SUTA	insect/ foliage	canopy	9	12
Downy Woodpecker ( <i>Picoides pubescens</i> )	DOWO	insect/bark	cavity	11	10
Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	YBCU	insect/foilage	canopy	8	12
Eastern Wood Pewee ( <i>Contopus virens</i> )	EWPE	insect/aerial	canopy	6	9
Mourning Dove ( <i>Zenaidura macroura</i> ) <sup>d</sup>	MODO	seeds/ground	canopy	7	6
Common Crow ( <i>Corvus brachyrhynchos</i> )	COCR	omnivore/ground	canopy	4	6

(continued)

## Appendix 1 (continued)

Species name	Code	Diet/foraging substrate	Nesting substrate	Number of plots occupied	
				on-frame	off-frame
Northern Bobwhite ( <i>Colinus virginianus</i> ) <sup>d</sup>	NOBO	seeds-veg/ground	ground	6	3
Brown Thrasher ( <i>Toxostoma rufum</i> )	BRTH	omnivore/ground	shrub	3	2
Northern Flicker ( <i>Colaptes auratus</i> ) <sup>d</sup>	NOFL	insect/ground	cavity	1	4
Bachman's Sparrow ( <i>Aimophila aestivalis</i> )	BASP	seeds/ground	ground	1	3
American Goldfinch ( <i>Carduelis tristis</i> )	AMGO	seeds/foilage	shrub	2	2
Red-shouldered Hawk ( <i>Buteo lineatus</i> ) <sup>e</sup>	RSHA	vertebrate/ground	canopy	2	1
Yellow-throated Vireo ( <i>Vireo flavifrons</i> ) <sup>e</sup>	YTVI	insect/foilage	canopy	3	0
Fish Crow ( <i>Corvus ossifragus</i> )	FICR	omnivore/ground	canopy	2	0
Ruby-throated Hummingbird ( <i>Archilochus colubris</i> )	RTHU	nectar/flowers	canopy	2	0
Chuck-will's-widow ( <i>Caprimulgus carolinensis</i> )	CWWI	insect/aerial	ground	1	1
Eastern Phoebe ( <i>Sayornis phoebe</i> )	EAPH	insect/aerial	building	1	1
Eastern Screech-Owl ( <i>Otus asio</i> )	EASO	vertebrate/ground	cavity	0	2
Common Nighthawk ( <i>Chordeiles minor</i> )	CONI	insect/aerial	ground	0	1
White-breasted Nuthatch ( <i>Sitta carolinensis</i> )	WBNU	insect/bark	cavity	0	1

<sup>a</sup>On-frame plots selected from regular geographic sampling grid; off-frame plots separate from grid.

<sup>b</sup>Modified from Martin et al. (1994).

<sup>c</sup>Alternatively grouped with habitat-generalist assemblage for sensitivity analysis.

<sup>d</sup>Alternatively grouped with forest-edge assemblage for sensitivity analysis.

<sup>e</sup>Alternatively grouped with mature-forest assemblage for sensitivity analysis.

