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THE BIRD COMMUNITY INDEX: A TOOL FOR ASSESSING BIOTIC INTEGRITY IN THE MID-ATLANTIC HIGHLANDS

FINAL REPORT

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August 1998

FOREWORD

This report documents the development and implementation of an indicator of biotic integrity based on songbird community composition. As part of the U.S. Environmental Protection Agency's (EPA's) Environmental Monitoring and Assessment Program (EMAP), this research is intended to facilitate assessments of ecological condition at regional and national scales. It is the first attempt to develop and apply a field indicator of ecological condition across the full extent of an EMAP reporting region, without stratifying by resource type.

Comprised of multiple biological metrics, our indicator is an index that ranks bird communities at sample sites according to the proportional representation of 16 behavioral and physiological response guilds. Relative proportions of "specialist" and "generalist" guilds, viewed as indicators of structural, functional, and compositional ecosystem elements, determine condition. Because songbirds are present throughout a wide variety of habitat types, the bird community index (BCI) is intended to integrate ecological conditions across a large physiographic region exhibiting diverse land-cover attributes and intensities of human use.

We developed the BCI from 34 reference sites in central Pennsylvania that represent a gradient of ecosystem condition from near pristine to severely degraded. The reference sites were independently ranked according to 1) a previously-developed human disturbance gradient and 2) bird guild representation (i.e., BCI). Upon satisfactory demonstration that the BCI could discriminate between categories of ecosystem condition identified from the human disturbance gradient, we applied the BCI to independent samples of 126 sites across the Mid-Atlantic Highlands Assessment (MAHA) area. Sites were selected using EMAP's probability-based sampling design, and therefore represent the total land area in the region. To verify the BCI's discriminatory properties, we compared the BCI assessment to independent gradients of landscape disturbance applied to both the 34 reference sites and the 126 MAHA sites.

The BCI identified four categories of biotic integrity in the MAHA area. Our assessment indicates that 16% of the area is in "excellent" condition, 27% is in "good" condition, 36% is in "fair" condition, and 21% is in "poor" condition. Urban and agricultural sites differ in their respective guild compositions, but are not separable by overall BCI score. Forested sites supporting the two highest integrity categories contain different site-level vegetation attributes, but cannot be separated by landscape-level land-cover composition. This research also defined thresholds of land-cover change where significant shifts in BCI categories were observed.

We provide a BCI model for determining ecological condition from bird species assemblage data collected across the MAHA area. We also provide a series of regression models for predicting BCI scores from explanatory habitat variables at plot and landscape scales.

ACKNOWLEDGMENTS

The challenge of collecting field data from randomly selected sites across four states was daunting to say the least. The success of this project was, therefore, predicated on the cooperation of many individuals. We are greatly indebted to Mary Gaudette, Randy Harrison, John Puschock, Jeff Larkin, Nathan Burkepile, and Rich Waynor for their assistance in the field. Penn State Cooperative Wetlands Center staff were also instrumental in gathering, compiling, and analyzing data from our central Pennsylvania reference sites, as well as providing additional technical assistance. In particular we thank Andy Cole, Denice Wardrop, Sarah Goslee, Laurie Bishel-Machung, Diann Prosser, Jen Perot, and Todd Fearer. The landscape analysis required for this project was absolutely dependent on the time and talents of Eric Warner and Mike Anderson from Penn State's Office of Remote Sensing of Earth Resources (ORSER). Don Stevens of Dynamac Corporation provided much-appreciated assistance with spatial statistics.

At the U. S. Environmental Protection Agency, we gratefully acknowledge the management support of Rick Linthurst, Steve Paulsen, Denise Shaw, Tom DeMoss, Ron Preston, Jim Green, and Gil Veith. Penn State staff from the School of Forest Resources, Environmental Resources Research Institute, and the Pennsylvania Cooperative Fish and Wildlife Research Unit, especially Sharon Goss and Kay Christine, cut through miles of red tape to keep the field work on schedule. The School of Forest Resources in the College of Agricultural Sciences provided essential laboratory space and computing facilities.

We extend a hearty "thank you" to every private landowner, from those with 1/4 acre lots to those controlling access to hundreds of square miles, for your permission to allow a group of rag-tag birdwatchers to wander across your land. We are grateful to the many public agencies who coordinated with our field crews to visit remote areas on public lands, especially the U.S. Forest Service, the National Park Service, the U.S. Army Corps of Engineers, the Pennsylvania Game Commission, and the Pennsylvania Bureau of Forestry. Thanks also go to Jim Green of the EPA's Wheeling, WV office for coordinating the landowner contact effort; and to the heroes of that effort, Phil Shriner and Tom Swimley. Phil and Tom visited every county courthouse in the MAHA area to identify the landowners of our random sample locations.

For your time, insight, and patience, thanks to all who provided advice on analysis. We are especially grateful to Margaret Brittingham, Wally Tzilkowski, Alan Taylor, C. R. Rao, Dave Bradford, Kevin Summers, Mary Jo Casalena, and Raymond O'Connor. Thanks especially to Tracy O'Connell, who endured countless soliloquies on this stuff from across the dinner table. And to Don Little from Sassafras Ridge, West Virginia: Thanks again for that tip about the "Y" restaurant.

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INTRODUCTION

The U. S. Environmental Protection Agency's (EPA's) Environmental Monitoring and Assessment Program (EMAP) is designed to estimate status and trends in ecological condition at regional and national scales. Research to meet EMAP objectives includes the development of ecological indicators that reflect key elements and processes of natural systems. Desirable indicators are differentially sensitive to a variety of stressors so that numerous impacts to a resource of concern may be evaluated. Further discussion of the indicator concept and development strategy within EMAP can be found in Hunsaker and Carpenter (1990) and Barber (1994).

To date, EMAP has produced regional reports on ecological condition for natural resources including forests, streams, and estuaries (e.g., Strobel et al. 1995,

U. S. EPA 1998). To complement this single-resource approach, EMAP also sponsors research on landscape indicators that address the interaction of multiple resources at watershed and other large-scale study units (e.g., Jones et al. 1997). Landscape indicators are intended to facilitate integrated assessments of ecological condition by reflecting the dynamics among terrestrial and aquatic, remote and human-dominated components of environmental systems.

This paper describes the development of a landscape indicator of ecological condition based on breeding songbird community composition. Research was conducted across the heterogeneous landscapes of the central Appalachians, and involved sampling in multiple natural resources as well as urban areas and ecotones. The design, therefore, captured ecologically significant landscape features that contribute to overall ecological condition, but are typically omitted from traditional field monitoring. This research is the first attempt to develop and apply a field indicator of ecological condition across the full extent of an EMAP reporting region without stratifying by resource type.

Songbirds exhibit numerous characteristics that suggest their potential as ecological indicators at regional and national scales:

- They are relatively ubiquitous.
- Species vary in sensitivity to physical, chemical, and biological stressors.
- Each species exhibits life-history characteristics (e.g., ground nester, granivore, short-distance migrant) that link to multiple environmental attributes. Therefore, one dataset on songbird community composition can be repeatedly re-organized to explore signs of impacts to different elements of the system.
- Survey methods are well-precedented and widely accepted by the scientific community.
- Survey methods are non-destructive, with low site impact.
- Methodology is inexpensive; no laboratory analyses are required.
- Taxonomy is well known.
- Many trained field observers are available.
- Long-term databases and ongoing programs exist to fortify analyses.
- Birds have strong public appeal.

Although birds themselves are a focus of societal concern, the purpose of this research is not to report on songbirds as an assessment endpoint. Rather, bird community composition across the region is intended to reflect system properties of concern, including structural complexity, interspecific dynamics, and landscape configuration; properties that are currently not well-addressed in large-scale monitoring programs. Figure 1 displays a conceptual model of system conditions that evoke songbird responses, and stressors from which these conditions can result.

Comprised of multiple biological metrics, our indicator is an index of biotic integrity (IBI) which we have termed the bird community index (BCI). It is modeled on previously-developed IBIs. The original IBI was developed to assess the condition of aquatic systems (Karr 1991, 1993; Fore et al. 1996) and the concept has since been adapted for use in upland environments (e.g., Bradford et al. 1998, Karr and Chu 1997). Biotic integrity refers to the capability of supporting and

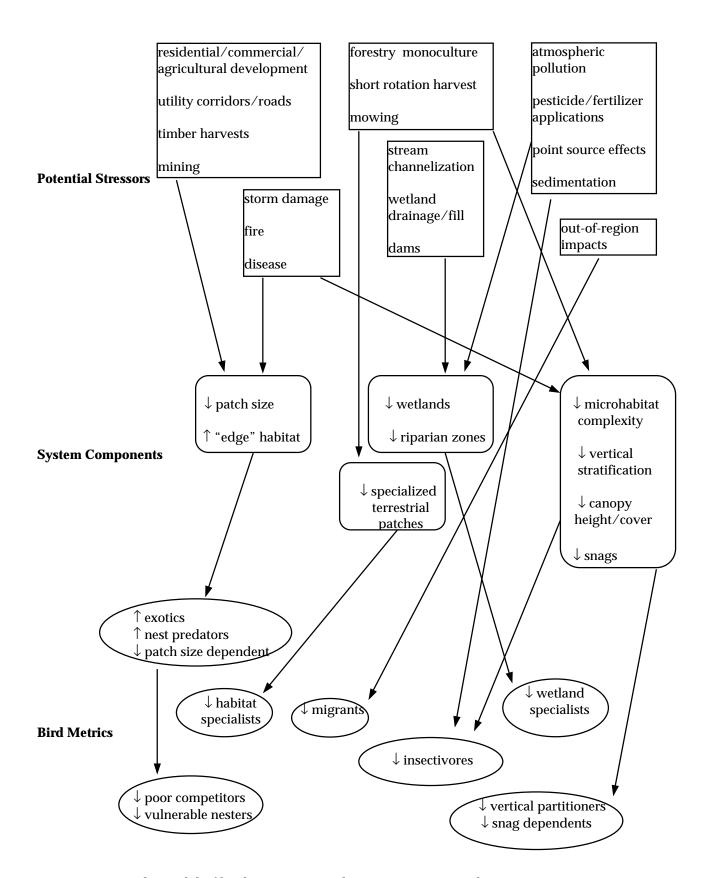


Figure 1. Example model of bird responses to changing system conditions.

maintaining "a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region" (Karr and Dudley 1981). The biotic integrity concept provides a system-specific framework in which species assemblage data can be ranked on a qualitative scale. This method of estimating condition is, therefore, more ecologically relevant than traditional analyses such as species richness and Shannon diversity (Blair 1996, Brooks et al. 1998).

The BCI is based on songbird response guilds, which are groups of species that require similar habitat, food, or other elements for survival (Verner 1984, Szaro 1986, Brooks and Croonquist 1990). Changes in specific resource availability are manifested as population responses in all of the species dependent on that resource. For example, the loss of snags in a forest stand can result in a decrease in the guild of bark-probing insectivores. Croonquist and Brooks (1991) have demonstrated that response guilds produce an effective indicator of habitat disturbance.

We consider a "high-integrity" condition to incorporate structural, functional, and compositional elements typical of the study area in the absence of human disturbance (Noss 1990, Karr and Chu 1997). A bird community that indicates high integrity, therefore, is dominated by guilds dependent on native system attributes. In our study, obligate tree-canopy nesters indicate high integrity because they are largely restricted to mature forests native to the region, while shrub nesters encounter appropriate nesting substrate in forested, residential, and agricultural areas (Brauning 1992). Obligate insectivores are limited to areas of high insect availability (e.g., Prosser and Brooks 1998), while omnivores can exploit a wide range of food resources in varied habitats. Many single-brooded species are restricted to areas that are relatively free from nest predators that concentrate around habitat edges (Wilcove 1985). While birds are inherently a compositional feature, the behavioral adaptations of different species and the roles they play in system processes can reflect system-level structure and function, as well as suggesting information about other organisms with which they interact.

This approach to evaluating biotic integrity results in high BCI scores for bird communities in which specialists are well-represented relative to generalists (O'Connell et al. 1998). We define specialists and generalists for 16 response guilds in eight guild categories: trophic, insectivore foraging behavior, population limiting, origin, migratory, number of broods, nest placement, and primary habitat. Because each species belongs simultaneously to several guild categories, we can iteratively analyze the bird species data to create a multi-metric index (Karr and Chu 1997). Based on guilds, the index can be calibrated for any region and be relevant regardless of species.

It is important to recognize, however, that the BCI in its current formulation is intended for use solely in the study area; both the reference high-integrity condition and the specific guilds used to formulate the index may differ in another region (e.g., Bradford et al. 1998). Furthermore, the BCI reflects biotic integrity at a fairly coarse level of resolution. In the central Appalachians, the land-cover and use types that are most likely to be encountered in a random sample are mature and regenerating forest, pasture and row crops, urban and suburban areas, and mined lands (Bailey 1980). In the absence of irreversible anthropogenic disturbance, most of the region would succeed to forest.

We recognize, however, that a minority of habitats in the region, such as shale barrens and cedar glades, are perpetually maintained by edaphic factors in states that resemble early-successional old-field or shrublands. These rare habitats, while entirely natural, may support native songbird communities that do not conform to our general definition of high biotic integrity for the region. In addition, other natural events, such as tornadoes and outbreaks of foliage-eating insects, may create natural, early successional conditions over large areas (e.g., thousands of acres). These areas, however, are relatively small and rare compared to the land area of the entire MAHA region, and are infrequently encountered in a random sample of the region. Key to understanding the utility of the BCI is that it is applied to individual sample sites, but the resulting assessment of biotic integrity takes place at the regional scale.

Objectives

Our specific research objectives were to: 1) develop a regional index of biotic integrity based on songbird community composition; 2) apply the index to a probability-based sample of field sites to determine the proportion of the study area exhibiting various categories of biotic integrity; 3) determine the combination of landscape configuration and local vegetation variables that are associated with different levels of biotic integrity; and 4) verify the bird community index with independent data collected from the same sample locations. The results of this study will ultimately be integrated with results from other ecological indicators to produce an overall assessment of ecological condition for the region.

METHODS

Study Area

Preliminary field research to develop the BCI began in 1994 with a sample of 34 sites from the Ridge and Valley physiographic province in central Pennsylvania. Data on multiple system attributes were collected from each site for research independent of this project (Brooks et al. 1996). All sites were centered on small (< 15 ha) wetlands, but were dominated by upland-cover types. We selected the 1994 sites to represent a reference gradient of ecological condition from nearly pristine to severely-degraded. A BCI developed with data collected from this reference gradient allowed a comparison between our bird community-based assessment of ecological condition and an independent assessment of the same sites based on multiple environmental variables.

In 1995 and 1996, we expanded our sampling to the entire MAHA area (Figure 2). The MAHA area encompasses approximately 168,420 km² in the mountainous physiographic provinces of EPA Region III, and is dominated by the Blue Ridge, Ridge and Valley, Allegheny Plateau, and Ohio Hills physiographic provinces of Pennsylvania, Maryland, Virginia, and West Virginia. The 58 sites sampled in 1995 and 68 sites sampled in 1996 are independent, blocked random samples from the EMAP

probability-based sampling grid (Overton et al. 1990). The probability-based design permits an estimate of condition across the entire study region, with known statistical confidence. We calculated confidence intervals for estimates of condition with the Yates-Grundy variance formula, using the edge correction described in Stevens and Kincaid (1997).

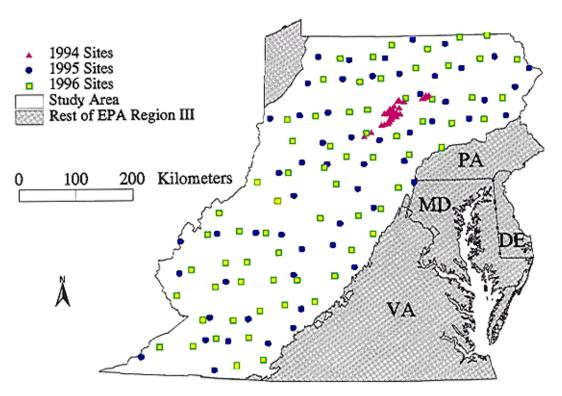


Figure 2. EPA Region III and the MAHA area with approximate locations of sample sites.

Sampling

Sample sites in 1994 consisted of a variable number of plots (3-11) placed every 50-200 m along a transect of up to 2 km. In 1995 and 1996, each site consisted of five plots spaced every 200 m along a randomly oriented 1 km transect (Figure 3). At each plot along a transect, we sampled songbirds with a 10-minute, 30 m-radius point count between sunrise and 10:00 hrs EDT (Hutto et al. 1986, Manuwal and Carey 1991, Ralph et al. 1993). For these analyses, we used a total species list compiled from unlimited radius point counts at each of the five plots. Sampling took place within the "safe

dates" for breeding birds, so we assumed that any birds detected were resident at each site through the breeding season (Brauning 1992).

At each bird sampling plot, we sampled a suite of vegetation variables to characterize the local habitat. We recorded the percentage herbaceous cover of graminoids, forbs, mosses, and ferns in three, 5-m radius, circular subplots located 15 m from plot center at 120, 240, and 360°. Also in the subplots, we recorded the percentage cover of shrubs from 0.00-0.50 m, 0.051-2.00 m, and 2.01-5.00 m, as well as the percentage canopy cover of overstory trees. From plot center, we used an angle gauge to sample trees over 10 cm dbh. All live trees were identified to species and the dbh was recorded for trees and snags. In addition, at each plot we recorded canopy height, slope, and assigned an Anderson Land Use Code (Anderson et al. 1976).

To characterize the local landscape configuration, we obtained aerial photographs of the circular area bisected by each transect. For the 1995 and 1996 sites, this resulted in a circular site (i.e., a "landscape circle") with a 0.5 km radius covering an area of approximately 79 ha. The photographs were interpreted and polygons of six cover types were digitized in a GIS and entered into a modified version of the spatial analysis software package SPAN (Miller et al. 1997). The SPAN output provides information on landscape diversity, dominance, and contagion, the amount of edge between cover types, and the areal coverage within the circular site of urban development, agricultural land, forest, woody shrubs, open water, and barren land.

We collected data for this project at several scales. We assessed vegetation structure and composition in three 79 m² subplots, and summarized these data at the "plot" scale (roughly 700 m² or 0.07 ha). Several of the vegetation variables (e.g., canopy height, number of conifer stems over 10 cm dbh) were further compiled and expressed as a site level variable (i.e., 79 ha). Bird data collected at the plot level were summarized as a total species pool for the entire site. We also analyzed landscape configuration with an aerial view of the entire 79 ha site. We intend the BCI assessment to be applied at the ecoregion scale which, in the case of the Mid-Atlantic Highlands, includes an area of over 150,000 km².

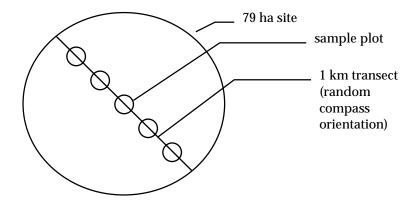


Figure 3. Sampling design for randomly selected sites in the MAHA area.

Response Guilds

We built the BCI with data on all the Passeriformes (perching birds), Piciformes (woodpeckers), Cuculiformes (cuckoos), and Columbiformes (doves) that we documented in the MAHA area from 1994-96 (112 total species; Appendix I). Birds were assigned to behavioral and physiological response guilds based on a literature review (Harrison 1975, Blake 1983, DeGraaf et al. 1985, Roberts 1987, Brooks and Croonquist 1990, Freemark and Collins 1992, Santner et al. 1992). From preliminary analyses of 32 guilds, we focused attention on the 24 guilds described in Appendix IV. Table 1 lists the 16 guilds in eight guild categories ultimately included in the BCI. We considered several factors (e.g., high correlation with other guilds, predictable response to land-cover change) in determining the final list of guilds to be included in BCI development. A complete list of species in each guild is included in Appendix III.

Because we selected guilds specifically to reflect different aspects of each species' life history traits, species belong simultaneously to several guilds. Guild assignments within each of the eight guild categories, however, are mutually exclusive, so species belong to no more than eight guilds. For example, in the Migratory category, species are classified as either residents or temperate migrants (we excluded tropical migrants

for statistical reasons) (Table 1). Also, guild assignments apply only to breeding season life history traits. For example, we consider the Eastern kingbird (*Tyrannus tyrannus*) to be an insectivore, even though this species subsists largely on fruit in its wintering range (Terborgh 1989).

Table 1. Summary of response guilds used in determination of the bird community index (BCI).

Integrity Element	Guild Category	Response Guild	Specialist	Generalist
Functional	Trophic	omnivore		X
Functional	Insectivore Foraging Behavior	bark prober	X	
Functional	Insectivore Foraging Behavior	ground gleaner	X	
Functional	Insectivore Foraging Behavior	upper-canopy forager	X	
Functional	Insectivore Foraging Behavior	lower-canopy forager	X	
Compositional	Population Limiting	nest predator/ brood parasite		X
Compositional	Origin	exotic		X
Compositional	Migratory	resident		X
Compositional	Migratory	temperate migrant		X
Compositional	Number of Broods	single-brooded	X	
Structural	Nest Placement	canopy nester	X	
Structural	Nest Placement	shrub nester		X
Structural	Nest Placement	open-ground nester	X	
Structural	Nest Placement	forest-ground nester	X	
Structural	Primary Habitat	forest generalist		X
Structural	Primary Habitat	interior forest obligate	X	

We categorized individual guilds as "specialist" or "generalist" based on each guild's relationship to specific elements of ecosystem structure, function, and composition. For example, the Nest Placement guilds relate directly to the availability of appropriate nesting substrate (a structural element). We consider shrub nesters to be generalists because a woody shrub layer is found throughout the Mid-Atlantic highlands in mature and regenerating forests, agricultural hedgerows, and suburban areas. In contrast, we consider tree canopy nesters to be specialists because a welldeveloped overstory canopy is absent from many agricultural and suburban areas in the MAHA area. The Trophic category (i.e., omnivore) reflects aspects of ecosystem function: Omnivores can function as primary or higher consumers, and therefore, exploit a wider range of energy sources than insectivores, which are obligate secondary or higher consumers. Thus, we consider omnivores to be generalists relative to insectivores. The nest predator/brood parasite guild is an example of a guild that reflects compositional elements of an ecosystem. Species in the nest predator/brood parasite guild can affect the abundance and distribution of other species. We consider nest predators and nest parasites to be generalists due to their relatively indiscriminate exploitation of other species as sources of food or surrogate parents.

It is important to recognize that not only are species assigned to several guilds simultaneously, but that a species may be assigned to both specialist and generalist guilds simultaneously. For example, the downy woodpecker (*Picoides pubescens*) is a generalist according to Primary Habitat and Migratory status, but a specialist according to its membership in four other guild categories (e.g., bark prober). A complete list of guilds with rationale for "specialist" and "generalist" interpretation is included in Appendix IV.

With species assigned to guilds, we summarized the proportional species richness of each guild at each site to construct a bird community profile. For example, if two of the species at a site containing a total of 10 species are single-brooded, then the bird community at the site would be summarized with a "0.20" for the single-brooded guild. We grouped sites according to their similarity in bird community profiles

through multivariate cluster analysis, and confirmed statistically separable differences in individual guild proportions among groups with analysis of variance (ANOVA).

BCI Development

The first step in BCI development was to establish a reference gradient of ecosystem condition for the 34 sites we sampled in 1994. The gradient assignments we applied to sites were the primary means to verify the independent ranking of ecological condition based solely on each site's bird guild composition. Brooks et al. (1996) examined the sediment deposition, soil properties, plant community, amphibian community, a Wildlife Community Habitat Profile (WCHP), and general landscape context of the reference sites and ranked them on a three-category scale of human disturbance from "pristine" to moderately-disturbed to severely-disturbed. Relative to disturbed sites, pristine sites experienced lower rates of sediment deposition and the soils contained a larger ratio of organic to mineral material. Plant communities exhibited higher Shannon diversity indices and were dominated by sediment-intolerant species at pristine sites. The amphibian community exhibited slightly higher species richness and was dominated by disturbance-intolerant species (e.g., wood frog [Rana *sylvatica*]) at the pristine sites. Habitat suitability indices for the WCHP averaged higher at pristine sites for species that occur in mature forested wetlands (e.g., wood frog, wood duck [Aix sponsa], southern red-backed vole [Clethrionomys gapperi]). Finally, the pristine sites exhibited larger areas of contiguous, mature forest than the moderately- or severely- disturbed sites (Penn State Cooperative Wetlands Center unpublished data, Brooks et al. 1996, Wardrop and Brooks 1998).

With a gradient of human disturbance established for the 1994 reference sites, we next developed an independent ranking of the same sites using only bird community data. We applied cluster analysis (complete linkage, squared Euclidean distance) to the 1994 matrix of bird community profiles to identify categories of sites with similar profiles. We intentionally identified three categories of bird community profiles to facilitate comparisons with the human disturbance gradient. We used one-way

ANOVA with Tukey's multiple comparisons procedure (alpha = 0.05) to identify statistically separable proportional species richness values of each guild among the three categories.

The next step in BCI development was to identify which bird community profiles indicate a low biotic integrity condition, and which are indicative of high biotic integrity. We ranked each category of occurrence for each guild on a scale of high integrity to low integrity. For specialist guilds, we ranked the highest- occurrence category a "3," the next highest a "2," etc. For generalist guilds, we reversed the ranking, assigning "3s" to the lowest-occurrence category. Therefore, a site can receive a rank of "3" for a guild if the site supports the highest category of proportional species richness for a specialist guild or the lowest category of proportional species richness for a generalist guild; a theoretical maximum-integrity site would have a "3" rank entered in every guild column.

The overall BCI score for a particular site is the sum of three subscores based on individual guild ranks: V_1 = the sum of the functional guild ranks, V_2 = the sum of the compositional guild ranks, and V_3 = the sum of the structural guild ranks. Because we assigned all the individual response guild ranks so that the highest-integrity condition received the highest rank, the sites exhibiting the highest BCI scores indicate the highest-integrity bird communities. Because the BCI preserves information from the three subscores, it is possible to compare rankings of functional, compositional, and structural integrity among sites with different overall BCI scores.

To compare independent rankings of the same sites based on the human disturbance gradient and the BCI, we applied Pearson correlation coefficients and one-way ANOVA. Prior to analyses, we tested all variables for normality (Anderson-Darling test) and homogeneity of variance (Levene's test). Variables that did not meet our assumptions of normality or homogeneity of variance for parametric statistics were transformed or omitted from analyses (Neter et al. 1990). All statistical analyses were performed with the Minitab 10.5 Xtra for the Power MacIntosh statistical software package (Minitab 1995).

BCI Application

Upon satisfactory demonstration that the BCI could discriminate between independently ranked categories on a human disturbance gradient, we applied the BCI methodology to data collected from the random sites representative of the entire MAHA area. First we constructed bird community profiles for all sites using the proportional species richness of 16 guilds. We then clustered sites (complete linkage, squared Euclidean distance) according to their bird community profiles. Unlike the clustering of the 1994 sample, however, for the 1995 and 1996 data we clustered the sites with no *a priori* decision on the number of clusters to be identified. Our objective was to identify the maximum number of categories of sites with statistically separable proportional species richness in the 16 guilds. We identified statistically separable bird community profiles using the cluster membership identifiers as factor levels in a one-way ANOVA with Tukey's multiple comparisons procedure (alpha = 0.05).

As with the 1994 sample, we applied ranks to the various levels of proportional species richness for each guild. We assigned high ranks for good representation of specialist guilds or poor representation of generalist guilds, and *vice versa*. The sum of functional, compositional, and structural scores is the overall BCI score for each site. The overall proportion of sites (out of 126 total) in each category of biotic integrity is the bird community-based assessment of ecological condition for the entire MAHA area.

Land-cover Analyses

In addition to demonstrating the value of the BCI model itself, the land-cover information we collected was used to help explain patterns of occurrence for specific bird community profiles. We identified linear regression models for predicting functional, compositional, structural, and total BCI score from a suite of landscape and plot level vegetation variables summarized for each site.

Verification is the process by which a model is tested on an independent sample of sites for its ability to indicate the system attributes for which it was designed (Brooks 1997). Verification of the BCI would involve a test of its ability to indicate the various

biotic and abiotic attributes of the human disturbance gradient. Because the human disturbance gradient developed by Brooks et al. (1996) included landscape condition as a ranking criterion and we collected land-cover data for each of our bird survey sites, we were presented with the unique opportunity of conducting a "transitive-verification" procedure of the BCI.

To verify the BCI, we first constructed an independent, three-category landscape disturbance gradient of the 34 reference sites to compare to the human disturbance gradient. We next used multivariate cluster analysis (Ward linkage, Euclidean distance) to group sites based on the landscape contagion and percentage of forested cover in each landscape circle (Miller et al. 1997). We considered a combination of low relative contagion and high-percentage forest to be indicative of low landscape disturbance (With and Crist 1995). We used Pearson correlation and one-way ANOVA with Tukey's multiple comparisons procedure (alpha = 0.05) to compare the human disturbance gradient with the landscape disturbance gradient and test for differences in land-cover configuration among the three categories of human disturbance (Neter et al. 1990).

The landscape disturbance and human disturbance gradients agreed well as independent rankings of the 34 reference sites ($r^2 = 0.812$). Sites labeled as pristine by the human disturbance gradient exhibited significantly higher percentage forest ($F_{2,33} = 53.28$, P = 0.00) and lower contagion ($F_{2,33} = 8.43$, P = 0.001) than sites labeled as moderately- or severely-disturbed. Thus, the landscape configuration of each site could serve as a reliable proxy for the information contained in the human disturbance gradient. We, therefore, applied a similar landscape disturbance ranking scheme to the 126 probability-based sites we sampled in 1995 and 1996. A high degree of agreement in the ranking of the probability-based sites between the BCI and landscape disturbance procedures constitutes verification that the BCI indeed functions as an indicator of overall system condition.

RESULTS

Objective 1: BCI Development

Brooks et al. (1996) identified three categories of human disturbance in the 34 reference sites we sampled in 1994. Fourteen sites were classified as pristine, ten were moderately-disturbed, and ten were severely-disturbed. We used the BCI scores determined for the 1994 reference sites to classify bird communities at nine sites as high-integrity, 12 sites as medium-integrity, and 13 as low-integrity ($r^2 = 0.821$ human disturbance X BCI).

Under the BCI gradient, sites with high-integrity bird communities exhibited significantly higher functional ($F_{2,33}=33.02$, P=0.000), compositional ($F_{2,33}=32.54$, P=0.000), structural ($F_{2,33}=27.16$, P=0.003) and overall BCI scores ($F_{2,33}=47.88$, P=0.000) than sites with either medium- or low-integrity bird communities. Medium-integrity sites exhibited significantly higher functional, compositional, and overall BCI scores than low-integrity sites (Tukey 95% C. I.s did not include zero). The difference between the structural integrity scores of medium- and low-integrity sites was not significant (Tukey 95% C. I. = -1.523, 0.703). Table 2 lists the mean proportional species richness of all 16 guilds across three levels of biotic integrity.

Likewise, bird community profiles of the BCI show significant differences between categories when the categories are determined by the three disturbance classes of the human disturbance gradient. Pristine sites contained significantly higher functional guild ranks ($F_{2,33} = 37.18$, P = 0.000), compositional ranks ($F_{2,33} = 22.37$, P = 0.000), structural ranks ($F_{2,33} = 16.31$, P = 0.000) and overall BCI score ($F_{2,33} = 38.82$, P = 0.000) than moderate- or severely-disturbed sites. Moderate sites contained significantly higher functional ranks than severely-disturbed sites, but differences between compositional rank (Tukey 95% C. I. = -2.846, 0.246), structural rank (Tukey 95% C. I. = -1.640, 1.240), and overall BCI score (Tukey 95% C. I. = -7.310, 0.110) were not significant.

Table 2. Proportion of total species at a site in each guild ($\bar{x} \pm SE$) in each of three ecological integrity categories: high, medium, and low. Significant differences in guild proportions are based on one-way ANOVA (df = 2, 33) with Tukey's test for multiple comparisons. Within rows, values with different superscripts are significantly different at P < 0.05.

Response Guild	high integrity	medium integrity	low integrity	P	
	n = 9	n = 12	n = 13		
omnivore	0.30 ± 0.02^{A}	0.47 ±0.02 ^B	0.57 ±0.02 ^C	0.000	
bark prober	0.12 ± 0.02^{A}	0.08 ±0.01 ^B	0.03 ±0.01 ^B	0.001	
ground gleaner	0.10 ±0.01 ^A	0.05 ±0.01 ^B	0.03 ±0.01 ^B	0.000	
upper-canopy forager	0.13 ±0.01 ^A	0.08 ±0.01 ^B	0.06 ±0.01 ^B	0.000	
lower-canopy forager	0.23 ± 0.02^{A}	0.19 ±0.01 ^{AB}	0.13 ±0.02 ^B	0.002	
nest predator/brood parasite	0.09 ±0.01 ^A	0.14 ±0.01 ^B	0.14 ±0.02 ^B	0.024	
exotic	0.00 ± 0.00^{A}	0.02 ±0.01 ^{AB}	0.06 ±0.02 ^B	0.020	
resident	0.29 ±0.02 ^A	0.40 ±0.02 ^B	0.40 ±0.02 ^B	0.004	
temperate migrant	0.22 ±0.02 ^A	0.24 ±0.01 ^A	0.32 ±0.01 ^B	0.000	
single-brooded	0.70 ±0.03 ^A	0.56 ± 0.02^{B}	0.41 ±0.02 ^C	0.000	
canopy nester	0.36 ± 0.02^{A}	0.32 ±0.02 ^{AB}	0.27 ±0.01 ^B	0.003	
shrub nester	0.20 ± 0.02^{A}	0.29 ±0.02 ^B	0.32 ±0.02 ^B	0.000	
open-ground nester	0.01 ±0.01 ^A	0.06 ±0.01 ^B	0.10 ±0.01 ^C	0.000	
forest-ground nester	0.22 ±0.01 ^A	0.08 ±0.01 ^B	0.03 ±0.01 ^C	0.000	
forest generalist	0.36 ± 0.02^{A}	0.44 ±0.02 ^B	0.31 ±0.02 ^A	0.000	
interior forest obligate	0.43 ±0.02 ^A	0.15 ±0.02 ^B	0.05 ±0.02 ^C	0.000	

Objective 2: BCI Application

A cluster analysis of bird community profiles of 16 guilds at the 126 probability-based sample locations in the entire MAHA area indicated five distinct groupings of sites with a mean within-cluster sum of squares of 1.28 (Figure 4). We ranked clusters according to the relative proportions of specialist and generalist guilds at the sites in each cluster. The ranking scheme allowed us to place the five clusters into four distinct categories of BCI scores. According to our bird community-based criteria for defining biotic integrity, approximately $16\pm5.5\%$ of the MAHA area supports the highest-integrity communities, $27\pm6.8\%$ is high-integrity, $36\pm7.3\%$ is medium-integrity, and 21% of the MAHA area supports two separate categories of low-integrity bird communities (i.e., "low 1" = $16\pm5.5\%$ and "low 2" = $5\pm3.4\%$) (Figure 5).

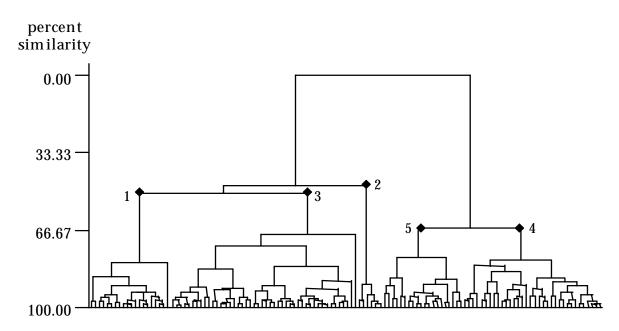


Figure 4. Cluster dendrogram of MAHA sites by guild composition. Node number indicates BCI category: 1 = low BCI score; 5 = high BCI score.

Table 3 lists the mean proportional species richness of all 16 guilds and biotic integrity ranks in five categories of biotic integrity. Although relationships among the five categories assume more complex patterns than under the three-category scheme developed for the 1994 reference sites, we found many significant differences in guild proportions among categories. When compared to sites in the lower-integrity categories, sites in the higher-integrity categories exhibited higher rankings for functional ($F_{4,125} = 102.27$, P = 0.000), compositional ($F_{4,125} = 58.94$, P = 0.000), structural ($F_{4,125} = 21.75$, P = 0.000) and overall BCI score ($F_{4,125} = 129.09$, P = 0.000).

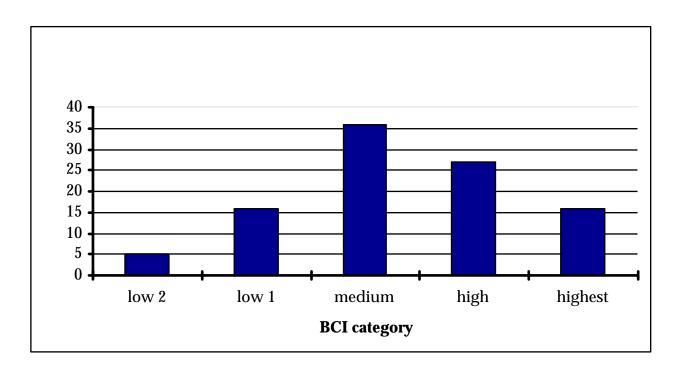


Figure 5. Percentage of sites in the MAHA area assigned to five categories of biotic integrity.

The low-2 and low-1 integrity categories could not be separated by functional (Tukey 95% C. I. = -3.450, 2.450), compositional (Tukey 95% C. I. = -4.495, 2.762), structural (Tukey 95% C. I. = -4.945, 1.495), or overall BCI scores (Tukey 95% C.I. = -9.400, 3.217), however, we found several significant differences in individual guilds between these two categories (Table 3). If we treat the low-2 and low-1 integrity categories as a single "low-integrity" group, then all four categories of biotic integrity exhibit statistically separable functional guild ranks, compositional guild ranks, and overall BCI scores (Tukey 95% C. I.s do not include zero). Structural guild ranks can only separate the highest- and high-integrity categories from the three lower- integrity categories (Tukey 95% C. I.s do not include zero). Figure 6 is a schematic representation of the gradient of biotic integrity among the five categories.

Table 3. Mean proportion of the total species per site in each guild ($\bar{x} \pm SE$) in each of five ecological integrity categories identified in the MAHA area. The indicated sample size refers to the number of sites in each category. Significant differences in guild proportions are based on one-way ANOVA (df = 4, 125) with Tukey's test for multiple comparisons. Within rows, values with different superscripts are significantly different at P < 0.05.

Response Guild	highest	high	medium	low 1	low 2	P
_	(n=20)	(n=34)	(n=46)	(n=20)	(n=6)	
omnivore	0.24 ±0.01 ^A	0.37 ± 0.01^{B}	$0.45 \pm 0.01^{\circ}$	0.61 ± 0.01^{D}	0.53 ± 0.00^{D}	0.000
bark prober	0.17 ±0.01 ^A	0.11 ± 0.01^{B}	0.08 ±0.01 ^C	0.03 ±0.01 ^D	0.03	0.000
					±0.01 ^{CD}	
ground gleaner	0.12 ± 0.01^{A}	0.10 ± 0.01^{A}	0.06 ± 0.01^{B}	$0.03 \pm 0.00^{\circ}$	0.03 ± 0.00^{BC}	0.000
upper-canopy	0.18 ± 0.01^{A}	0.15 ± 0.01^{A}	0.10 ± 0.01^{B}	0.04 ±0.01 ^C	$0.01 \pm 0.01^{\circ}$	0.000
forager						
lower-canopy	0.21 ± 0.01^{A}	0.17 ± 0.01^{A}	0.17 ± 0.01^{A}	0.12 ± 0.01^{B}	0.14 ± 0.02^{AB}	0.000
forager						
nest predator/	0.07 ± 0.01^{A}	0.11 ± 0.01^{B}	0.10 ± 0.01^{B}	$0.16 \pm 0.01^{\circ}$	0.21 ± 0.02^{D}	0.000
brood parasite						
exotic	0.00 ± 0.00^{A}	0.00 ± 0.00^{A}	0.02 ± 0.00^{B}	$0.07 \pm 0.01^{\circ}$	0.16 ± 0.03^{D}	0.000
resident	0.28 ± 0.02^{A}	0.34 ± 0.01^{B}	0.35 ± 0.01^{AB}	$0.42 \pm 0.02^{\circ}$	0.69 ± 0.03^{D}	0.000
temperate	0.16 ± 0.02^{A}	0.18 ± 0.01^{A}	0.26 ± 0.01^{B}	$0.36 \pm 0.01^{\circ}$	0.19 ± 0.01^{AB}	0.000
migrant						
single-brooded	0.74 ± 0.01^{A}	$0.68~\pm0.01^{\mathrm{B}}$	$0.53 \pm 0.01^{\circ}$	0.35 ± 0.01^{D}	0.38 ± 0.03^{D}	0.000
canopy nester	0.37 ± 0.02^{A}	0.37 ±0.01 ^A	0.30 ± 0.01^{B}	$0.25 \pm 0.01^{\circ}$	0.29 ± 0.01^{BC}	0.000
shrub nester	0.19 ±0.01 ^A	0.22 ± 0.01^{A}	0.27 ±0.01 ^B	0.29 ±0.01 ^B	0.19 ± 0.04^{A}	0.000
open-ground	0.01 ±0.00 ^A	0.02 ±0.01 ^{AB}	0.07 ±0.01 ^C	0.13 ± 0.01^{D}	0.06 ± 0.01^{BC}	0.000
nester						
forest-ground	0.21 ± 0.01^{A}	0.18 ± 0.01^{A}	0.09 ± 0.01^{B}	0.03 ±0.01°	$0.00 \pm 0.00^{\circ}$	0.000
nester						
forest generalist	0.35 ± 0.01^{A}	0.38 ± 0.01^{A}	0.37 ±0.01 ^A	0.27 ± 0.02^{B}	0.30 ± 0.02^{AB}	0.000
interior forest	0.49 ±0.01 ^A	0.36 ± 0.01^{B}	0.17 ±0.01 ^C	0.06 ± 0.01^{D}	0.05 ± 0.01^{D}	0.000
obligate						

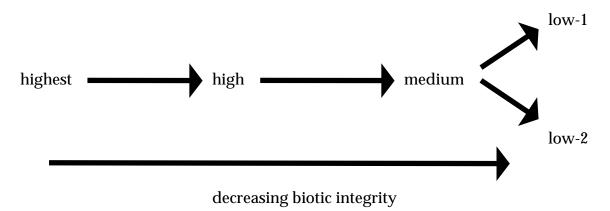


Figure 6. Schematic representation of BCI biotic integrity categories in the MAHA area. There are five categories of sites with distinct guild compositions, but the BCI does not distinguish between integrity values for the two lowest-integrity categories.

Figures 7-11 illustrate the mean bird community profiles of sites in five categories of ecological integrity defined by the BCI. Statistically significant differences in individual guilds among groups are indicated in Table 3.

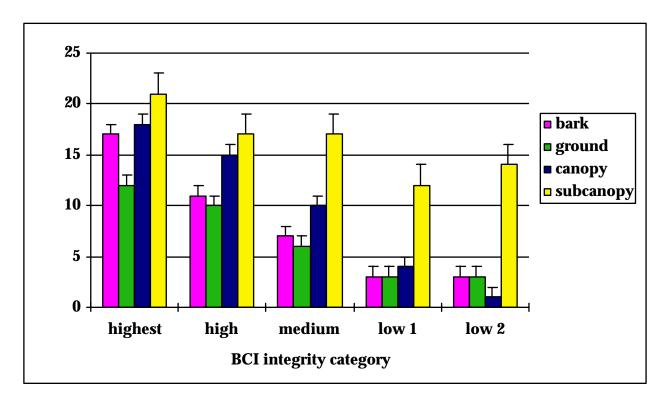


Figure 7. Proportion of insectivore foraging behavior guilds (functional) among five categories of biotic integrity. The guilds are bark probers, ground gleaners, upper-canopy foragers and subcanopy (i.e., lower-canopy) foragers.

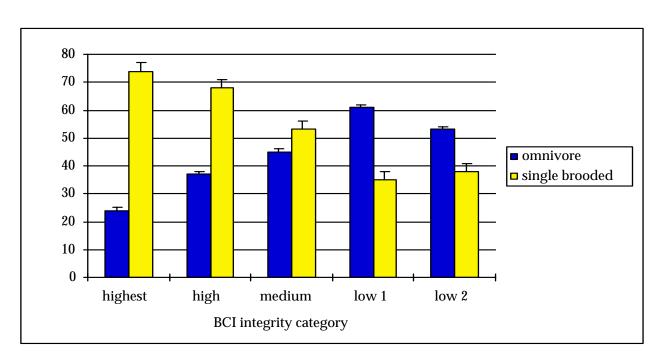


Figure 8. Proportion of omnivores (functional) and single-brooded species (compositional) among five categories of biotic integrity.

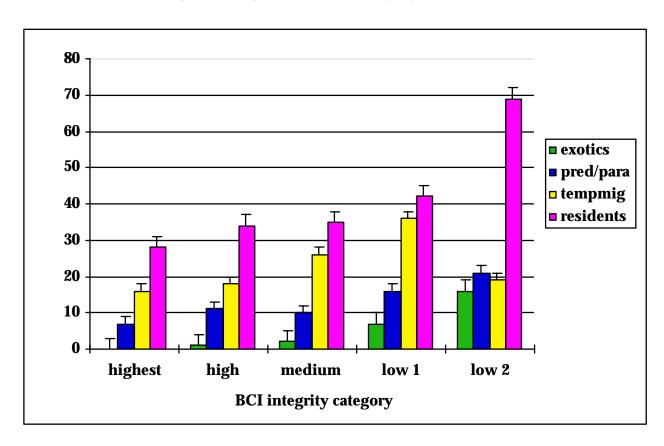


Figure 9. Proportion of compositional guilds among five categories of biotic integrity. "Pred/para" is the guild of nest predators and brood parasites; "tempmig" refers to temperate (i.e., short distance) migrants.

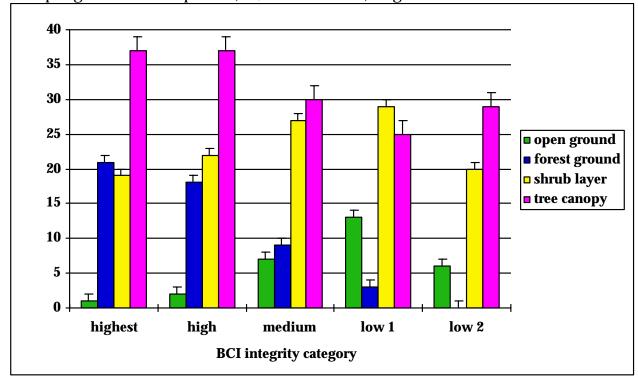


Figure 10. Proportion of nest placement guilds (structural) among five categories of biotic integrity.

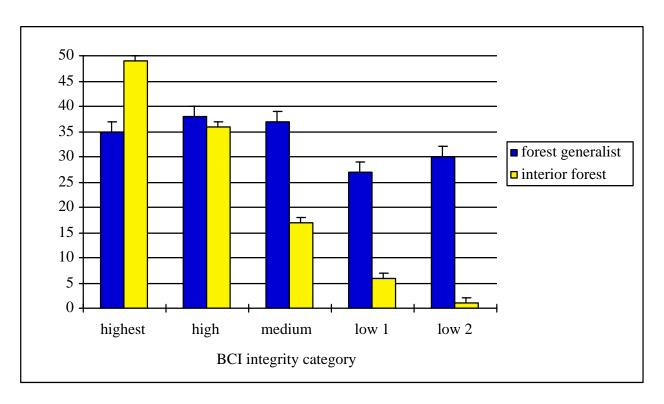


Figure 11. Proportion of forest generalists and interior-forest obligates (structural) among five categories of biotic integrity.

Objective 3. Land-cover Associations

Significant differences occur in many landscape and vegetation variables at the site scale among the five bird-based categories of biotic integrity (Table 4). For example, the low-2 sites, which are not separable from the low-1 sites according to BCI, contain significantly higher percentages of developed cover than sites in any other category ($F_{2,125} = 35.91$, P = 0.000). The low-1 sites contain significantly more agricultural cover than sites in any other category ($F_{4,125} = 40.16$, P = 0.000). Medium-integrity sites exhibit roughly equivalent proportions of forested and non-forested cover, and differ in this regard from sites in all other categories ($F_{4,125} = 63.38$, P = 0.000). Sites in the high- and highest-integrity categories cannot be separated by any of the landscape patch variables interpreted from aerial photographs (all pairwise Tukey 95% C. I.s include zero). The high- and highest-integrity categories, which differ significantly according to BCI, can only be separated by plot level vegetation variables. The highest-integrity sites contain significantly higher mean canopy height (Tukey 95% C. I. = -8.030, -0.254) and greater mean canopy closure (Tukey 95% C. I. = -0.265, -0.025). Figures 12-16 illustrate the

SPAN landscape circles for representative sites in each category of biotic integrity. Figure 17 illustrates mean proportions of forest, agricultural, and urban cover in each category.

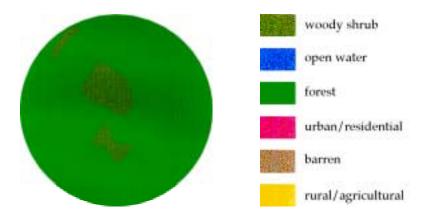


Figure 12. Representative land-cover configuration of a typical 79 ha site supporting the highest-integrity bird community. This site is 91% forested.

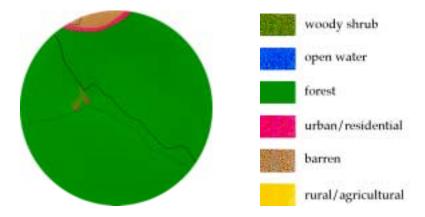


Figure 13. Representative land-cover configuration of a typical 79 ha site supporting a high-integrity bird community. This site is 94% forested.

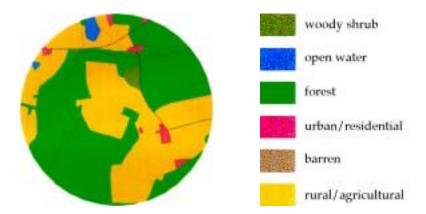


Figure 14. Representative land-cover configuration of a typical 79 ha site supporting a medium-integrity bird community. This site contains roughly equal proportions of forest (52%) and rural/agricultural cover (44%).

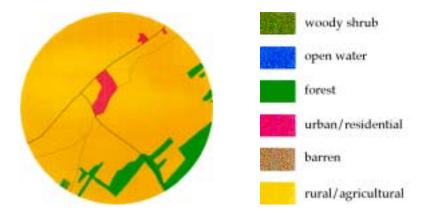


Figure 15. Representative land-cover configuration of a typical 79 ha site supporting a low-integrity (rural) bird community. This site contains 90% rural/agricultural cover.

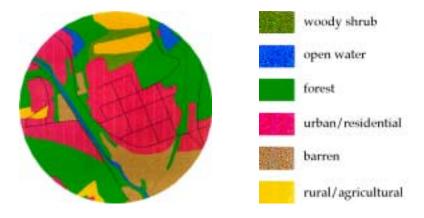


Figure 16. Representative land-cover configuration of a typical 79 ha site supporting a low-integrity (urban) bird community. This site exhibits a mix of cover types but is dominated by urban/residential cover (37%).

Table 4. Landscape and plot level land-cover variables ($\bar{x} \pm SE$) in each of five ecological integrity categories identified in the MAHA area with the BCI. Significant differences are based on one-way ANOVA (df = 4, 125) with Tukey's test for multiple comparisons. Within rows, values with different superscripts are significantly different at P < 0.05.

Land-cover	highest	high (n=34)	medium	low 1	low 2	P
Variables	(n=20)	_	(n=46)	(n=20)	(n=6)	
diversity	$0.08 \pm 0.02 \mathrm{A}$	0.13 ±0.02 A	0.34 ±0.02 B	0.33 ±0.03 B	0.40 ±0.06 B	0.000
dominance	0.20 ±0.04	0.22 ± 0.03	0.27 ±0.02	0.27 ± 0.02	0.29 ± 0.06	0.275
contagion	1.61 ±0.46 A	1.88 ±0.28 A	4.28 ±0.24 B	4.09 ±0.26 B	5.58 ±0.70 B	0.000
% urban/residential	1 ±1 ^A	1 ±0 A	4 ±1 A	3 ±1 ^A	43 ±14 ^B	0.000
% herbaceous/agricultural	1 ±1 ^A	5 ±2 AB	31 ±4 ^C	$66 \pm 5^{\mathrm{D}}$	29 ±14 ^{BC}	0.000
% woody shrub	4 ±2	3 ±1	6 ±2	3 ±1	2 ±1	0.290
% forested	94 ±2 A	89 ±2 A	57 ±4 ^B	25 ±3 ^C	21 ±5 ^C	0.000
forest edge (m)	1313 ±337 A	2108 ±323 A	4864 ±295 B	4706 ±565 B	6589 ±612 ^B	0.000
mean % slope	29 ±4 ^A	23 ±2 ^{AB}	16 ±1 ^{BC}	9 ±1 ^C	7 ±3 °C	0.000
mean #stems > 10 cm dbh	10.2 ±0.6 A	8.2 ±0.6 A	5.2 ±0.5 B	1.6 ±0.3 °C	2.9 ±0.9 ^{BC}	0.000
mean % canopy cover	61 ±3 ^A	47 ±3 B	33 ±3 ^C	11 ±3 ^D	21 ±4 ^C	0.000
mean canopy height (m)	23.8 ±1.0 ^A	19.7 ±0.7 B	15.2 ±0.8 ^C	$8.0 \pm 1.4^{\rm D}$	14.5 ±2.0 ^{BC}	0.000
mean % shrub cover	58 ±8 ^A	57 ±5 ^A	36 ±3 ^B	18 ±5 B	16 ±5 B	0.000

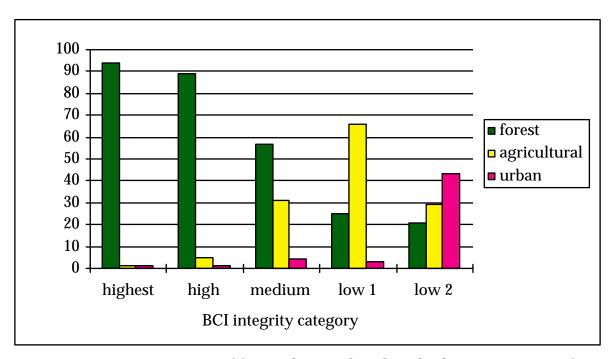


Figure 17. Mean proportions of forested, agricultural, and urban cover among five categories of biotic integrity determined with the BCI.

To further illustrate the relationship between landscape and vegetation variables and various levels of biotic integrity, we developed linear regression models using the BCI score as the response variable in the regression equation. Functional score is best predicted by a four variable model including landscape diversity (-), percentage of agricultural land (-), mean total shrub cover (+), and percentage canopy closure (+) ($r^2 = 0.733$, $F_{4,125} = 83.210$, P = 0.000). The compositional score model includes the three variables, percentage forested land (+), mean canopy height (+), and mean slope (+) ($r^2 = 0.709$, $F_{4,125} = 98.940$, P = 0.000). The structural score model includes the three variables, landscape diversity (-), mean number of stems per plot > 10 cm (+), and percentage of agricultural land (-) ($r^2 = 0.399$, $F_{4,125} = 26.980$, P = 0.000). Total BCI score is best predicted by a five variable model including percentage forested land (+), mean slope (+), mean canopy height (+), mean number of stems per plot > 10 cm (+), and land-cover contagion (-) ($r^2 = .816$, $F_{4,125} = 106.320$, P = 0.000). Table 5 outlines the specific multipliers in each equation.

Table 5. Regression equations for predicting functional, compositional, structural, and total BCI scores from vegetation and land-cover variables. Unless otherwise indicated, variables refer to land-cover at the scale of the 79 ha site: "divers" = land-cover diversity, "agland" = percentage of agricultural land, "shrub" = mean shrub cover per plot, "%can" = mean tree canopy cover per plot, "forest" = percentage of forested land, "canht" = mean tree canopy height (m) per plot, "slope" = mean percentage slope per plot, "stems" = mean number of stems over 10.0 cm dbh per plot, "contag" = land-cover contagion.

BCI	n	regression equation	r	F	P
Subscore					
Functional (V1)	126	14.300 - 7.810divers - 4.620agland + 3.860shrub + 6.440%can	0.733	83.210	0.000
Compositional (V2)	126	7.180 + 8.800forest + .0147canht + 6.820slope	0.709	98.940	0.000
Structural (V3)	126	17.600 - 5.500divers + 0.229stems - 2.000agland	0.399	26.980	0.000
Total BCI	1	30.000 + 18.700forest + 12.800slope + 0.255canht + 0.387stems - 0.612contag	0.816	106.320	0.000

Objective 4: BCI Verification

The landscape disturbance gradient we developed on the 1994 reference data classified sites as undisturbed, moderately-disturbed, and disturbed. Under the landscape disturbance gradient, undisturbed sites contained significantly higher percentage forest ($F_{2,33} = 216.61$, P = 0.000), mean forest patch size ($F_{2,33} = 36.08$, P = 0.000) and contagion ($F_{2,33} = 17.52$, P = 0.000) than either moderately-disturbed or undisturbed sites. Moderately-disturbed sites contained significantly higher percentage forest and larger mean forested patch sizes than disturbed sites, but did not differ in contagion (95% C. I. for Tukey pairwise comparison = -1.705, 1.993).

Like the human disturbance gradient (Brooks et al. 1996), the landscape disturbance gradient we developed to verify the BCI identified differences in BCI scores among sites. Undisturbed sites supported significantly higher functional ($F_{2,33} = 43.61$, P = 0.000), compositional ($F_{2,33} = 41.52$, P = 0.000), structural ($F_{2,33} = 20.11$, P = 0.000), and overall BCI scores ($F_{2,33} = 59.84$, P = 0.000) than either the moderately- disturbed or

disturbed sites. Differences between the structural guild ranks of moderately-disturbed and disturbed sites were not significant (Tukey 95% C.I. = -2.168, 0.285).

Likewise, the BCI gradient identified landscape disturbance differences among sites in different categories of biotic integrity. High-integrity sites contained significantly lower contagion ($F_{2,33} = 13.03$, P = 0.000), higher percentage forest ($F_{2,33} = 106.93$, P = 0.000), and larger mean forest patch size ($F_{2,33} = 19.19$, P = 0.000), than either medium- or low-integrity sites. Medium-integrity sites exhibited significantly larger forest patch size and higher percentage forest than low-integrity sites, but differences in contagion were not significant (Tukey 95% C.I. = -1.926, 2.026). The landscape disturbance and BCI gradients applied to the 1994 reference sites are highly correlated ($r^2 = 0.932$ landscape disturbance XBCI).

To verify the BCI methodology on an independent sample of probability-based sites from the entire MAHA area, we developed a landscape disturbance gradient for the 126 sample sites. We clustered the sites (complete linkage, squared Euclidean distance) into five categories according to contagion, percentage residential development, percentage forest, mean number of stems > 10 cm dbh per plot, mean canopy height per plot, and mean total shrub cover per plot. We then ordered the clusters along a landscape disturbance gradient. The Pearson correlation between this landscape disturbance gradient and the five category BCI was $r^2 = 0.785$.

DISCUSSION

BCI Development

The first phase of this research revealed that BCI scores were highly correlated with the known ecological condition of the 1994 reference sites. Furthermore, bird community profiles and BCI scores were similar within groups of sites, whether the groups were determined by the BCI or the human disturbance gradient. Thus, our response guilds proved useful, not only in ordinating sites into three categories of ecological condition, but in demonstrating significantly different biological aspects of

the bird community between categories. These findings confirm our primary assumption that songbird community structure is a valid biological index: It reflects, at a minimum, the selected physical, chemical, and biological aspects of ecological condition that had previously been documented at our reference sites. As with any useful indicator, the BCI may serve as a substitute for more numerous and intensive measurements of condition and disturbance.

Under the three-category classification of high, medium, and low BCI scores we developed for the 1994 reference sites, all 16 guilds comprised significantly different proportions of the bird community between at least two categories. For six of the guilds (bark prober, ground gleaner, upper-canopy forager, nest predator/brood parasite, resident, and shrub nester), it was the proportion in the high-integrity sites that was different from the proportion in the medium- and low-integrity sites. Lower-canopy foragers, canopy nesters, and exotics differed in proportion between high-integrity and low-integrity sites, with medium-integrity sites supporting intermediate proportions. Temperate migrants were best represented at low-integrity sites, while forest generalists were most prevalent at medium-integrity sites. Five of the guilds (omnivore, single-brooded, open-ground nester, forest-ground nester, and interior-forest obligate) occurred in significantly different proportions in sites in each category. For example, interior-forest obligates comprised 43% of the species in high-integrity sites, 15% in medium-integrity sites, and 5% of the species in the low-integrity sites.

Differences in bird community profiles were largely preserved as they were ranked and compiled as structural, functional, and compositional elements of the BCI. Total BCI score, functional score, and compositional score were significantly different among sites in all three categories. Structural scores, however, could discriminate only between high-integrity sites and sites labeled as either medium- or low-integrity. The inability of structural scores to discriminate between medium- and low-integrity sites is likely due to the fact that two major structural guilds (canopy nesters and shrub nesters) did not differ between sites in these two categories. Approximately 60% of the species at medium- and low-integrity sites were either shrub or canopy nesters. The similarities

in these two guilds between sites in the medium- and low-integrity categories may overpower the differences evident in other structural guilds. Interpretation of the forest generalists presents another complicating factor in the structural guilds. Because we ranked low occurrence of this guild as a high-integrity condition, both low- and high-integrity sites ranked higher than medium-integrity sites for forest generalists.

BCI Application

When applied to the probability-based random sample of sites from the entire MAHA area, the BCI indicated five distinct bird community types. In general, the bird communities documented at sites with the higher BCI scores were separable from the communities at sites with the lower scores by functional, compositional, structural, and overall BCI scores. The two community types with the lowest overall BCI scores, however, could not be distinguished from each other by functional, compositional, structural, or total BCI score. A close examination of these two communities reveals that one supports significantly more open-ground nesters, while the other supports the highest proportions of exotics, nest predators/brood parasites, and resident species. These guild differences indicate that the former community is typical of a grassland or agricultural setting, while the latter is typical of urban environments. We conclude that ecological condition in the MAHA area cannot be characterized by a linear gradient from pristine to disturbed landscapes. Rather, both rural and urban land-cover modification may have equally adverse effects on ecological condition.

BCI scores increase from low-integrity rural and low-integrity urban to the medium-integrity communities. Specifically, medium-integrity communities contain fewer omnivores, nest predators/brood parasites, residents, and exotics; but significantly more upper-canopy foragers, single-brooded species, forest-ground nesters, and interior-forest obligates. Relative to medium-integrity communities, high-integrity communities support fewer omnivores, exotics, temperate migrants, shrub nesters, and open-ground nesters; but more bark probers, ground gleaners, upper-canopy foragers, single-brooded species, canopy nesters, forest-ground nesters, and

interior-forest obligates. Relative to the high-integrity communities, bird communities from the sites with the highest BCI scores exhibited fewer omnivores, nest predators/brood parasites, and residents; but more bark probers, single-brooded species, and interior-forest obligates.

If we track the response of each guild down the gradient from a high-integrity to a low-integrity condition, several interesting patterns emerge. In the functional guilds, omnivores increase from roughly 25% to more than 50% of the species in the community. The overall low proportion of insectivores in the lower-integrity communities relative to higher-integrity communities may indicate a diminished insect biomass, loss of specialized foraging opportunities (e.g., Pettersson et al. 1995), or factors unrelated to insect availability. A more in-depth look at insectivore foraging behaviors, however, provides evidence for loss of specific foraging opportunities: Lower-canopy foragers are well-represented in all five integrity categories, but bark probers, ground gleaners, and upper-canopy foragers all decrease from more than 10% of the species at a site to fewer than 5 percent.

Compositional changes down the gradient from high- to low- integrity include the decrease in single-brooded species from nearly 75% of the bird community to less than 40 percent. Exotic species increase from 0% of the species in the highest- and high-integrity communities to approximately 16% of the species in the low-integrity urban communities (e.g., Blair 1996). Nest predators/brood parasites increase from fewer than 10% of the species at a site to more than 20% (e.g., Donovan et al. 1995). Non-migratory resident species increase from fewer than 30% to roughly 70% of the species at a site (e.g., Schmiegelow et al. 1997). Temperate migrants are most prevalent at the low-integrity rural sites, where they occupy 36% of the bird community. Temperate migrants comprise 15 to 20% of the bird community at both ends of the biotic integrity gradient, but the balance of the species are residents at the low-integrity urban sites and neotropical migrants at the highest- and high-integrity sites (e.g., Askins and Philbrick 1987, Croonquist and Brooks 1991). The compositional guilds describe a bird community that is characterized by opportunistic species at the low-integrity sites.

Interpretation of the trends in structural guilds down a gradient of biotic integrity is less dramatic than for functional or compositional guilds, but informative nonetheless. Canopy nesters and forest generalists decrease from roughly 40% to 30% of the species in the community. Shrub nesters increase from about 20% of the community toward a peak of nearly 30% at the medium- and low-integrity rural sites, only to decrease again to near 20% for the low-integrity urban sites. Open-ground nesters occupy about 13% of the bird community at the low-integrity rural sites, and less than 7% at sites in all other categories. The loss of forest, both in terms of extent and maturity, is evident down the integrity gradient from the prevalence of forest-ground nesters and interior-forest obligates. Forest-ground nesters drop steadily through the gradient from about 20% of the bird community to 0% at the low-integrity urban sites. Interior-forest obligates comprise almost 50% of the species at the highest-integrity sites, but only about 5% at the low-integrity sites (e.g., Freemark and Collins 1992).

The great benefit of the probability-based sampling design we employed to characterize the MAHA area is that the proportion of sample sites we assigned to different categories of biotic integrity equates to the land area of the Mid-Atlantic Highlands with known statistical confidence. We can, therefore, report on the proportion of land area in various states of biotic integrity using the 95% confidence intervals for our estimates. Thus, areas supporting the highest-integrity bird communities occupy between 10.5 and 21.5% (i.e., 17,684 - 36,210 km²); high-integrity areas comprise 20.2-33.8% (34,020-56,926 km²); medium-integrity is 28.7-43.3% (48,336-72,925 km²); low-integrity rural falls between 10.5 and 21.5% (17,684-36,210 km²); and low-integrity urban bird communities occupy 1.6-8.4% (2,694-14,147 km²) of the MAHA area.

Land-Cover and Vegetation Associations

The five bird community types identified with the BCI in the MAHA area coincide with specific attributes of land-cover configuration at the 79 ha scale, as well as

vegetation characteristics observed on the ground. This finding supports our objective to develop a biological indicator for large-scale habitats that contain a mosaic of terrestrial, aquatic, and urban elements. This finding also documents a unit size of landscape within which bird communities respond significantly to land-cover disturbance.

The general relationship between the BCI and remotely-sensed land-cover pattern indicates that good ecological condition is associated with extensive forest cover. This is to be expected in the MAHA region, where the native landscape matrix is forested and undisturbed areas naturally succeed into forest. In addition to forest extent, the BCI also indicated a relationship with ground-level forest structure: The highest- and high-integrity sites identified with the BCI exhibit no significant differences in the percentage of forest, agricultural land, urban development, or woody shrubs at the 79 ha scale. Differences in landscape diversity, dominance, and contagion are also insignificant. Vegetation measures taken on the ground, however, indicate that sample sites in the highest-integrity category support a significantly taller and more closed tree canopy than the equally forested high-integrity sites. Thus, the forests are no more extensive at the highest-integrity sites, but the vegetation is more mature. According to the BCI, the portion of the MAHA area in the best ecological condition is that characterized by mature forest vegetation in units of at least 79 ha.

Land-cover and vegetation attributes at medium-integrity sites exhibit several significant shifts away from conditions present at the high- and highest-integrity sites. At the 79 ha scale, medium-integrity sites contain significantly higher landscape diversity, contagion, forest edge, and percentage agricultural cover; but significantly less percentage forest, shrub cover, and canopy cover, as well as lower canopy height, and fewer tree stems per plot when compared to sites in the high- and highest-integrity categories. Despite the loss of mature forest relative to higher-integrity sites, medium-integrity sites still support more than twice the forest area present at low-integrity rural and low-integrity urban sites. Medium-integrity sites are unique among all categories in being roughly 50-66% forested at the 79 ha scale. Thus, medium-integrity sites provide

critical habitat needs for forest species in a landscape setting close to a matrix shift away from forest.

Sites in the two low-integrity categories have undergone matrix shifts from forest to another major land-cover type at the 79 ha scale. Neither category includes sites supporting any more than 30% forested cover. Low-integrity rural sites are dominated by herbaceous/agricultural cover encompassing roughly 60-70% of the land area. At the ground level, low-integrity rural sites also support the smallest trees and most open canopy in the MAHA area. Low-integrity urban sites are characterized by a variable mix of forested, agricultural, and urban/residential cover, with urban conditions typically comprising the matrix at roughly 30-55% of the land area. Interestingly, ground-level canopy cover and canopy height at low-integrity urban sites are significantly greater than at low-integrity rural sites, and similar to conditions present at medium-integrity sites. The taller and more closed canopy at the low-integrity urban sites, however, is insufficient to inflate the BCI scores of low-integrity urban sites above low-integrity rural sites. This phenomenon may be due to the fact that low-integrity sites simply do not provide large enough forest patch sizes to support bird species that require a tall, closed forest canopy. Alternatively, the amount of canopy closure and canopy height at low-integrity urban sites may still fall below thresholds of habitat suitability for mature-forest obligates. Other factors, such as artificially elevated populations of human-associated nest predators (e.g., cats, raccoons), may also be operating in low-integrity urban environments.

The best subsets multiple regression approach we employed to further explore relationships between BCI scores and habitat variables identified highly significant regression equations for determining functional, compositional, structural, and total BCI score. We found that total BCI score, and, by association, overall biotic integrity, is best predicted by a five-variable model that consists of landscape-level contagion and percentage forest, and the ground-level attributes canopy height, density of trees, and slope. The importance of "forest," both in terms of land-cover and size and number of individual stems, is again apparent. Landscape contagion, which relates to the

interspersion of different land-cover patches, emerges from the model as a significant negative variable. Mean slope at ground level is positively associated with BCI scores, although it is unclear whether this relationship derives from microhabitat features provided in areas of high topographic relief, or from the fact that most extensive forests in the MAHA area occur on mountain slopes and ridges.

While we cannot state a causal mechanism in the relationship between regression variables and biotic integrity, we can apply the model to land-cover data from the Mid-Atlantic Highlands to identify areas with a high probability of supporting various degrees of biotic integrity. For example, to explore the spatial distribution of biotic integrity, we could access GIS databases with the capacity to identify forested land, landscape contagion, and slope. Within this population of sites, additional information on canopy height and stocking density could be obtained and added to the model for a prediction of BCI scores. The regression model can also aid in identifying specific thresholds of land-cover and vegetation variables at which critical shifts in BCI scores, equating to shifts in biotic integrity, occur.

BCI Verification

The human disturbance gradient represented by the 1994 reference sites allowed a direct comparison between the BCI assessment of biotic integrity, and independent assessments of several physical, chemical, and biological attributes of the same sites. The high level of agreement between the ranking of sites under the human disturbance gradient and the three-category BCI provided confidence that the BCI indicates the condition of system attributes in addition to birds.

An independent landscape disturbance gradient applied to the 1994 reference sites demonstrated a strong correlation with both the human disturbance gradient and the BCI. This finding established land-cover configuration as a means to verify the BCI application to the 1995 and 1996 sites from the probability-based sample of the MAHA area. We compared the five-category BCI gradient developed for the probability-based sites to an independent gradient of the same sample sites using land-cover and

vegetation variables. Because land-cover data were strongly associated with the data used to build the human disturbance gradient at the reference sites, close agreement between the landscape and BCI assessments of the MAHA area sample sites provides additional evidence that the BCI indicates overall ecosystem condition.

The correlation in site rankings between the independent BCI and landscape disturbance gradients was high, even though the number of categories (5) was higher than that used for the 1994 reference sites (3). Not only do the two ranking methods ordinate sites similarly, but the values for individual variables (e.g., proportion of omnivores, percentage forest) are similar within categories under either method. For example, sites that the BCI determined to be in "good" condition were also in "good" condition based on their land-cover configuration. Also, individual guilds, e.g., omnivores, assumed the same general pattern of occurrence under the BCI's five categories of biotic integrity as they did under the landscape gradient's five categories of landscape disturbance. These findings provided the additional verification that the BCI accurately reflects overall system condition, and does not merely indicate the condition of the bird community.

The use of bird guilds to discriminate between habitats of varying quality has been both lauded and questioned. For example, Croonquist and Brooks (1991) and Miller et al. (1997) noted strong associations between the representation of response guilds and the amount of human-dominated land cover in two central Pennsylvania watersheds. Conversely, DeGraaf and Chadwick (1984) working in New Hampshire and Szaro (1986) in Arizona found individual species variables to better distinguish discrete habitat types than did guild variables. Most of the response guilds we employed in this study successfully discriminated between varying degrees of land-cover condition. Our success is using guilds for this purpose was likely due to the fact that we selected guilds based on habitat use (Szaro 1986) and that the range of habitat conditions in the study area was large (DeGraaf and Chadwick 1984).

The bird community profiles we constructed for each sample site were ultimately based on the presence of singing males, and the BCI did not incorporate information on

reproductive success. Due to the influences of source and sink dynamics on metapopulations of breeding songbirds (Dunning et al. 1992, Donovan et al. 1995), it is possible that the BCI may have assigned high rankings for biotic integrity to sites where reproductive success is compromised. Because of the relationships between BCI scores and the 1994 reference sites, however, we are confident that BCI-derived proportions of the MAHA area represent different degrees of biotic integrity, rather than just different bird species assemblages.

Management Implications

To assess the ecological condition of the MAHA area and prioritize management prescriptions, it can be helpful to think of the various biotic integrity categories as representing "excellent" (highest-integrity), "good" (high-integrity), "fair" (medium-integrity), and "poor" (low-integrity rural and low-integrity urban) ecological condition. Because BCI scores are highly correlated with land-cover and vegetational features at the 79 ha scale, we expect that large-scale management activities can affect BCI scores and ecological condition.

This study begins to define thresholds of vegetation and land-cover change at which shifts in ecological integrity are observed. At the 79-ha scale, both good and excellent ecological condition were associated with a minimum of 87% forest cover. Poor ecological condition was observed when agricultural/herbaceous cover exceeded 61%, or urban/residential cover exceeded 29%. One interpretation of these results is to consider areas in good ecological condition as desirable by society, and to manage them so as to maintain current land cover. Longer rotation sequences in forested areas of good condition could create more areas with the potential to support excellent condition. Conversely, many of the areas in poor ecological condition are justified by societal requirements for agricultural and urban land uses. Community planning efforts may focus instead on those marginal landscapes of fair condition, guiding development such that they are not transformed beyond critical land-cover thresholds into areas of poor ecological condition.

In summary, we have demonstrated that the BCI is a valid biological indicator of ecological condition at landscape scales. As with any single metric, however, we recommend that information from the BCI be combined with that from additional indicators for a robust ecological assessment of the MAHA area. We also recognize that the field monitoring design we have developed and tested for the BCI may not be practical for annual implementation across multiple states. The strong association between remotely-sensed landscape pattern and breeding bird community composition may permit remote imagery to substitute for bird data in, for example, four out of every five years. Comprehensive field monitoring would then be required only intermittently to ascertain that the bird-landscape correlation had not been affected by chemical pollution or other large-scale disturbances which this study did not address.

Future Research

We intend to pursue additional questions raised by this research in order to increase the practical utility of the BCI, and to improve guidance on the amount of land-cover change that is compatible with high-integrity ecological systems. To refine our preliminary thresholds of land-cover change, we plan to study additional MAHA sites that exhibit land-cover configurations under-represented in our 1995-96 sample. We are continuing to explore the range of landscape scales within which the BCI can reflect land-cover pattern. Using Thematic Mapper satellite imagery, we are currently quantifying pattern metrics in successively larger landscapes around our sampling transects. Correlation of these metrics with the BCI will determine the largest landscape scale at which the association between bird communities and landscape pattern persists.

As another way to address the issue of scale, and to provide linkage between BCI methodology and established bird monitoring programs, we intend to apply the BCI to subsections of Breeding Bird Survey (BBS) routes for which we can obtain land-cover data. In the BBS, bird sampling plots along each survey route are separated by 1/2 mi or 0.8 km. Rather than using landscape circles here, a more relevant approach at the larger scale of BBS routes would be land-cover analysis within a rectangular strip of

land surrounding the survey route. For example, a five-stop subsample from a BBS route (about two miles long) could be analyzed within a surrounding strip of 5.2 km by 2 km. The area in this landscape sample would encompass 1040 ha; roughly 13 times the area of the landscape circles employed for the BCI. Thus, the BBS provides the advantage of rapid increase in the land area characterized with each additional bird sampling point included. Should significant correlations emerge with landscape pattern at larger BBS scales, the BCI could be considered for broad application within an established monitoring framework, with appropriate regional calibration and testing.

In addition to spatial scaling, the BBS also provides the benefit of analysis through time. Once an appropriate scale of BCI application is identified for use with BBS data, we can apply the BCI to annual BBS results. From a methodological perspective, such an application can lead to improvements in the BCI itself, by empirically identifying the inter-annual variance of BCI assessments. More importantly, BCI application through time can reveal changes in bird community integrity, and changes in biotic integrity, that have taken place in the 32 years since the establishment of the BBS.

Finally, we are interested in deconstructing the BCI data from our landscape sites into plot-level units. We will calculate BCI scores separately for forested and agricultural plots, and compare the resulting ecological assessments for these two discrete natural resources with the results from EMAP's forest and agricultural monitoring components in the same region. The purpose of this analysis will be to determine if the BCI adds useful information to more traditional, resource-specific monitoring through its integrated perspective of ecological condition at the landscape scale. We will calculate BCI scores for urban and ecotone plots as well, to provide condition information for these areas that are not generally included in ecological monitoring programs. We will also quantify differences in BCI scores between forested plots in forested landscapes versus forested plots in agricultural and mixed landscapes, performing equivalent comparisons for selected non-forested plot types, to explore various relationships in ecological condition between spatial scales.

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Appendix I. Scientific name, common name, and four-letter common name code for 112 "songbirds" documented at probability-based sampling locations in the MAHA area. Taxonomoy follows A. O. U. (1983) and Supplements.

SCIENTIFIC NAME	COMMON NAME	4 LETTER CODE
Columba livia	Rock Dove	RODO
Zenaida macroura	Mourning Dove	MODO
Coccyzus americanus	Yellow-billed Cuckoo	YBCU
Coccyzus erythrophthalmus	Black-billed Cuckoo	BBCU
Chaetura pelagica	Chimney Swift	CHSW
Archilochus colubris	Ruby-throated Hummingbird	RTHU
Melanerpes erythrocephalus	Red-headed Woodpecker	RHWO
Melanerpes carolinus	Red-bellied Woodpecker	RBWO
Sphyrapicus varius	Yellow-bellied Sapsucker	YBSA
Picoides pubescens	Downy Woodpecker	DOWO
Picoides villosus	Hairy Woodpecker	HAWO
Colaptes auratus	Northern Flicker	NOFL
Dryocopus pileatus	Pileated Woodpecker	PIWO
Contopus virens	Eastern Wood-Pewee	EWPE
Empidonax virescens	Acadian Flycatcher	ACFL
Empidonax alnorum	Alder Flycatcher	ALFL
Empidonax traillii	Willow Flycatcher	WIFL
Empidonax minimus	Least Flycatcher	LEFL
Sayornis phoebe	Eastern Phoebe	EAPH
Myiarchus crinitus	Great Crested Flycatcher	GCFL
Tyrannus tyrannus	Eastern Kingbird	EAKI
Eremophila alpestris	Horned Lark	HOLA
Progne subis	Purple Martin	PUMA
Tachycineta bicolor	Tree Swallow	TRSW
Stelgidopteryx serripennis	Northern Rough-winged Swallow	NRWS
Hirundo pyrrhonota	Cliff Swallow	CLSW
Hirundo rustica	Barn Swallow	BARS
Cyanocitta cristata	Blue Jay	BLJA
Corvus brachyrhynchos	American Crow	AMCR
Corvus ossifragus	Fish Crow	FICR
Corvus corax	Common Raven	CORA
Poecile carolinensis	Carolina Chickadee	CACH
Poecile atricapillus	Black-capped Chickadee	BCCH
Baeolophus bicolor	Tufted Titmouse	TUTI
Sitta canadensis	Red-breasted Nuthatch	RBNU
Sitta carolinensis	White-breasted Nuthatch	WBNU
Certhia americana	Brown Creeper	BRCR
Thryothorus ludovicianus	Carolina Wren	CARW

Troglodytes aedon	House Wren	HOWR
Troglodytes troglodytes	Winter Wren	WIWR
Regulus satrapa	Golden-crowned Kinglet	GCKI
Polioptila caerulea	Blue-Gray Gnatcatcher	BGGN
Sialia sialis	Eastern Bluebird	EABL
Catharus fuscescens	Veery	VEER
Catharus guttatus	Hermit Thrush	HETH
Hylocichla mustelina	Wood Thrush	WOTH
Turdus migratorius	American Robin	AMRO
Dumetella carolinensis	Gray Catbird	GRCA
Mimus polyglottos	Northern Mockingbird	NOMO
Toxostoma rufum	Brown Thrasher	BRTH
Bombycilla cedrorum	Cedar Waxwing	CEDW
Sturnus vulgaris	European Starling	EUST
Vireo griseus	White-eyed Vireo	WEVI
Vireo griscus Vireo solitarius	Blue-headed Vireo	BHVI
Vireo flavifrons	Yellow-throated Vireo	YTVI
Vireo gilvus	Warbling Vireo	WAVI
Vireo olivaceus	Red-eyed Vireo	REVI
Vermivora pinus	Blue-winged Warbler	BWWA
Vermivora chrysoptera	Golden-winged Warbler	GWWA
Vermivora ruficapilla	Nashville Warbler	NAWA
Parula americana	Northern Parula	NOPA
Dendroica petechia	Yellow Warbler	YEWA
Dendroica pensylvanica	Chestnut-sided Warbler	CSWA
Dendroica magnolia	Magnolia Warbler	MAWA
Dendroica caerulescens	Black-throated Blue Warbler	BTBW
Dendroica coronata	Yellow-rumped Warbler	YRWA
Dendroica virens	Black-throated Green Warbler	BTNW
Dendroica fusca	Blackburnian Warbler	BNWA
Dendroica dominica	Yellow-throated Warbler	YTWA
Dendroica pinus	Pine Warbler	PIWA
Dendroica discolor	Prairie Warbler	PRWA
Dendroica cerulea	Cerulean Warbler	CERW
Mniotilta varia	Black-and-white Warbler	BAWW
Setophaga ruticilla	American Redstart	AMRE
Helmitheros vermivorus	Worm-eating Warbler	WEWA
Seiurus aurocapillus	Ovenbird	OVEN
Seiurus noveboracensis	Northern Waterthrush	NOWA
Seirus motacilla	Louisiana Waterthrush	LOWA
Oporornis formosus	Kentucky Warbler	KEWA
Oporornis philadelphia	Mourning Warbler	MOWA

Coathlymic triches	Common Yellowthroat	COYE
Geothlypis trichas	Hooded Warbler	
Wilsonia citrina		HOWA
Wilsonia canadensis	Canada Warbler	CAWA
Icteria virens	Yellow-breasted Chat	YBCH
Piranga rubra	Summer Tanager	SUTA
Piranga olivacea	Scarlet Tanager	SCTA
Cardinalis cardinalis	Northern Cardinal	NOCA
Pheucticus ludovicianus	Rose-breasted Grosbeak	RBGR
Guiraca caerulea	Blue Grosbeak	BLGR
Passerina cyanea	Indigo Bunting	INBU
Pipilo erythrophthalmus	Eastern Towhee	EATO
Ammodramus savannarum	Grasshopper Sparrow	GRSP
Ammodramus henslowii	Henslow's Sparrow	HESP
Pooecetes gramineus	Vesper Sparrow	VESP
Passerculus sandwichensis	Savannah Sparrow	SASP
Melospiza melodia	Song Sparrow	SOSP
Melospiza georgiana	Swamp Sparrow	SWSP
Spizella pusilla	Field Sparrow	FISP
Spizella passerina	Chipping Sparrow	CHSP
Junco hyemalis	Dark-eyed Junco	DEJU
Zonotrichia albicollis	White-throated Sparrow	WTSP
Dolichonyx oryzivorus	Bobolink	BOBO
Sturnella magna	Eastern Meadowlark	EAME
Agelaius phoeniceus	Red-winged Blackbird	RWBL
Molothrus ater	Brown-headed Cowbird	ВНСО
Quiscalus quiscula	Common Grackle	COGR
Icterus spurius	Orchard Oriole	OROR
Icterus galbula	Baltimore Oriole	BAOR
Passer domesticus	House Sparrow	HOSP
Carduelis tristis	American Goldfinch	AMGO
Carpodacus purpureus	Purple Finch	PUFI
Carpodacus mexicanus	House Finch	HOFI
r		

Appendix II. Four-letter common name codes for 112 "songbirds" documented in the MAHA area, sorted alphabetically.

COMMON NAME	CODE	COMMON NAME	CODE
Acadian Flycatcher	ACFL	Eastern Meadowlark	EAME
Alder Flycatcher	ALFL	Eastern Phoebe	EAPH
American Crow	AMCR	Eastern Towhee	EATO
American Goldfinch	AMGO	European Starling	EUST
American Redstart	AMRE	Eastern Wood-Pewee	EWPE
American Robin	AMRO	Fish Crow	FICR
Baltimore Oriole	BAOR	Field Sparrow	FISP
Barn Swallow	BARS	Great Crested Flycatcher	GCFL
Black-and-white Warbler	BAWW	Golden-crowned Kinglet	GCKI
Black-billed Cuckoo	BBCU	Gray Catbird	GRCA
Black-capped Chickadee	BCCH	Grasshopper Sparrow	GRSP
Blue-Gray Gnatcatcher	BGGN	Golden-winged Warbler	GWWA
Brown-headed Cowbird	BHCO	Hairy Woodpecker	HAWO
Blue-headed Vireo	BHVI	Henslow's Sparrow	HESP
Blue Grosbeak	BLGR	Hermit Thrush	HETH
Blue Jay	BLJA	House Finch	HOFI
Blackburnian Warbler	BNWA	Horned Lark	HOLA
Bobolink	BOBO	House Sparrow	HOSP
Brown Creeper	BRCR	Hooded Warbler	HOWA
Brown Thrasher	BRTH	House Wren	HOWR
Black-throated Blue Warbler	BTBW	Indigo Bunting	INBU
Black-throated Green Warbler	BTNW	Kentucky Warbler	KEWA
Blue-winged Warbler	BWWA	Least Flycatcher	LEFL
Carolina Chickadee	CACH	Louisiana Waterthrush	LOWA
Carolina Wren	CARW	Magnolia Warbler	MAWA
Canada Warbler	CAWA	Mourning Dove	MODO
Cedar Waxwing	CEDW	Mourning Warbler	MOWA
Cerulean Warbler	CERW	Nashville Warbler	NAWA
Chipping Sparrow	CHSP	Northern Cardinal	NOCA
Chimney Swift	CHSW	Northern Flicker	NOFL
Cliff Swallow	CLSW	Northern Mockingbird	NOMO
Common Grackle	COGR	Northern Parula	NOPA
Common Raven	CORA	Northern Waterthrush	NOWA
Common Yellowthroat	COYE	Northern Rough-winged Swallow	NRWS
Chestnut-sided Warbler	CSWA	Orchard Oriole	OROR
Dark-eyed Junco	DEJU	Ovenbird	OVEN
Downy Woodpecker	DOWO	Pine Warbler	PIWA
Eastern Bluebird	EABL	Pileated Woodpecker	PIWO
Eastern Kingbird	EAKI	Prairie Warbler	PRWA

Appendix II (cont.)

COMMON NAME	CODE
Purple Finch	PUFI
Purple Martin	PUMA
Rose-breasted Grosbeak	RBGR
Red-breasted Nuthatch	RBNU
Red-bellied Woodpecker	RBWO
Red-eyed Vireo	REVI
Red-headed Woodpecker	RHWO
Rock Dove	RODO
Ruby-throated Hummingbird	RTHU
Red-winged Blackbird	RWBL
Savannah Sparrow	SASP
Scarlet Tanager	SCTA
Song Sparrow	SOSP
Summer Tanager	SUTA
Swamp Sparrow	SWSP
Tree Swallow	TRSW
Tufted Titmouse	TUTI
Veery	VEER
Vesper Sparrow	VESP
Warbling Vireo	WAVI
White-breasted Nuthatch	WBNU
White-eyed Vireo	WEVI
Worm-eating Warbler	WEWA
Willow Flycatcher	WIFL
Winter Wren	WIWR
Wood Thrush	WOTH
White-throated Sparrow	WTSP
Yellow-breasted Chat	YBCH
Yellow-billed Cuckoo	YBCU
Yellow-bellied Sapsucker	YBSA
Yellow Warbler	YEWA
Yellow-rumped Warbler	YRWA
Yellow-throated Vireo	YTVI
Yellow-throated Warbler	YTWA

Appendix III. Species assignments in the 16 response guilds included in the BCI.

INTEGRITY ELEMENT	GUILD CATEGORY	RESPONSE GUILDS			
Functional	Trophic	Omnivore	Omnivore	Omnivore	Omnivore
		AMCR	CORA	HESP	SOSP
		AMGO	DEJU	HOLA	SWSP
		AMRO	EABL	INBU	VEER
		BAOR	EAME	NOCA	VESP
		BHCO	EATO	NOMO	WOTH
		BLJA	EUST FICR	RBGR	WTSP
		ВОВО		RODO	YBCH
		BRTH CHSP	FISP GRCA	RTHU RWBL	YBSA
		COGR	GRSP	SASP	
Functional	Insectivore Foraging Behavior	Bark Prober	Ground Gleaner	Upper-canopy	
	rotaging Denavior	BAWW	HETH	Forager BGGN	
		BRCR	KEWA	BNWA	
		DOWO	MOWA	BTNW	
		HAWO	NOFL	CERW	
		PIWA	OVEN	GWWA	
		PIWO	WEWA	NOPA	
		RBNU	WIWR	OROR	
		RBWO		REVI	
		RHWO		SCTA	
		WBNU		SUTA	
		YTWA		WAVI	
		11,111		YTVI	
				YTWA	
Functional	Insectivore Foraging Behavior	Lower-canopy Forager AMRE	Lower-canopy Forager GCKI		
		BBCU	HOWA		
		ВССН	HOWR		
		BHVI	MAWA		
		BTBW	NAWA		
		BWWA	PRWA		
		CACH	TUTI		
		CARW	WEVI		
		CAWA	YBCU		
		CAWR	YEWA		
		COYE	YRWA		
		CSWA			

Appendix III (cont.)

Compositional	Population Limiting	Nest Predator/ Brood Parasite AMCR BHCO BLJA COGR CORA EUST FICR			
Compositional	Origin	Exotic EUST HOFI HOSP RODO			
Compositional	Migratory	Resident	Resident	Temperate Migrant	Temperate Migrant
		AMCR	HOFI	BGGN	HETH
		AMGO	HOLA	ВНСО	HOWR
		AMRO	HOSP	BHVI	PIWA
		BCCH	MODO	BRTH	RHWO
		BLJA	NOCA	CHSP	RWBL
		BRCR	NOFL	COGR	SASP
		CACH	NOMO	COYE	SWSP
		CARW	PIWO	EAME	TRSW
		CEDW	PUFI	EAPH	VESP
		CORA	RBNU	EATO	WEVI
		DEJU	RBWO	FISP	WIWR
		DOWO	RODO	GCKI	WTSP
		EABL	SOSP	GRCA	YBSA
		EUST	TUTI	GRSP	YRWA
		FICR	WBNU	HESP	YTWA
		HAWO			

Compositional	Number of Broods	Single-brooded	Single-brooded	Single-brooded	Single-brooded
		ALFL	CEDW	MAWA	SUTA
		AMCR	CERW	MOWA	TRSW
		AMGO	CHSW	NAWA	TUTI
		AMRE	CLSW	NOFL	VEER
		BAOR	COGR	NOPA	WAVI
		BAWW	CORA	NOWA	WBNU
		BBCU	CSWA	NRWS	WEVI
		ВССН	DOWO	OROR	WEWA
		BGGN	EAKI	OVEN	WIFL
		BHVI	EWPE	PIWA	WIWR
		BNWA	FICR	PIWO	WTSP
		BOBO	GCFL	PRWA	YBCU
		BRCR	GWWA	PUFI	YBSA
		BTBW	HAWO	RBGR	YEWA
		BTNW	HOWA	RBNU	YTVI
		BWWA	KEWA	RBWO	YTWA
		CACH	LEFL	REVI	
		CAWA	LOWA	SCTA	
Structural	Nest Placement	Forest-ground Nester	Open-ground Nester	Shrub Nester	Shrub Nester
		BAWW	BOBO	ALFL	NOMO
		CAWA	BWWA	AMGO	PRWA
		DEJU	EAME	BBCU	REVI
		EATO	FISP	BLGR	RWBL
		HETH	GRSP	BRTH	WEVI
		KEWA	GWWA	BTBW	WIFL
		LOWA	HESP	CHSP	YBCH
		MOWA	HOLA	COYE	YBCU
		NAWA	SASP	CSWA	YEWA
		NOWA	SOSP	GRCA	
		OVEN	SWSP	HOWA	
		VEER	VESP	INBU	
		WEWA		MAWA	
		WTSP		NOCA	

Appendix III (cont.)

Structural	Nest Placement	Canopy Nester	Canopy Nester		
		ACFL	GCKI		
		AMCR	LEFL		
		AMRE	MODO		
		AMRO	NOPA		
		BAOR	OROR		
		BGGN	PIWA		
		BHVI	PUFI		
		BLJA	RBGR		
		BNWA	RTHU		
		BTNW	SCTA		
		CEDW	SUTA		
		CERW	WAVI		
		COGR	WOTH		
		CORA	YRWA		
		EAKI	YTVI		
		EWPE	YTWA		
		FICR			
a			_		
Structural	Primary Habitat	Forest Generalist	Forest Generalist	Interior Forest	Interior Forest
		BBCU	NOFL	Obligate ACFL	Obligate KEWA
		ВССН	NOPA	AMRE	LOWA
		BGGN	PUFI	BAWW	MAWA
		BLJA	RBGR	BHVI	NOWA
		CARW	RBWO	BNWA	OVEN
		COYE	REVI	BRCR	PIWA
		DEJU	SUTA	BTBW	PIWO
		DOWO	TUTI	BTNW	RBNU
		EAPH	WEVI	CAWA	SCTA
		EATO	WOTH	CERW	VEER
		EWPE	YBCU	CORA	WBNU
		GCFL	YBSA	GCKI	WEWA
		CDCA	3/T3/I	TTANA	MANA

 GRCA

NOCA

YTVI

HAWO

HETH

HOWA

WIWR

YRWA

YTWA

Appendix IV. Interpretation of response guilds used in development and application of the Bird Community Index. We include in our discussion of each guild the basis for our treating each guild as a "specialist" or a "generalist." Note that we apply these terms broadly: In the BCI, a specialist can be a species with a narrow range of habitat tolerances, or one that exhibits a low intrinsic rate of population increase. For our purposes, specialist guilds may be thought of as "guilds indicative of a high-integrity condition" while generalist guilds are "guilds indicative of a low-integrity condition." From this group of 24 response guilds, we selected 16 to comprise the BCI. Response guilds marked with an asterisk (*) were removed from direct inclusion in the BCI due to a high degree of correlation with other guilds, or a lack of discernible response along a gradient of human disturbance.

Integrity Element
Guild Category
Response Guild

Functional

Trophic Level

Omnivore: Species that routinely consume both animal and plant material during the breeding season. We ranked omnivores as generalists because of the wide variety of food items available to omnivores .

*Insectivore: Species with breeding season diets restricted to, or largely dominated by, insects and other invertebrates. We consider insectivores to be specialists because of their high trophic position in the ecosystem and the potential for prey availability to be reduced in disturbed environments. We removed this guild from the BCI due to its high correlation with other guilds.

Insectivore Foraging Behavior: We consider all guilds under this guild category to be specialists due to the patchy distribution of their respective primary food source. For example, bark probers rely on a well-developed arthropod community that includes wood-boring species and species that occupy spaces on the bark of trees. Both upper and lower-canopy foragers depend on an abundance of insect prey occupying leaf surfaces. While the guilds in this category might just as easily be considered "structural" in nature, we treat them as "functional" in terms of their relationship to specific pathways of energy flow in the ecosystem. For example, the structural guild "forest-ground nester" indicates the physical condition of the forest floor; while the functional guild "ground gleaner" indicates the degree to which trophic energy flow provides an abundant food source for top predators that forage on the forest floor.

Bark Prober: Species that obtain prey from the bark of tree trunks,

branches, or twigs.

Ground Gleaner: Species that forage for invertebrates at ground level. **Upper-canopy Forager:** Species that forage in the leafy canopy, generally

above 5 m.

Lower-canopy Forager: Species that forage in the leafy canopy, generally

below 5 m.

*Aerial Screener: Species that forage in the air column, by flying with mouth agape to funnel in flying insects. This guild was removed from the BCI because of its ambiguous interpretation along a gradient of human disturbance. For example, chimney swifts and barn swallows, which we consider foraging specialists, nest almost exclusively on man-made structures and are most common in severely-degraded environments.

*Aerial Sallier: Species that fly out from exposed perches to snatch flying insects, and then often return to the same perch. We removed the guild from the BCI due to ambiguous response along a human disturbance gradient. For example, the acadian, least, and great crested flycatchers typical of forested areas are replaced by Eastern phoebes, willow flycatchers, and Eastern kingbirds in more open environments.

Compositional

Migratory

Resident: Species that commonly occur within the Mid-Atlantic Highlands throughout the year. Some of these species, e.g., American robin, may be at least partially migratory within the region. We consider residents to be generalists because they are present in the landscape in which they breed, if not their specific home range, throughout the year. Relative to migrants, we expect resident species to be better able to locate critical resources during times of stress (e.g., ephemeral water sources during drought). Because residents establish breeding territories earlier than migrants and do not have to curtail breeding late in the season to prepare for a lengthy and arduous migration, residents also have more opportunities throughout the breeding season to re-nest after a nesting failure.

Temperate Migrant: Species that winter south of the Mid-Atlantic Highlands, but mainly within temperate North America, i.e., generally north of 30° latitude. We consider temperate migrants to be generalists because, like residents, they enjoy a long potential breeding season relative to tropical migrants. Earlier arrival and later departure dates than tropical migrants should make temperate migrants comparatively better able to cope with breeding season stresses.

*Tropical Migrant: Species that winter primarily within the New World subtropics and tropics, generally south of 30° latitude. We consider tropical migrants to be specialists for several reasons. First, they typically arrive on their breeding grounds later and leave earlier than temperate migrants and residents, leaving less time for tropical migrants to attempt to re-nest following a nesting failure. Second, tropical migrants endure long-distance migrations across inhospitable barriers (e.g., the Gulf of Mexico). Thus, the very nature of their migration poses hazards which temperate migrants and residents do not face. Finally, tropical migrants face impacts on their wintering grounds (e.g., pesticide exposure, critical habitat loss) that may deplete populations below levels that can be sustained by a stressed breeding population. We removed tropical migrants from the BCI due to high correlation with other guilds.

Number of Broods

Single-brooded: Species limited to the production of one brood per breeding season. Some species in this guild may be able to re-nest following an early season nesting failure. We consider single-brooded species to be specialists because their intrinsic rate of population increase is lower than that of multi-brooded species. Thus, single-brooded species are more vulnerable to population level disturbances than are multi-brooded species.

*Multi-Brooded: Species that typically attempt to produce two or more broods per breeding season. We consider multi-brooded species to be generalists relative to single-brooded species because multi-brooded species exhibit a higher intrinsic rate of population increase. Consequently, multi-brooded species should be more resilient to the effects of population level stessors than single-brooded species. We removed this guild from the BCI due to high correlation with other guilds.

Origin

Exotic: Species native to ecosystems other than the Mid-Atlantic Highlands, but introduced and naturalized in the study region through human activities. We consider exotics to be generalists due to their close association with human-dominated environments and their adaptability in surviving and thriving in "new" environments.

Population Limiting

Nest Predator/Brood Parasite: Species whose activities as nest robbers or brood parasites can affect populations of target species. We consider members of this guild to be generalists because of their relatively indiscriminate attacks on the nests of other species.

Structural

Nest Placement

Canopy Nester: Species that nest in the tree canopy, generally above 5 m in height. We consider canopy nesters to be specialists due to the absence of a well-defined canopy in most agricultural and urban environments.

Shrub Nester: Species that nest among herbaceous or woody vegetation, above ground level, but generally below 5 m in height. We consider shrub nesters to be generalists due to the prevalence of a well-developed shrub layer in forested, agricultural, and many urban environments.

*Native Cavity Nester: Species native to the Mid-Atlantic Highlands that nest in natural tree cavities or artificial nest boxes. We consider native cavity nesters to be specialists due to the patchy distribution of suitable nest cavities across the landscape. We removed this guild from the BCI due to ambiguous behavior of the guild across a human disturbance gradient. For example, the woodpeckers typical of forested environments tend to be replaced by Eastern bluebirds and tree swallows in more disturbed environments.

Open-ground Nester: Species that nest at ground level in environments that lack a forest overstory canopy. We specifically selected this guild as a means to help rank bird communities in agricultural .settings. We consider the guild to be specialist due to the guild's dependence on thick herbaceous ground cover in large patch sizes.

Forest-ground Nester: Species that nest at ground level in forested environments. We consider forest-ground nesters to be specialists due to their dependence on appropriate forest floor ground cover and isolation from nest predators.

Primary Habitat

*Grassland: Species that occur primarily in herbaceous old-fields, hayfields, and other prairie-like environments. We consider grassland species to be specialists due to the rarity of their primary habitat type in the study area. We removed this guild from the BCI due to its correlation with other guilds.

*Edge: Species that occur in residential and shrub-dominated environments, or literally within ecotones of two or more habitat types. We consider edge species to be generalists because of the abundance of "edge" habitat in the Mid-Atlantic Highlands. We removed this guild from the BCI due to its correlation with other guilds.

Forest Generalist: Species that occur primarily in forested areas, but use these forests relatively indiscriminately. These species display no obvious trends toward requiring forest interior versus forest edge habitat, and no specific relationship to forest patch size larger than the home range. We consider members of this guild to be generalists due to the abundance of forested terrain in the study area.

Interior Forest Obligate: Species that occur in forest, but tend to partition forest patches and make preferential use of interior forest conditions within a core area of the forest patch. Unlike area sensitive species, which simply require large forest patches, species in the interior forest obligate guild demonstrate an avoidance of forest edge in the patches in which they reside. We consider the species in this guild to be specialists due to their dependence on interior forest conditions within blocks of forest.

Appendix V. Biotic integrity ranks for proportional species richness of guilds at sample sites: the Bird Community Index.

This document provides specific guidelines for application of the Bird Community Index, a multi-metric indicator of ecological condition. The Bird Community Index (i.e., BCI) assigns ranks to the proportional species richness of structural, compositional, and functional songbird response guilds. The ranks determined for 16 separate guilds are compiled to produce an overall BCI score for the individual sampling unit (e.g., a sample site). The overall BCI score places the sampling unit into one of five categories of ecological condition.

A complete explanation of the development and application of the BCI is contained within the technical report, "The Bird Community Index: A Tool for Assessing Biotic Integrity in the Mid-Atlantic Highlands" (report 98-4, Penn State Cooperative Wetlands Center). The authors strongly advise against any application of the BCI without a thorough understanding of the technical report. Please do not reproduce or distribute this document without the expressed permission of the authors. All inquiries pertaining to the BCI should be directed to Tim O'Connell at the Penn State Cooperative Wetlands Center, (814) 863-3194, tjo111@psu.edu.

The BCI was specifically developed as one component of the USEPA's Mid-Atlantic Highlands Assessment. Thus, the ranks that comprise the BCI are specific to the species sampled during fieldwork, the geographic area sampled, and the scale at which the samples were obtained. The authors provide no guarantee that the BCI will behave as predicted if applied to data collected at different scales or from different

geographic regions. Also, the BCI was developed with bird community data on the Passeriformes (perching birds), Columbiformes (pigeons), Cuculiformes (cuckoos), Apodiformes (swifts and hummingbirds), and Piciformes (woodpeckers) only: Any attempt to incorporate species from other orders into the existing BCI will render the index null and void. The species assignments to individual guilds must come only from those in the Appendix of the aforementioned report.

The following table outlines specific ranks applied to various proportions of guilds in the BCI. For example, a bird community in which 20% of the species are ground-gleaning insectivores receives a rank of "5" for the ground-gleaner guild. Ranks for individual guilds range from 1 to 5, with 1 indicating "low" biotic integrity and 5 indicating "high" biotic integrity. (Note, however, that some ranks are split between categories, so that the actual range for an individual guild may be smaller than 1-5, e.g., canopy-nesters range from 1.5 to 4.5.) The BCI score for a sampling unit is simply the sum of the ranks for all 16 guilds. A theoretical "minimum integrity" community would receive a BCI score of 20.5; the theoretical "maximum integrity" score is 77. Further development of the BCI may include an effort to calibrate the index to provide BCI scores between 0 and 1.

guild type	guild	proportion	rank
structural	forest birds	0.000-0.280	4.5
		0.281-1.000	2.5
	interior forest birds	0.000-0.010	1
		0.011-0.080	1.5
		0.081-0.260	3
		0.261-0.430	4
		0.431-1.000	5
	forest ground-nesters	0.000	1
		0.001-0.020	1.5
		0.021-0.160	3
		0.161-0.240	4.5
		0.241-1.000	5
	open ground-nesters	0.000-0.020	1
		0.021-0.110	2.5
		0.111-1.000	5
	shrub-nesters	0.000-0.210	4
		0.211-0.330	1.5
		0.331-1.000	1
	tree canopy-nesters	0.000-0.280	1.5
		0.281-0.320	2
		0.321-1.000	4.5

guild type	guild	proportion	rank
functional	bark-probing insectivores	0.000-0.060	1.5
		0.061-0.110	3
		0.111-0.170	4
		0.171-1.000	5
	ground-gleaning insect.	0.000-0.050	1.5
		0.051-0.070	2
		0.071-0.140	4.5
		0.141-1.000	5
	tree canopy insectivores	0.000-0.030	1.5
		0.031-0.050	2
		0.051-0.120	3
		0.121-0.200	4.5
		0.201-1.000	5
	shrub-gleaning insect.	0.000-0.140	1.5
		0.141-0.230	2.5
		0.231-1.000	5
	omnivores	0.000-0.290	5
		0.291-0.410	4
		0.411-0.480	3
		0.481-0.580	1
		0.581-1.000	2

guild type	guild	proportion	rank
compositional	nest predator/brood parasite	0.000-0.100	5
		0.101-0.150	3.5
		0.151-0.180	2
		0.181-1.000	1
	exotic species	0.000	5
		0.001-0.020	4.5
		0.021-0.050	3
		0.051-0.110	2
		0.111-1.000	1
	residents	0.000-0.260	5
		0.261-0.390	3.5
		0.391-0.570	2
		0.571-1.000	1
	temperate migrants	0.000-0.210	4
		0.211-0.300	2
		0.301-1.000	1
	single-brooded	0.000-0.410	1.5
		0.411-0.450	2

0.451-0.610 3 0.611-0.730 4 0.731-1.000 5

With ranks assigned to each proportion of each guild at a sampling unit, the ranks are summed to arrive at a total BCI score for the sampling unit. BCI scores break out like this:

highest integrity: 60.1-77.0

high integrity: 52.1-60.0

medium integrity: 40.1-52.0

low integrity: 20.0-40.0

To determine if a "low-integrity" sample is a "rural" or "urban" bird community, return to the following guilds:

The bird community is "low-integrity rural" if the total BCI score falls between 20.0 and 40.0, and

>31% of the species are temperate migrants

>28% of the species are shrub-nesters

>8% of the species are open ground-nesters

The bird community is "low-integrity urban" if the total BCI score falls between 20.0 and 40.0, and

- >17% of the species are nest predators/brood parasites
- >11% of the species are exotics
- >56% of the species are residents