BIRD GUILDS AS INDICATORS OF ECOLOGICAL CONDITION IN THE CENTRAL APPALACHIANS

TIMOTHY J. O'CONNELL,1,3 LAURA E. JACKSON,2 AND ROBERT P. BROOKS1

1Penn State Cooperative Wetlands Center, Forest Resources Laboratory, Pennsylvania State University, University Park, Pennsylvania 16802 USA
2U.S. Environmental Protection Agency, Office of Research and Development, Research Triangle Park, North Carolina 27711 USA

Abstract. We developed an index of biotic integrity based on bird communities in the central Appalachians. As one component of the U.S. Environmental Protection Agency, Environmental Monitoring and Assessment Program’s (EPA-EMAP) Mid-Atlantic Highlands Assessment (MAHA), the index is intended to indicate landscape-scale stressors to upland environments in the central Appalachians. The Bird Community Index (BCI) ranks bird communities according to the proportional representation of 16 behavioral and physiological response guilds. We developed the index from 34 sites in central Pennsylvania that represented a gradient of human disturbance from near pristine to degraded. Upon satisfactory demonstration that the BCI could discriminate between categories of biotic integrity identified from the human disturbance gradient, we applied it to an independent, probability-based sample of 126 sites across 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. Sites in poor condition were dominated by either urban or agricultural bird communities, but these communities could not be numerically distinguished from each other by BCI score. Forested sites in good and excellent condition supported different bird communities and ground-level vegetation attributes but could not be separated by land cover composition alone. In general, the shift from medium to poor ecological condition defined by bird communities coincided with a shift in land cover composition from forested to nonforested.

Key words: anthropogenic disturbance; assessment; biotic integrity; bird communities; ecological condition; indicator; landscape; Mid-Atlantic Highlands; response guilds.

INTRODUCTION

The U.S. Environmental Protection Agency’s (EPA’s) Environmental Monitoring and Assessment Program (EMAP) seeks 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 sensitive to a variety of stressors, so that numerous impacts to a resource of concern may be evaluated (Hunsaker and Carpenter 1990, Barber 1994).

To date, EMAP has produced regional reports on ecological condition for forests, streams, and estuaries (e.g., USEPA 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).

We describe the development of a landscape indicator of ecological condition based on bird community composition. Because we sampled random sites across the central Appalachians, our design captured ecologically significant landscape features that contribute to overall ecological condition, but that are often 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 (e.g., forest).

Birds exhibit numerous characteristics that suggest their potential as ecological indicators at large scales. For example, many species’ distributions are affected by habitat fragmentation or other habitat structure parameters (Askins and Philbrick 1987, Freemark and Collins 1992, Murray and Stauffer 1995, Wilson et al. 1995, Schmiegelow et al. 1997). Many birds occupy high trophic levels and may integrate functional disturbance at lower levels (Cody 1981, Sample et al. 1993, Pettersson et al. 1995, Rodewald and James 1996). Bird community composition reflects interspecific dynamics and population trends (Cody 1981). Birds are also attractive as ecological indicators because, relative to other taxa, they can be readily sampled and their taxonomy is well known. Although birds are a focus of societal concern, the purpose of this research is not to report on birds as an assessment
endpoint. Rather, the condition of bird communities across the region is intended to reflect the overall structural, functional, and compositional condition of ecosystems.

Birds, however, are no less likely to exhibit problematic variability in community species composition or abundance estimates than any other taxa. For example, Gibbs and Wenny (1993) examined common survey practices for songbirds, and documented large differences between numbers detected and numbers present. Thus, for use as metrics in a bioindicator, bird data should be grouped at an ecologically relevant higher order of organization (Brooks et al. 1998, Karr and Chu 1999). The Bird Community Index (BCI) is based on 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 the species dependent on that resource. For example, the loss of snags in a forest stand can result in a decrease in a guild of bark-probing insectivores. Croonquist and Brooks (1991) demonstrated that response guilds could produce an effective indicator of habitat disturbance.

The BCI functions like an index of biotic integrity (IBI). 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 (Bradford et al. 1998, Karr and Chu 1999). Biotic integrity refers to the capability of supporting and 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. Thus, a biotic integrity assessment provides a means to estimate condition that, unlike species richness or Shannon diversity, is not confounded by intermediate levels of disturbance as suggested in Brooks et al. (1998), and demonstrated empirically in Blair (1996).

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 1999). A bird community that indicates high integrity, therefore, is dominated by guilds dependent on native system attributes. Our guild-based 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. Because each species simultaneously belongs to several guild categories, we can iteratively analyze bird species data to create a multimetric index. Based on guilds, the index can be calibrated for many different regions and be relevant regardless of species composition.

It is important to recognize that the BCI is intended solely for use in the study area; both the reference high-integrity condition, and the specific guilds used to formulate the index may differ in other regions (e.g., Bradford et al. 1998). Furthermore, the BCI reflects ecological condition at a coarse level of resolution. In the central Appalachians, the most prevalent land cover types are forest, pasture and row crops, residential/commercial areas, and mined lands. In the absence of irreversible anthropogenic disturbance, most of the study region would succeed to the Northern Hardwoods, Appalachian Oak, or Mixed Mesophytic forest types (Bailey 1978).

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 fields or shrublands. These rare habitats, while entirely natural and valuable as conservation priorities, may support bird communities that do not conform to our general definition of high biotic integrity for the region. In addition, other natural events, such as tornados and outbreaks of defoliating insects, may create natural, early-successional conditions over large areas (e.g., thousands of hectares). These areas, however, are relatively small and rare compared to the land area of the central Appalachians. Rather than suppress our estimate of regional ecological condition, the presence of natural, early-successional communities within the study region indicates that the scale at which we make our assessment is large enough to incorporate natural disturbance regimes. Key to understanding the utility of the BCI is that it is a tool applied at individual sample sites, but the resulting assessment of ecological condition takes place at the regional scale.

Our specific research objectives were to: (1) develop an index of biotic integrity based on bird community composition, (2) apply the index to a probability-based sample of sites to produce an assessment of regional ecological condition, (3) verify the index with independent land cover data from the probability-based sample locations, and (4) determine the combination of landscape configuration and ground-level vegetation variables that are associated with different levels of biotic integrity.

**METHODS**

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. These sites had been ordered on a gradient of ecological condition based on an a priori analysis of multiple system attributes (Brooks et al. 1996). We selected these sites of known condition to serve as examples of baseline bird communities in different states of biotic integrity. A BCI developed with data collected from this
reference gradient allowed comparison between our bird-community-based assessment of biotic integrity, and an independent assessment of the same sites based on multiple environmental variables.

In 1995 and 1996, we expanded our sampling to the entire Mid-Atlantic Highlands Assessment (MAHA) area (Fig. 1). The MAHA area encompasses ≈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, comprised independent, blocked random samples from the EMAP probability-based sampling grid (Overton et al. 1990). The blocked random site selection from this grid permitted samples from subsequent years to be combined while preserving the spatial distribution of sites across the region. No site was sampled in both 1995 and 1996. The sampling design was intended to capture a “snapshot” of bird species assemblages across the study region. The probability-based design permitted an estimate of ecological 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).

Sample sites from the central Pennsylvania reference gradient consisted of a variable number of plots (3–11) placed every 50–200 m along a transect of up to 2 km. Each probability-based sample site from the MAHA area consisted of five plots spaced every 200 m along a randomly oriented 1-km transect. We decided to use 1-km transects for the probability-based samples to ensure that the area sampled was larger than any individual bird’s breeding territory, but small enough for the entire site to be potentially contained within a single land cover type. At the 1-km transect length, our probability-based sites included ≈61 sites wholly contained within either urban, agricultural, mining, or forested land cover types, as well as sites incorporating ecotones between these cover types. This sampling scale maximized the degree to which randomly selected sites from the MAHA area would reflect the full spectrum of landscape scale stressors relevant to breeding birds.

At each plot along a transect, we sampled birds with a 10-min, unlimited-radius point count between sunrise and 1000 Eastern Daylight Time (Hutto et al. 1986, Manuwal and Carey 1991, Ralph et al. 1993). 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 also sampled a suite of vegetation variables to characterize ground-level 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°. In these subplots, we also recorded the percentage cover of shrubs from 0.00–0.50 m, 0.51–2.00 m, and 2.01–5.00 m, as well as the percentage canopy cover of overstory trees. Recording shrub data in three vertical strata allowed us to analyze relationships among the strata individually, as well as compiling data from the strata to examine total shrub cover. All estimates of percentage cover were made via ocular estimation with direct comparison to a percent-
an angle gauge to conduct a plotless sample of trees
age cover template design. From plot center, we used
an angle gauge to conduct a plotless sample of trees
>10-cm dbh (Stoddard and Stoddard 1987). All live
trees were identified to species, and the dbh was re-
corded for trees and snags. In addition, at each plot,
we recorded canopy height, slope, and aspect, and as-
signed an Anderson Land Use Code (Anderson et al.
1976). We used a clinometer to estimate canopy height
and percentage slope.

Because we relied on multiple observers to collect
data in the field, we conducted training sessions for all
observers prior to the field season. All observers dem-
onstrated at least 90% agreement in assessments of
percent cover, tree heights, slope measurements, au-
ditory bird species identification, and abundance of
bird species before any data were collected.

To characterize the local landscape configuration, we
obtained aerial photographs of the circular area bi-
sected by each transect. For the MAHA area sample,
this resulted in 126 circular sites (i.e., “landscape cir-
cles”) of 0.5 km radius covering an area of ≈79 ha
each. We examined the photographs, and digitized
polygons of seven cover types into a Geographic In-
formation System (GIS) with a modified version of the
spatial analysis software package, SPAN (Miller et al.
1997). We digitized polygons of forest, woody shrubs,
open water, herbaceous wetland, barren land, residen-
tial/commercial development, and agricultural/herba-
ceous land. SPAN provides data on landscape diversity,
dominance, contagion, and length of edge between land
cover types, as well as the areal extent of cover types.
In addition to these remotely sensed vegetation attrib-
utes, we recorded the maximum elevation (in meters
above sea level), and geographic latitude of each site
from USGS topographic maps. We included elevation,
and the product of elevation and latitude, in our anal-
yses as site-level indices of growing season length.

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

### Response guilds

We built the BCI with data on all the Passeriformes
(perching birds), Piciformes (woodpeckers), Cuculi-
formes (cuckoos), Apodiformes (swifts and humming-
birds), and Columbiformes (doves) that we documented
in the MAHA area from 1994 to 1996 (112 total spe-
cies). We assigned birds to 32 behavioral and physi-
ological response guilds based on a literature review
(Harrison 1975, Blake 1983, DeGraaf et al. 1985, Rob-
erts 1987, Brooks and Croonquist 1990, Freemark and
Collins 1992, Santner et al. 1992). Table 1 lists the 16
guilds in eight guild categories ultimately included in
the BCI. We considered several factors (e.g., high cor-
relation with other guilds, predictable response to land
cover change) in determining the final list of guilds to
be included in BCI development.

Because we selected guilds specifically to reflect dif-
ferent aspects of each species’ life history traits, spe-
cies simultaneously belong to several guilds. Guild as-
signments within each of the eight guild categories,
however, are mutually exclusive, so species belong to
no more than eight guilds. For example, in the Migrat-
tory category, we classified species as either residents
or temperate migrants (we excluded tropical migrants
for statistical reasons) (Table 1). Also, guild assign-
ments apply only to breeding season life history traits.

### Table 1. Biotic integrity elements, guild categories, response guilds, and guild interpretations used in the Bird Community
Index (BCI).

<table>
<thead>
<tr>
<th>Functional element</th>
<th>Guild category</th>
<th>Response guild</th>
<th>Specialist</th>
<th>Generalist</th>
</tr>
</thead>
<tbody>
<tr>
<td>trophic</td>
<td>insectivore foraging behavior</td>
<td>omnivore</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>insectivore foraging behavior</td>
<td>bark prober</td>
<td>ground gleaner</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>insectivore foraging behavior</td>
<td>upper canopy forager</td>
<td>lower canopy forager</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Functional</td>
<td>origin</td>
<td>exotic</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>migratory</td>
<td>migratory</td>
<td>temperate migrant</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Compositional</td>
<td>migratory</td>
<td>resident</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Compositional</td>
<td>number of broods</td>
<td>single-brooded</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Compositional</td>
<td>population limiting</td>
<td>nest predator/brood parasite</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Structural</td>
<td>nest placement</td>
<td>canopy nester</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Structural</td>
<td>nest placement</td>
<td>shrub nester</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Structural</td>
<td>nest placement</td>
<td>open-ground nester</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Structural</td>
<td>nest placement</td>
<td>forest-ground nester</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Structural</td>
<td>primary habitat</td>
<td>forest generalist</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Structural</td>
<td>primary habitat</td>
<td>interior forest obligate</td>
<td>X</td>
<td></td>
</tr>
</tbody>
</table>

We also analyzed landscape configuration with an aero-
rial view of the entire 79-ha site. We intend that the
BCI assessment be applied at the ecoregional scale,
which, in the case of the Mid-Atlantic Highlands, in-
cludes an area of >150 000 km².
For example, we consider the Eastern Kingbird (Tyr
annus tyrannus) to be an insectivore, even though this
species subsists largely on fruit in its wintering range
(Terborgh 1989).

We made all guild assignments specific to the MAHA
area because many species exhibit plasticity in certain
life history traits across their breeding range. For ex-
ample, American Robins (Turdus migratorius) behave
as temperate migrants in the New England states, where
they breed during spring and summer, but are largely
absent during winter. In contrast, robins regularly win-
ter in the mid-Atlantic states (Santner et al. 1992), and
we consider them to be residents for the purpose of our
study. We recognize variability in the expression of life
history traits within the MAHA area, but our guild
assignments are intended to represent the typical be-
behavior of the species in our study.

We categorized individual guilds as “specialist” or
“generalist” based on each guild’s relationship to spe-
cific 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). In our study, obligate
tree-canopy nesters (specialists) indicate high integrity
because they are largely restricted to mature forests
native to the region, while shrub nesters (generalists)
also encounter appropriate nesting substrate in regener-
ating forests, agricultural hedgerows, and suburban
areas (Brauning 1992). The Trophic category reflects
aspects of ecosystem function: Obligate insectivores
are limited to areas of high insect availability (e.g.,
Prosser and Brooks 1998), while omnivores can exploit
the range of food resources found in varied habitats.
Thus, we consider omnivores to be generalists relative
to insectivores. Ecosystem composition reflects organ-
ization induced by factors other than structure and
function (e.g., interspecific dynamics). For example,
species in the nest predator/brood parasite guild can
affect the abundance and distribution of other species.
We consider nest predators and brood parasites to be
generalists due to their relatively indiscriminate ex-
plotation of other species as sources of food or sur-
rrogate parents. Perhaps as a consequence of the nest
preda$on and brood parasitism, many single-brooded
species (specialists) are restricted to large patches that
are relatively free from nest predators and brood par-
sites that concentrate around habitat edges (Freemark

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 gener-
alist guilds simultaneously. For example, the Downy
Woodpecker (Picoides pubescens) is a generalist ac-
gording to Primary Habitat and Migratory status, but
a specialist according to its membership in four other
guild categories (e.g., bark prober).

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 0.20 for the single-
brooded guild. We grouped sites according to their simi-
arity in bird community profiles through cluster anal-
ysis, and conrmed 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 ecological condition for the 34
sites we sampled in 1994. While all reference sites
encompassed a land area of >300 ha, each site was
centered on a small (<15-ha) wetland to maximize the
number of biotic and abiotic indicators that could be
applied to rank the sites on a gradient of condition.
The gradient assignments we applied to sites were the
primary means to test the independent ranking of biotic
integrity based solely on each site’s bird guild com-
position.

Brooks et al. (1996) examined the sediment depo-
sition, soil properties, plant community, amphibian
community, a Wildlife Community Habitat Proile
(WCHP), and general landscape context of the refer-
ence sites and ranked them on a three-category scale
of human disturbance from pristine to moderately dis-
turbed to severely disturbed. Ranks were assigned
based on best professional judgment of the field biol-
gists familiar with the sites once all required pieces
of data had been collected. Relative to disturbed sites,
pristine sites had lower rates of sediment deposition,
and the soils contained a larger ratio of organic to min-
eral material. Plant communities exhibited higher
Shannon diversity indices, and were dominated by sed-
iment-intolerant species at pristine sites. The amphib-
ian community exhibited slightly higher species rich-
ness, and was dominated by disturbance-intolerant spe-
cies (e.g., wood frog [Rana sylvatica]) at the pristine
sites. Habitat suitability indices for the WCHP aver-
aged higher at pristine sites for species that occur in
mature forested wetlands (e.g., wood frog, Wood Duck
[Aix sponsa], and southern red-backed vole [Cleth-
ritionomys gapperi]). Finally, the pristine sites exhibited
larger areas of contiguous, mature forest than the mod-
erately or severely disturbed sites (Brooks et al. 1996,
Cole et al. 1997, Wardrop and Brooks 1998; Penn State
Cooperative Wetlands Center unpublished data).

With a gradient of human disturbance established for
the 1994 reference sites, we next developed an inde-
pendent ranking of the same sites using only bird com-
unity data. We applied cluster analysis (complete
linkage, squared Euclidean distance) to identify cate-
gories of sites with similar bird community profiles.
We intentionally identied three categories of bird
community profiles to facilitate comparisons with the
human disturbance gradient. We used one-way ANO-
VA 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 low biotic integrity, 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 receive a rank of “3” for every guild.

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 Spearman rank correlation coefficients and one-way ANOVA. The ANOVAs took the form of establishing statistical significance among categories of variables defined through analysis of independent data sources. For example, to determine if BCI scores of the three categories identified through cluster analysis of bird community profiles from the 34 reference sites were separable by category, we applied ANOVA to BCI scores using category codes as the factor levels in the ANOVA model. As another means to establish the strength of association between the independent BCI gradient and the a priori human disturbance gradient applied to the same sites, we applied ANOVA again, and simply substituted category codes from the human disturbance gradient as the ANOVA factor levels. We applied this same technique to land cover data from the 1994 reference sites, and to the bird and land cover data collected from the probability based sites.

Prior to analyses, we tested all variables (e.g., guild proportions, vegetation data, and landscape data) 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). We conducted all statistical analyses 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 determined 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 (i.e., different bird communities). 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.

**BCI verification and land cover analyses**

Verification is the process by which a model’s ability to indicate the system attributes for which it was designed is tested on an independent sample of sites (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. As an alternative to model validation, which would involve measurements of all variables used to construct the human disturbance gradient on the independent sample of sites, verification necessitates only that the new sample of sites be independently ranked by some method that correlates with the human disturbance gradient criteria.

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 used 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). (In this case,
only Ward’s linkage yielded a clear three-category cluster that was essential to examine the correlation between the landscape and human disturbance gradients.) 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 Spearman rank 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 ($r = 0.825$). Contagion was significantly lower at pristine sites relative to moderately and severely disturbed sites ($F_{2,33} = 8.43, P = 0.001$); although contagion could not separate sites in the two disturbed categories from one another. Percentage of forest differed significantly among the sites in all three categories ($F_{2,33} = 53.28, P < 0.001$), with the pristine sites supporting the most forest. Thus, the landscape configuration of each site could serve as a reliable proxy for the information contained in the human disturbance gradient. Therefore, we applied the landscape disturbance-ranking scheme to the 126 probability-based sites we sampled in 1995 and 1996. As with the 1994 reference data, we clustered the sites (complete linkage, squared Euclidean distance) into categories according to percentage of forest and contagion. We then ordered the clusters along a landscape disturbance gradient, ranking high-percentage forest and low relative contagion as indicators of low landscape disturbance. To gauge the strength of the similarity between independent rankings of the same sites by BCI and landscape disturbance as the test for model verification, we applied Spearman rank correlation and a $t$ test for pairwise differences in ranks. 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 ecological condition.

To identify land cover configurations typical of sites with similar bird communities, we applied one-way ANOVA with Tukey’s multiple comparisons procedure ($\alpha = 0.05$) to the SPAN-generated land cover variables. We used the specific bird community profiles identified from cluster analysis as factor levels in the ANOVA model. We also used best subsets multiple regression to explore the relationship between BCI score and 24 landscape and ground-level vegetation variables summarized for each site. We used multiple criteria (i.e., uncorrelated predictor variables, high adjusted $r^2$ value, small error variance terms) to make our decision on the regression model that provided the best fit to the data.

**Results**

**BCI development**

Brooks et al. (1996) identified three categories of human disturbance at the 34 reference gradient sites we sampled in 1994. Fourteen sites were classified as pristine, 10 were moderately disturbed, and 10 were severely disturbed. Independently derived BCI scores determined for the 1994 reference sites classified bird communities at 9 sites as high integrity, 12 sites as medium integrity, and 13 as low integrity ($r = 0.831$ human disturbance $\times$ BCI).

Under the BCI gradient, sites with high-integrity bird communities exhibited significantly higher functional ($F_{2,33} = 33.02, P < 0.001$), compositional ($F_{2,33} = 32.54, P < 0.001$), structural ($F_{2,33} = 27.16, P = 0.003$), and overall BCI scores ($F_{2,33} = 47.88, P < 0.001$) 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 (i.e., Tukey 95% CIs did not include zero). The difference between the structural integrity scores of medium- and low-integrity sites was not significant (Tukey 95% CI = $-1.523, 0.703$). Table 2 lists the mean proportional species richness of all 16 guilds among three levels of biotic integrity.

Likewise, bird community profiles of the BCI show significant differences among the three classes of the human disturbance gradient. pristine sites contained significantly higher functional ($F_{2,33} = 37.18, P < 0.001$), compositional ($F_{2,33} = 22.37, P < 0.001$), structural ($F_{2,33} = 16.31, P < 0.001$), and overall BCI scores ($F_{2,33} = 38.82, P < 0.001$) than moderately or severely disturbed sites. Moderately disturbed sites contained significantly higher functional scores than severely disturbed sites, but differences between compositional (Tukey 95% CI = $-2.846, 0.246$), structural (Tukey 95% CI = $-1.640, 1.240$), and overall BCI scores (Tukey 95% CI = $-7.310, 0.110$) were not significant.

The BCI also highlighted landscape disturbance differences among sites in different categories of biotic integrity. High-integrity sites contained significantly lower contagion ($F_{2,33} = 13.03, P < 0.001$), higher percentage forest ($F_{2,33} = 106.93, P < 0.001$), and larger mean forest patch size ($F_{2,33} = 19.19, P < 0.001$), 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% CI = $-1.926, 2.026$). The landscape disturbance and BCI gradients applied to the 1994 reference sites were highly correlated ($r = 0.938$ landscape disturbance $\times$ BCI).

**BCI application**

A cluster analysis of bird community profiles of 16 guilds at the 126 probability-based sample locations across the entire MAHA area yielded five distinct clus-
TABLE 2. Proportion (mean ± 1 SE) of total species in each guild in each of the three biotic integrity categories determined by the Bird Community Index (BCI) at the 34 reference sites.

<table>
<thead>
<tr>
<th>Response guild</th>
<th>High integrity (n = 9, rank = 3)</th>
<th>Medium integrity (n = 12, rank = 2)</th>
<th>Low integrity (n = 15, rank = 1)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Omnivore</td>
<td>0.30 ± 0.02^a</td>
<td>0.47 ± 0.02^a</td>
<td>0.57 ± 0.02^a</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bark prober</td>
<td>0.12 ± 0.02^a</td>
<td>0.08 ± 0.01^a</td>
<td>0.03 ± 0.01^a</td>
<td>0.001</td>
</tr>
<tr>
<td>Ground gleaner</td>
<td>0.10 ± 0.01^a</td>
<td>0.05 ± 0.01^b</td>
<td>0.03 ± 0.01^b</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Upper-canopy forager</td>
<td>0.13 ± 0.01^a</td>
<td>0.08 ± 0.01^b</td>
<td>0.06 ± 0.01^b</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Lower-canopy forager</td>
<td>0.23 ± 0.02^a</td>
<td>0.19 ± 0.01^a</td>
<td>0.13 ± 0.02^b</td>
<td>0.002</td>
</tr>
<tr>
<td>Nest predator/brood parasite</td>
<td>0.09 ± 0.01^a</td>
<td>0.14 ± 0.01^a</td>
<td>0.14 ± 0.02^a</td>
<td>0.024</td>
</tr>
<tr>
<td>Exotic</td>
<td>0.00 ± 0.00^a</td>
<td>0.02 ± 0.01^a</td>
<td>0.06 ± 0.02^a</td>
<td>0.020</td>
</tr>
<tr>
<td>Resident</td>
<td>0.29 ± 0.02^a</td>
<td>0.40 ± 0.02^a</td>
<td>0.40 ± 0.02^a</td>
<td>0.004</td>
</tr>
<tr>
<td>Temperate migrant</td>
<td>0.22 ± 0.02^a</td>
<td>0.24 ± 0.01^a</td>
<td>0.32 ± 0.01^b</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Single-brooded</td>
<td>0.70 ± 0.03^a</td>
<td>0.56 ± 0.02^a</td>
<td>0.41 ± 0.02^a</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Canopy nester</td>
<td>0.36 ± 0.02^a</td>
<td>0.32 ± 0.02^a</td>
<td>0.27 ± 0.01^b</td>
<td>0.003</td>
</tr>
<tr>
<td>Shrub nester</td>
<td>0.20 ± 0.02^a</td>
<td>0.29 ± 0.02^a</td>
<td>0.32 ± 0.02^b</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Open-ground nester</td>
<td>0.01 ± 0.01^a</td>
<td>0.06 ± 0.01^b</td>
<td>0.10 ± 0.01^c</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Forest-ground nester</td>
<td>0.22 ± 0.01^a</td>
<td>0.08 ± 0.01^b</td>
<td>0.03 ± 0.01^c</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Forest generalist</td>
<td>0.36 ± 0.02^a</td>
<td>0.44 ± 0.02^a</td>
<td>0.31 ± 0.02^a</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interior forest obligate</td>
<td>0.43 ± 0.02^a</td>
<td>0.15 ± 0.02^a</td>
<td>0.05 ± 0.02^a</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Notes: 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.

ters of sites with a mean within-cluster sum of squares of 1.28 (Fig. 2). We interpret these clusters as five distinct bird community types, based on the relative proportions of the various guilds represented in the species that occur at the sites in each cluster. We ranked clusters according to the relative proportions of specialist and generalist guilds at the sites in each cluster. The ranking scheme, however, produced only four distinct categories of BCI scores among the five community types. According to our bird-community-based criteria for defining biotic integrity, ~16 ± 5.5% of the MAHA area supports the highest integrity communities, 27 ± 6.8% is high-integrity, 36 ± 7.3% is medium-integrity, and 21% of the MAHA area supports two separate categories of low-integrity bird communities (i.e., “low 1” = 16 ± 5.5% and “low 2” = 5 ± 3.4%) (Fig. 3). Raw BCI scores ranged from 26.5 to 68.5, with the following ranges of scores in each category: highest integrity >60.1, high integrity 52.1–60.0, medium integrity 40.1–52.0, and low integrity <40.0. Theoretical minimum and maximum BCI scores are 20.0 and 77.0, respectively.

Table 3 lists the mean proportional species richness of all 16 guilds 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 low 1- and low 2-integrity categories, sites in the...
high- and highest integrity categories exhibited higher functional ($F_{4, 125} = 102.27, P < 0.001$), compositional ($F_{4, 125} = 58.94, P < 0.001$), structural ($F_{4, 125} = 21.73, P < 0.001$), and overall BCI scores ($F_{4, 125} = 129.09, P < 0.001$).

The low 2- and low 1-integrity categories could not be separated by functional (Tukey 95% CI $= -3.450, 2.450$), compositional (Tukey 95% CI $= -4.495, 2.762$), structural (Tukey 95% CI $= -4.945, 1.495$), or overall BCI scores (Tukey 95% CI $= -9.400, 3.217$). We found, however, 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, compositional, and overall BCI scores (Tukey 95% CIs do not include zero). Structural guild scores can separate only the highest and high-integrity categories from the three lower integrity categories (Tukey 95% CIs do not include zero).

### BCI verification

The landscape disturbance gradient we developed using the 1994 reference data classified sites as undisturbed, moderately disturbed, and disturbed. Under the landscape disturbance gradient, undisturbed sites contained significantly higher percentage forest ($F_{2, 33} = 216.61, P < 0.001$), mean forest patch size ($F_{2, 33} = 36.08, P < 0.001$), and contagion ($F_{2, 33} = 17.52, P < 0.001$) 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% CI 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 ($F_{2, 33} = 43.61, P < 0.001$), compositional ($F_{2, 33} = 41.52, P < 0.001$), structural ($F_{2, 33} = 20.11, P < 0.001$), and overall BCI scores ($F_{2, 33} = 59.84, P < 0.001$) than either the moderately disturbed or disturbed sites. Moderately disturbed sites exhibited significantly higher functional and compositional scores than disturbed sites, but differences between the structural guild ranks were not significant (Tukey 95% CI $= -2.168, 0.285$).

To verify the BCI on the independent sample of probability-based sites from the entire MAHA area, we developed a landscape disturbance gradient for the 126 sample sites. The Spearman rank correlation between

---

### Table 3. Mean proportion (± 1 se) of the total species in each guild in each of five BCI biotic integrity categories at the 126 MAHA area sample sites.

<table>
<thead>
<tr>
<th>Response guild</th>
<th>Highest (n = 20)</th>
<th>High (n = 34)</th>
<th>Medium (n = 46)</th>
<th>Low 1 (n = 20)</th>
<th>Low 2 (n = 6)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Omnivore</td>
<td>0.24 ± 0.01a</td>
<td>0.37 ± 0.01c</td>
<td>0.45 ± 0.01c</td>
<td>0.61 ± 0.01d</td>
<td>0.53 ± 0.00d</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bark prober</td>
<td>0.17 ± 0.01a</td>
<td>0.11 ± 0.01b</td>
<td>0.08 ± 0.01d</td>
<td>0.03 ± 0.01e</td>
<td>0.03 ± 0.01e</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Ground gleanser</td>
<td>0.12 ± 0.01a</td>
<td>0.10 ± 0.01c</td>
<td>0.06 ± 0.01c</td>
<td>0.03 ± 0.00e</td>
<td>0.03 ± 0.00e</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Upper-canopy forager</td>
<td>0.18 ± 0.01a</td>
<td>0.15 ± 0.01c</td>
<td>0.10 ± 0.01c</td>
<td>0.04 ± 0.01c</td>
<td>0.01 ± 0.01c</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Lower-canopy forager</td>
<td>0.21 ± 0.01a</td>
<td>0.17 ± 0.01c</td>
<td>0.17 ± 0.01c</td>
<td>0.12 ± 0.01c</td>
<td>0.14 ± 0.02c</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Nest predator/brood</td>
<td>0.07 ± 0.01a</td>
<td>0.11 ± 0.01b</td>
<td>0.10 ± 0.01b</td>
<td>0.16 ± 0.01c</td>
<td>0.21 ± 0.02d</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Exotic</td>
<td>0.00 ± 0.00c</td>
<td>0.00 ± 0.00c</td>
<td>0.02 ± 0.00c</td>
<td>0.07 ± 0.01c</td>
<td>0.16 ± 0.03d</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Resident</td>
<td>0.28 ± 0.02a</td>
<td>0.34 ± 0.01c</td>
<td>0.35 ± 0.01c</td>
<td>0.42 ± 0.02c</td>
<td>0.69 ± 0.03d</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temperate migrant</td>
<td>0.16 ± 0.02a</td>
<td>0.18 ± 0.01c</td>
<td>0.26 ± 0.01c</td>
<td>0.36 ± 0.01c</td>
<td>0.19 ± 0.01b</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Single-brooded</td>
<td>0.74 ± 0.01c</td>
<td>0.68 ± 0.01b</td>
<td>0.53 ± 0.01c</td>
<td>0.35 ± 0.01d</td>
<td>0.38 ± 0.05d</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Canopy nester</td>
<td>0.37 ± 0.02a</td>
<td>0.37 ± 0.01c</td>
<td>0.30 ± 0.01c</td>
<td>0.25 ± 0.01c</td>
<td>0.29 ± 0.01c</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Shrub nester</td>
<td>0.19 ± 0.01c</td>
<td>0.22 ± 0.01c</td>
<td>0.27 ± 0.01c</td>
<td>0.29 ± 0.01c</td>
<td>0.19 ± 0.04c</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Open-ground nester</td>
<td>0.01 ± 0.00a</td>
<td>0.02 ± 0.01c</td>
<td>0.07 ± 0.01c</td>
<td>0.13 ± 0.01d</td>
<td>0.06 ± 0.01c</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Forest-ground nester</td>
<td>0.21 ± 0.01c</td>
<td>0.18 ± 0.01c</td>
<td>0.09 ± 0.01c</td>
<td>0.03 ± 0.01c</td>
<td>0.00 ± 0.00d</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Forest generalist</td>
<td>0.35 ± 0.01c</td>
<td>0.38 ± 0.01c</td>
<td>0.37 ± 0.01c</td>
<td>0.27 ± 0.02c</td>
<td>0.30 ± 0.02d</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interior forest obligate</td>
<td>0.49 ± 0.01a</td>
<td>0.36 ± 0.01b</td>
<td>0.17 ± 0.01c</td>
<td>0.06 ± 0.01d</td>
<td>0.05 ± 0.01d</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

*Note: Within rows, superscript letters indicate significant differences at $P < 0.05$ (one-way ANOVA, df = 4, 125, Tukey’s multiple comparisons).*
Within rows, values with different superscripts are significantly different at \( P < 0.001 \). Medium-integrity sites exhibit roughly equivalent proportions of forested and nonforested cover, and differ in this regard from sites in all other categories \( F = 63.38, P < 0.001 \). Sites in the high- and highest integrity categories cannot be separated by any of the landscape variables (see Table 4) interpreted from aerial photographs (all pairwise Tukey 95% CIs include zero). The high- and highest integrity categories, which differ significantly according to BCI, can be separated only by ground-level vegetation variables. The highest integrity sites contain significantly higher mean canopy height (Tukey 95% CI = \(-0.254\)) and greater mean canopy cover (Tukey 95% CI = \(-0.254\)) and greater mean canopy cover (Tukey 95% CI = \(-0.254\)). Example landscape circles from sites in each BCI category are illustrated in Fig. 5.

The best subsets multiple regression of BCI score (dependent variable) on landscape and ground-level variables (independent variables) indicated a four-variable model as the best fit to the data. Total BCI score is best predicted by the equation:

\[
\text{BCI score} = 30.200 + 20.400 \times \text{percentage forested land} - 10.100 \times \text{landscape diversity} + 0.326 \times \text{mean canopy height} + 12.900 \times \text{mean slope}
\]

with \( n = 122 \), \( r^2 = 0.830 \), \( F = 142.980 \), \( P < 0.001 \).

**DISCUSSION**

**Summary of major findings**

We successfully developed an indicator of biotic integrity based on bird communities, applied the indi-

Table 4. Landscape and ground-level land cover variables (mean ± 1 se) in each of five biotic integrity categories identified in the MAHA area with the BCI.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Highest (n = 20)</th>
<th>High (n = 34)</th>
<th>Medium (n = 46)</th>
<th>Low 1 (n = 20)</th>
<th>Low 2 (n = 6)</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Landscape variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diversity</td>
<td>0.08 ± 0.02*</td>
<td>0.13 ± 0.02*</td>
<td>0.34 ± 0.02*</td>
<td>0.33 ± 0.03*</td>
<td>0.40 ± 0.06*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Dominance</td>
<td>0.20 ± 0.04</td>
<td>0.22 ± 0.03</td>
<td>0.27 ± 0.02</td>
<td>0.27 ± 0.02</td>
<td>0.29 ± 0.06</td>
<td>0.275</td>
</tr>
<tr>
<td>Contagion</td>
<td>1.61 ± 0.46*</td>
<td>1.88 ± 0.28*</td>
<td>4.28 ± 0.24*</td>
<td>4.09 ± 0.26*</td>
<td>5.58 ± 0.70*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Residential/commercial (%)</td>
<td>1 ± 1*</td>
<td>1 ± 0*</td>
<td>4 ± 1*</td>
<td>3 ± 1*</td>
<td>43 ± 14*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Herbaceous/agricultural (%)</td>
<td>1 ± 1*</td>
<td>5 ± 2*</td>
<td>31 ± 4*</td>
<td>66 ± 5*</td>
<td>29 ± 14*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Woody shrub (%)</td>
<td>4 ± 2</td>
<td>3 ± 1</td>
<td>6 ± 2</td>
<td>3 ± 1</td>
<td>2 ± 1</td>
<td>0.290</td>
</tr>
<tr>
<td>Forested (%)</td>
<td>94 ± 2*</td>
<td>89 ± 2*</td>
<td>57 ± 4*</td>
<td>25 ± 3*</td>
<td>21 ± 5*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Forest edge (m)</td>
<td>1313 ± 337*</td>
<td>2108 ± 323*</td>
<td>4864 ± 295*</td>
<td>4706 ± 565*</td>
<td>6589 ± 612*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Maximum elevation (m)</td>
<td>628 ± 45*</td>
<td>641 ± 45*</td>
<td>505 ± 27*</td>
<td>440 ± 53*</td>
<td>261 ± 44*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Ground-level variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope (%)</td>
<td>29 ± 4*</td>
<td>23 ± 2*</td>
<td>16 ± 1*</td>
<td>9 ± 1*</td>
<td>7 ± 3*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Basal area m(^2)/ha</td>
<td>47.2 ± 2.8*</td>
<td>38.3 ± 2.9*</td>
<td>24.2 ± 2.5*</td>
<td>7.6 ± 1.5*</td>
<td>13.6 ± 4.3*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>61 ± 3*</td>
<td>47 ± 3*</td>
<td>33 ± 3*</td>
<td>11 ± 3*</td>
<td>21 ± 4*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Canopy height (m)</td>
<td>23.8 ± 1.0*</td>
<td>19.7 ± 0.7*</td>
<td>15.2 ± 0.8*</td>
<td>8.0 ± 1.4*</td>
<td>14.5 ± 2.0*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Shrub cover (%)</td>
<td>58 ± 8*</td>
<td>57 ± 5*</td>
<td>36 ± 3*</td>
<td>18 ± 5*</td>
<td>16 ± 5*</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Notes: 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 \( P < 0.05 \).
cator to a random sample of sites to assess ecological condition over a large region, and gauged the ability of our indicator to convey information on ecological condition across the sample region. General results of the research include:

1) Independent assessments of site condition via multiple biological and land cover attributes agree well with BCI scores.

2) Five distinct bird community types occur in the Mid-Atlantic Highlands.

3) The five bird community types in the MAHA area comprise four categories of biotic integrity; the lowest integrity condition is associated with either urban or agricultural bird communities.

4) BCI scores are positively associated with the percentage of forest cover at the landscape scale, but remotely sensed land cover data alone are insufficient to effectively model bird community composition or overall biotic integrity.

**BCI development**

The methods we employed to develop the BCI differ from those used to produce IBIs in other systems. For example, Karr and Chu (1999) make an a priori decision as to the conditions that constitute biological integrity, and then test the response of potential metrics against a gradient that tracks deviation away from the condition of greatest integrity. This approach is straightforward, and is of great utility in systems in which the stressors and desirable condition are readily identified. For example, the presence of chemical pollutants or excess sedimentation in headwater streams is clear evidence of the stressors affecting the resource, and a high-integrity condition indicating the absence of these stressors is unambiguously desirable. In our study, incorporating a heterogeneous ecoregion comprising several physiographic provinces and landscape types, a more insidious stressor (i.e., land cover disturbance) operates. While we assumed that forested areas would ultimately rank higher on an integrity scale than urban areas, we made no a priori attempt to define the most forested areas as necessarily “the best.” Rather, we made decisions regarding which metrics exhibited ecologically desirable traits, and then determined the combination of habitat variables that supported those metrics.

The first phase of this research revealed that BCI scores were significantly correlated with the known ecological condition of the 1994 reference sites. Response guilds proved useful, not only in orderining sites into three categories of biotic integrity, but in demonstrating significantly different biological aspects of the bird community between categories (Table 2). These findings confirm our primary assumption that bird community structure is a valid biological index: It reflects, at a minimum, the selected physical, chemical, and biological aspects of ecological condition 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.

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 structural guilds (canopy nesters and shrub nesters) did not differ between sites in these two categories. In addition, because we ranked low occurrence of forest generalists 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 identified five distinct bird community types. In general, we observed differences in structural, functional, compositional, and total BCI scores among community types. The two community types with the lowest overall BCI scores, however, could not be distinguished 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 an agricultural/herbaceous (i.e., rural) setting, while the latter is typical of residential/commercial (i.e., urban) environments.

We have not determined if it is possible to characterize ecological condition in the MAHA area by a linear gradient of disturbance from pristine to degraded landscapes. Our data indicate that rural and urban land-cover modifications may have different, but equally adverse, effects on biotic integrity at the ecoregional scale. Thus, for the purpose of this assessment, there is no need for the BCI to be able to order one type of altered environment ahead of another on a gradient of biotic integrity.

We recognize, however, scenarios in which an index that can separate and rank various urban and agricultural bird communities relative to each other would be highly desirable. For example, similar assessments in ecoregions dominated by an agricultural matrix would be severely limited if the indicators employed were not able to rank various agricultural land uses on a gradient of ecological structure, function, and composition. This ability in the index becomes crucial when the natural vegetative condition of the matrix, in the absence of anthropogenic disturbance, is grassland rather than for-
Figure 5. SPAN-generated landscape circles of representative sites in each category of biotic integrity determined with the BCI. Note that the landscape configuration of sites supporting the “high” and “highest” integrity communities are statistically identical.

est. Simple substitutions in the metrics that form the index (e.g., “grassland obligates” or relative abundance of individual indicator species), or unequal weightings of various metrics may be sufficient to provide the necessary ordering of disturbed environments.

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 >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 >10% of the species at a site to <5%.

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 <40%. Exotic species increase from 0% of the species in the highest and high-integrity communities to ≈16% of the species in the low-integrity urban communities (e.g., Blair 1996). Nest predators/brood parasites increase from <10% of the species at a site to >20% (e.g., Donovan et al. 1995). Resident species increase from <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 15–20% 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, Cronquist 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 generally decrease down the gradient. Shrub nesters peak at nearly 30% of the species at the medium- and low-integrity rural sites, but are less well represented at either end of the integrity gradient. Open-ground nesters occupy ≈13% of the bird community at the low-integrity rural sites, but <7% at sites in all other cat-
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 ≈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 ≈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% CI for our estimates. Thus, areas supporting the highest integrity bird communities occupy between 10.5% and 21.5% of the MAHA area (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.

**BCI verification**

The human disturbance gradient represented by the 1994 reference sites allowed direct comparison between the BCI assessment of biotic integrity, and an independent assessment 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 bird community composition.

The correlation in site rankings of the 126 MAHA area sites between the independent BCI and landscape disturbance gradients was high, even though the number of categories was higher than that used for the 1994 reference sites (5 vs. 3). The ranks assigned to sites by BCI and landscape disturbance are, in fact, statistically identical, i.e., the sum of the pairwise differences between methods is zero. Furthermore, 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.

**Land cover and ground-level 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 ground-level vegetation characteristics summarized at the site level (Table 4). These findings support our objective to develop a biological indicator for large-scale habitats that contain a mosaic of terrestrial, aquatic, and urban elements. Our results also document a unit size of landscape within which bird communities respond significantly to land cover disturbance.

The relationship between BCI scores and remotely-sensed land cover pattern indicates that high biotic integrity is generally 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 to forest. In addition to forest extent, the BCI also indicated a relationship with ground-level forest structure: While the highest and high-integrity sites identified with the BCI exhibit no significant differences in landscape configuration, 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.

Land cover and ground-level vegetation attributes at medium-integrity sites exhibit several significant shifts away from conditions present at the high- and highest integrity sites. Despite the loss of mature forest relative to the high- and highest 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 ≈37–77% forested at the 79-ha scale. Thus, medium-integrity sites may provide critical habitat needs for forest species in a landscape context approaching a matrix shift from forested to nonforested.

Sites in the two low-integrity categories have undergone matrix shifts from forest to another major land cover type at the 79-ha scale. In neither category do sites typically support >36% forested cover. Low-integrity rural sites are dominated by herbaceous/agricultural cover encompassing ≈57–81% of the land area. Low-integrity urban sites are characterized by a variable mix of forested, agricultural, and residential/commercial cover, with urban conditions typically comprising the matrix at ≈43% 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 cover and the 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 among BCI scores and habitat variables identified a highly significant regression equation for determining total BCI score. We found that total BCI score, and, by association, overall biotic integrity, is best predicted by a four-variable model that consists of landscape-level diversity and percentage forest, and the ground-level attributes canopy height and slope. The importance of 'forest,' both in terms of land cover and size of individual stems, is again apparent. Landscape diversity, which increases with the number of different land cover patches, emerges from the model as a significant negative variable. Mean slope 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. It is important to note that other variables, e.g., landscape contagion and field-measured canopy cover, when combined with percentage of forest, produce significant regression models for predicting BCI score as well. While these variables are not included in the model that best fit our data, their use in prescriptive management may have merit. Our data suggest that a general predictive model for BCI score should incorporate landscape-level forest cover, some measure of the interspersion of nonforest cover types (e.g., contagion or diversity), and some indication of stand maturity (e.g., canopy height or canopy cover).

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 diversity, and slope. Within this population of sites, additional information on canopy height 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 ground-level vegetation variables at which critical shifts in BCI scores, equating to shifts in biotic integrity, occur.

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 in the MAHA area are correlated with land cover 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 land cover change at which shifts in biotic integrity are observed. At the 79-ha scale, both good and excellent ecological condition were associated with an approximate minimum forest cover of 82%. Poor ecological condition was observed when agricultural/herbaceous cover exceeded ≈56%, or residential/commercial cover ex-
ceeded \approx 39\%$. Relative proportions of forested, agricultural/herbaceous, and residential/commercial cover in each BCI category are illustrated in Fig. 6. One interpretation of these results is to consider areas in good ecological condition as desirable to 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, most of the land area in poor ecological condition is justified by societal requirements for agricultural and urban land uses, and does not warrant management actions to increase BCI scores. Community planning efforts may focus instead on those marginal landscapes in 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 biotic integrity at landscape scales. As with any multimetric index, 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, general 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 only be required intermittently to confirm that chemical pollution or other large-scale disturbances that this study did not address had not affected the correlation between land cover and bird community composition.

**ACKNOWLEDGMENTS**

We wish to thank the many people who supported this study through their invaluable contributions in planning, research, and logistics. For regional field data collection, we are indebted to Mary Gaudette, Randy Harrison, John Puscheck, Jeff Larkin, Nathan Burklepilch, and Rich Waynor. For research associated with our reference sites, we thank Andy Cole, Denice Wardrop, Sarah Goslee, Laurie Bishel-Machung, Diann Prosser, and Todd Fearer. At the U.S. Environmental Protection Agency, we gratefully acknowledge the management support of Rick Linthurst, Steve Paulsen, Dentric Shaw, Tom DeMoss, Ron Preston, Jim Green, Terry Slonecker, and Gil Veith. For administrative and technical assistance, we thank staff from the Pennsylvania State University College of Agricultural Sciences, School of Forest Resources, Environmental Resources Research Institute, and the Pennsylvania Cooperative Fish and Wildlife Research Unit. We thank Eric Warner and Mike Anderson of Penn State’s Office of Remote Sensing of Earth Resources for landscape pattern analyses, and Don Stevens of Dynamac Corporation for his assistance with spatial statistics. Sincere thanks are due to every private landowner who granted access to properties that emerged from our random sample, and to Phil Shriner and Tom Swinley for identifying them all. Finally, we are grateful to those who have provided research advice and review, especially Paul Adamus, Robert Blair, Dave Bradford, Margaret Brittingham, Mary Jo Casanela, Raymond O’Connor, C. R. Rao, Alan Taylor, Wally Tzilkowski, and an anonymous reviewer.

The U.S. Environmental Protection Agency has funded the research reported herein, and the National Health and Environmental Effects Research Laboratory has reviewed this document and approved it for publication. Approval for publication does not signify that the contents reflect the views of the Agency, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

**LITERATURE CITED**


