

Sensitivity of breeding birds to the “human footprint” in western Great Lakes forest landscapes

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Abstract. Breeding birds in forest ecosystems are generally diverse, habitat selective, and easily sampled. Because they must integrate environmental variables over space and time, local populations of forest birds (like other animal and plant taxa) may provide meaningful signals of local forest health or degradation. We evaluated 949 breeding bird surveys in areas ranging from degraded urban/suburban forest remnants to relatively pristine old growth forests in the western Laurentian Great Lakes region of North America. The “human footprint” across this landscape was represented by a one-dimensional numeric gradient derived from land cover variables, forest fragmentation metrics, and publicly available data on housing density and transportation corridors. We used an iterative, maximum likelihood approach to quantify species-specific responses to this human disturbance gradient. Many species showed significant directional responses, consistent with known life history attributes. Other species were most commonly detected at intermediate levels of anthropogenic disturbance, yielding unimodal responses. Relationships between the “human footprint” and occurrences of 38 bird species were illustrated by general Gaussian functions that represented both unidirectional and unimodal patterns. These biotic response (BR) functions were combined into a bird-based index of ecological condition (IEC) ranging from 0 (maximally degraded) to 10 (minimally degraded). We described a successful application of the IEC method at the Wild Rivers Legacy Forest (WRLF), a >260 km² conservation landscape in northeastern Wisconsin, USA, managed primarily under a working forest conservation easement established in 2006. In general, areas within the WRLF yielded high IEC values (7.0–9.0), but nearby forest areas not under the conservation easement were characterized by significantly lower IEC values based on breeding bird assemblages.

Key words: bird assemblage; disturbance gradient; ecological indicator; forestry management; northern mesic forest; western Great Lakes (USA).

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INTRODUCTION

The western Laurentian Great Lakes region, including portions of Michigan, Wisconsin, Minnesota, and Ontario, is covered by one of the

largest relatively contiguous areas of mixed conifer-hardwood forest in North America (Stearns 1949, Heilman et al. 2002). Despite widespread glaciation as recently as 11,000 yr BP and intensive logging during the past century,

these forests support a particularly rich diversity of breeding bird species, most of which (>80%) migrate annually to southern wintering grounds (Curtis 1959, Howe et al. 1992, Price et al. 1995). Today, forest ecosystems in northern Wisconsin and nearby states face several real or potential threats, including unsustainable logging (Frelich 1995), residential development (Radeloff et al. 2005, Hawbaker et al. 2006), invasive species introductions (Holdsworth et al. 2007, Corio et al. 2009), deer overbrowsing (Alverson et al. 1988), and regional climate change (Scheller and Mladenoff 2005, Duveneck et al. 2014). We explored the general manifestation of human activities, or the “human footprint,” on breeding bird assemblages in northern Wisconsin landscapes. In particular, we evaluated the relationship between measurable landscape variables like housing density, road density, and habitat loss on the occurrences of breeding birds in standardized point counts. We used a maximum likelihood approach to estimate species responses to a gradient of human disturbance, modeled after the classical analysis of Whittaker (1967) and subsequent investigators. In this case, our gradient ranged from pristine, minimally disturbed old growth forests of northern Wisconsin and Upper Michigan to highly fragmented forest landscapes in urban-suburban landscapes near Green Bay and Wausau, Wisconsin (USA).

A simple, but effective way to monitor the condition of complex ecological systems is to identify a suite of sensitive species or biotic variables that vary in response to environmental degradation (Karr and Chu 1999, Niemi and McDonald 2004). During the past several decades, researchers have developed new approaches for quantifying biotic sensitivity to ecosystem degradation (Niemi and McDonald 2004). Although some ecologists are skeptical about the utility or validity of indicator species (Simberloff 1999), the use of biotic indicators has grown steadily because of a demand for accountability of resource management policies and land use practices (Karr 1987, Croonquist and Brooks 1991, Karr and Chu 1997, Carignan and Villard 2002, Niemi and McDonald 2004, Kotwal et al. 2008).

Our approach extends the Index of Ecological Condition (IEC) model originally created by Howe et al. (2007b) for Great Lakes coastal

wetlands. Contributions of species to the index are based on documented species' responses to an environmental reference gradient ranging from maximally-degraded to nearly pristine (undisturbed) conditions. Our quantitative biotic indicator based on forest bird assemblages can be used to compare the impacts of alternative forest management strategies or to track changes in forest condition over time.

In addition to its practical application as a forest assessment tool, this analysis illustrates the relevance of ecological gradient analysis to anthropogenic landscape-level stressors. Human environmental impacts are easily observed almost everywhere on earth, but until recently few studies (e.g., Fore et al. 1996) have quantified and compared species responses to these impacts. The idea that the complex, multidimensional influences of human activities can be meaningfully reduced to a single environmental disturbance gradient implies that strong, unifying gradients in nature are not limited to abiotic conditions like climate, topography, or nutrient concentrations. We test this idea with results from breeding bird distributions in a predominately forested landscape that has been disturbed extensively by human activities during the past 150 years.

METHODS

Study area

Northern Wisconsin is covered primarily by mesic mixed deciduous/conifer forests interspersed with lowland forests, lakes, rivers, bogs, sedge meadows, and managed or developed lands, creating a diverse and complex landscape mosaic (Curtis 1959). Before European settlement, northern mesic forests in this region were dominated by sugar maple (*Acer saccharum* Marshall) and varying proportions of eastern hemlock (*Tsuga canadensis* [L.] Carrière), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), American basswood (*Tilia americana* L.), white ash (*Fraxinus americana* L.), ironwood (*Ostrya virginiana* [Mill.] K.Koch), red oak (*Quercus rubra* L.), and white pine (*Pinus strobus* L.; Curtis 1959). During the late 1800s and early 1900s, logging removed nearly all mature hardwoods, leaving very little old growth forest (Stearns 1949, Curtis 1959,

Table 1. Bird data were collected at a total of 949 bird survey sites in Wisconsin and the Upper Peninsula of Michigan, USA between 1993 and 2010 (Fig. 1) and were used to develop the environmental reference gradient of condition.

Bird dataset	Sites	Year(s)	Source
Old Growth and Managed Forest Study	36	1993, 1994	1
Marshfield Ecological Study Area Bird Study	202	2003	2
Peshigo River State Forest Bird Study	81	2003	3
Wild Rivers Legacy Forest	197	2010	4
Wisconsin Department of Natural Resources	105	2010	5
Nicolet National Forest Bird Survey	268	2009, 2010	6, 7
Highly Disturbed Sites	60	2010	4

Note: Sources are: 1, Howe and Mossman (1996); 2, Cassini (2005); 3, Wisconsin Department of Natural Resources (2006); 4, Gnass (2012); 5, Wisconsin Department of Natural Resources (2011); 6, Howe and Roberts (2005); 7, Niemi et al. (2015).

Frelich 1995). Selective removal of white pine, eastern hemlock, and yellow birch led to increased dominance by sugar maple, and extensive logging led to the expansion of early successional species such as quaking aspen (*Populus tremuloides* Michx.), big-tooth aspen (*Populus grandidentata* Michx.), white birch (*Betula papyrifera* Marshall), and pin cherry (*Prunus pensylvanica* L.f.; Stearns 1949, Curtis 1959). The extent and continuity of forests in northern Wisconsin have recovered significantly since the early 20th century, but human-related (anthropogenic) land uses including forestry management, agriculture, residential development, and road development (Frelich 1995, Saunders et al. 2002, Hawbaker et al. 2006, Wolter et al. 2006, Gonzalez-Abraham et al. 2007) dominate the northern Wisconsin landscape today. All of these activities may affect the suitability of the landscape for breeding bird species.

Bird-landscape relationships

We derived biotic response (BR) functions (Howe et al. 2007b) from publicly available landscape variables and seven bird survey datasets collected in northern and central Wisconsin and a small area in Michigan's Upper Peninsula between 1993 and 2010. In order to assess a broad gradient of forest condition, we selected bird survey sites ($n = 949$; Table 1) in a geographic area where the "human footprint" varied significantly (Fig. 1). We excluded sites with 25% or more of non-target habitats (e.g., grasslands, open wetlands, water) or lacking any natural habitat (see *Model development and analyses*) within a 500-m circular GIS buffer. All sites were at least 250 m apart to avoid double counting of birds (Ralph et al. 1995). Point counts

from the predominantly forested landscapes of northern Wisconsin included an analysis of old growth and managed forest birds funded by the Wisconsin Department of Natural Resources (WDNR; Howe and Mossman 1996), the 2009 and 2010 Nicolet National Forest Bird Survey (NNFBS; Howe and Roberts 2005, Niemi et al. 2015), and point counts in north central and northeastern Wisconsin by biologists from the WDNR's Natural Heritage Inventory (NHI) Program (Wisconsin Department of Natural Resources 2011). In cases where multiple point counts were conducted at a sampling site, we randomly selected a single count from only a single year to include in our analysis. Because only half of the NNFBS points are sampled each year (Howe and Roberts 2005, Niemi et al. 2015), we used sites from the NNFBS that were sampled during either 2009 ($n = 134$) or 2010 ($n = 134$). Non-forest sites from the NNFBS were excluded except for disturbed areas that were once occupied by forest (Howe and Roberts 2005). For example, some sites were located along forest roads or within relatively disturbed urban environments (e.g., small towns). The WDNR's NHI bird study was conducted in northeastern Wisconsin in northern mesic and lowland forests (Wisconsin Department of Natural Resources 2011). Bird surveys in the Wild Rivers Legacy Forest (WRLF) represented landscapes with intermediate and low levels of human impact. Most WRLF sites were located in the interior of northern mesic forests, but some were located on small forest roads or trails.

Bird point counts in relatively degraded forest landscapes were provided by a study of the Marshfield Ecological Study Area (MESA) funded by the Marshfield Clinic (Cassini 2005), a

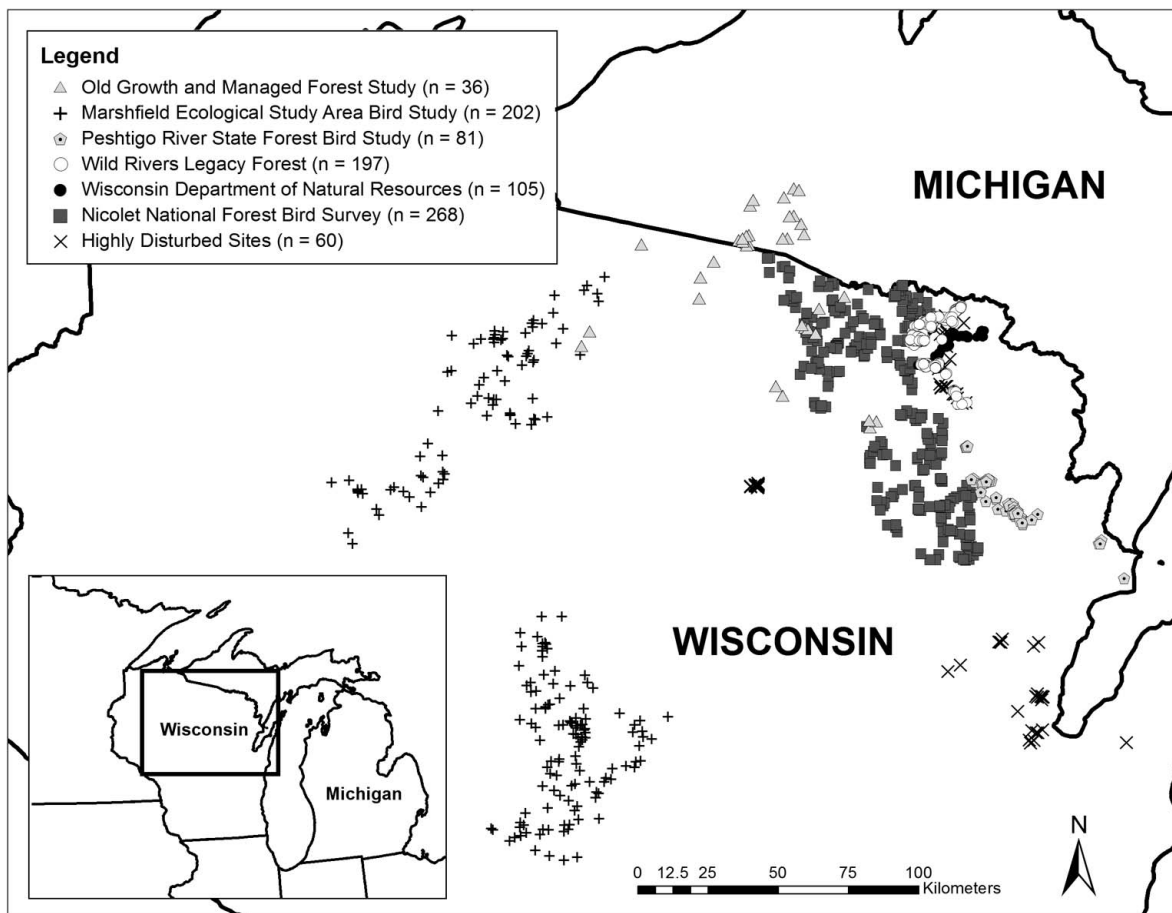


Fig. 1. Project study area in northern Wisconsin and the Upper Peninsula of Michigan, USA indicating bird survey sites ($n = 949$) from seven datasets (Table 1). Map was created using ArcGIS 10.1 software (Environmental Systems Research Institute, Redlands, California, USA; Environmental Systems Research Institute 2012). U.S. Census Bureau state boundary lines (U.S. Census Bureau 2000b) are displayed for reference.

WDNR-funded analysis of the Peshtigo River State Forest and Governor Thompson State Park (Wisconsin Department of Natural Resources 2006), and point counts in highly fragmented, disturbed forested landscapes conducted by us during 2010 (Table 1). MESA sites were located in northern and central Wisconsin (Fig. 1). Central Wisconsin sites were located in agricultural landscapes, urban (high and low intensity) areas, and near roads; northern Wisconsin sites were located in deciduous or mixed-deciduous/conifer forests, coniferous forests, or forested wetlands (Cassini 2005). The Peshtigo River State Forest and Governor Thompson State Park bird survey sites were located in a variety of fragmented and relatively contiguous forest areas in northeastern

Wisconsin including stands of northern mesic forests, red pine (*Pinus resinosa* Aiton), aspen (*Populus* sp.), and mixed forest-open woodlands (Wisconsin Department of Natural Resources 2006). Our 2010 “Highly Disturbed Sites” were located in landscapes with relatively high levels of urban and agricultural development. Sampling locations ranged from small, isolated forest patches (where counts were conducted at least 100 m from forest edge) to heavily managed forests. Some sites were located on small roads, forest roads, or trails.

Bird sampling

All sites, except those in the old growth bird study, were surveyed using a standard unlimit-

Table 2. Variables ($n = 20$) used to develop the environmental reference gradient of condition collected at all bird survey sites ($n = 949$).

Variable code	Variable description
500m_RA2	percent of developed area in 500-m buffer (logit transformation)
500m_RA3	percent of natural habitat area in 500-m buffer (logit transformation)
500m_RA4	percent of non-cultivated agriculture/silviculture area in 500-m buffer (logit transformation)
1km_RA1	percent of cultivated agriculture area in 1-km buffer (logit transformation)
1km_RA2	percent of developed area in 1-km buffer (logit transformation)
1km_RA3	percent of natural habitat area in 1-km buffer (logit transformation)
1km_RA4	percent of non-cultivated agriculture/silviculture area in 1-km buffer (logit transformation)
500m_CA3	core area (m^2) of natural habitat in 500-m buffer (squared transformation)
500m_ED3	total natural habitat edge density (km/km^2) per 500-m buffer (square root transformation)
1km_ED3	total natural habitat edge density (km/km^2) per 1-km buffer (square root transformation)
500mPA3	average perimeter to area ratio (m/m^2) of natural habitat in 500-m buffer (square root transformation)
1km_PA3	average perimeter to area ratio (m/m^2) of natural habitat in 1-km buffer (square root transformation)
500SP2_3	shared perimeter (m) between developed lands and natural habitat in 500-m buffer (square root transformation)
500SP3_4	shared perimeter (m) between natural habitat and non-cultivated agriculture/silviculture lands in 500-m buffer (square root transformation)
1kmSP2_3	shared perimeter (m) between developed lands and natural habitat in 1-km buffer (square root transformation)
1kmSP3_4	shared perimeter (m) between natural habitat and non-cultivated agriculture/silviculture lands in 1-km buffer (square root transformation)
RdDen500	total road/railroad (summed) density (km/km^2) per 500-m buffer ($\log_{10}(x + 1)$ transformation)
RdDen1km	total road/railroad (summed) density (km/km^2) per 1-km buffer ($\log_{10}(x + 1)$ transformation)
Dist2RdM	distance (m) to nearest road or railroad (square root transformation)
HDen500m	weighted average number of houses per census block (km/km^2) per 500-m buffer ($\log_{10}(x + 1)$ transformation)

Notes: Using ArcGIS 10.0 (Environmental Systems Research Institute 2011), LANDFIRE's land cover Existing Vegetation Type class names (Rollins 2009) based on LANDFIRE (2001 and 2008) were reclassified into four general categories: cultivated agriculture (1), developed (2), natural habitat (3), and non-cultivated agriculture/silviculture (4; Gnass 2012). Percentages of class types and fragmentation variables (core area, edge density, perimeter to area ratio, and shared perimeter) were calculated using IAN image analysis program (DeZonia and Mladenoff 2004) developed at the University of Wisconsin–Madison (<http://forestandwildlifeecology.wisc.edu/staticsites/mladenofflab/Projects/IAN/index.htm>, 5 April 2012). All variables were transformed to improve normality.

ed-distance 10-min bird point count, following methods described by Howe et al. (1997) and Knutson et al. (2008). Observers from the old growth study conducted two consecutive 5-min unlimited-radius point counts (Howe and Mossman 1996), which we converted into 10-min point counts by determining the maximum number of individuals recorded for each species during the two 5-min counts. Trained observers recorded all birds seen or heard during the 10-min census period. We only included surveys performed during the breeding bird season from 25 May to 15 July. During the early breeding season (25 May–30 June) we included bird surveys conducted between 30 min before sunrise and 10:00 h. To account for diminished levels of bird activity later in the breeding season (1 July–15 July), we excluded bird surveys completed after 09:00 h. We also restricted our analysis to bird surveys conducted during optimal or near-optimal weather conditions; surveys conducted during reported wind speeds

>19.3 km/h or continuous rain were excluded.

Corrections to bird point count data have been applied to account for biases in detectability among species or habitats (MacKenzie et al. 2006). Such methods, however, require several critical assumptions (e.g., accurate distance estimation by observers, uniform rates of movement or no movement by species into and out of the sampling area) that themselves can introduce unwanted bias or uncertainty (Johnson 2007, Etterson et al. 2009). Because our stressor-response analyses treat each species independently and apply only to forest habitats, we did not adjust point count data for species-specific or habitat-specific differences in detectability (Johnson 2007).

Model development and analyses

Environmental reference gradient.—For each of the bird sampling sites, we collected independent landscape variables (Table 2) obtained from GIS land cover data and other public domain

information associated with human activities. Variables were selected because of their documented or potential effects on forest ecosystems and biota, particularly birds (Kroodsma 1984, Brooks et al. 1998, Knutson et al. 1999, Jones et al. 2000, Cadenasso and Pickett 2001, Radeloff et al. 2005, Miller et al. 2007, Pidgeon et al. 2007, Minor and Urban 2010).

Initially we used ArcGIS 10.0 (Environmental Systems Research Institute, Redlands, California, USA; Environmental Systems Research Institute 2011) and public domain databases to assemble 202 variables related to human presence (e.g., population density), landscape composition (e.g., percent land cover), and landscape pattern (e.g., fragmentation metrics) at 500 m or 1 km circular buffers around the census sites (Saab 1999, Boscolo and Metzger 2009). Many of these variables were highly correlated or could not be ordered along a gradient of maximally to minimally degraded condition, so we reduced the list to 20 relatively uncorrelated variables that correspond monotonically to the degree of human environmental impacts (Table 2). Where appropriate, we transformed variables to improve normality. For variables (e.g., housing density) that were highly correlated ($r > 0.90$) at 500 m and 1 km buffers, we only kept the variable calculated at a 500 m buffer because the territory sizes of most forest bird species are well within this range.

We calculated a weighted average of the number of houses per census block in order to quantify the average housing density per 500 m buffer. We combined U.S. Census Bureau TIGER/Line block units (U.S. Census Bureau 2001, 2012) and U.S. Census housing units per census block (U.S. Census Bureau 2001, 2011a) using tools in ArcGIS 10.0 (Environmental Systems Research Institute 2011). Because we used bird studies that were conducted during different years (1993–2010), we used GIS variables collected from the year that best matched the year when a sampling site was surveyed. For example, we used U.S. 2000 Census data to calculate average housing densities for survey sites from the old growth and managed forest bird study (1993, 1994), MESA bird study (2003), and Peshtigo River State Forest and Governor Thompson State Park bird study (2003). For the NNFBS (2009, 2010), WDNR forests (2010), WRLF (2010), and our

“Highly Disturbed Sites” (2010), we used U.S. 2010 Census data. We used TIGER road data (U.S. Census Bureau 2000a, 2007, 2011b, 2012) to calculate road density at 500 m and 1 km buffers, even though TIGER road data have been shown to underestimate road density in northern Wisconsin (Hawbaker and Radeloff 2004). At both buffer distances, we also calculated railroad density (U.S. Census Bureau 2000a, 2007, 2011b, 2012) and pooled these densities with road densities. We then calculated the distance to the nearest road or railroad (U.S. Census Bureau 2000a, 2007, 2011b, 2012) using the ArcGIS 10.0 *Near* tool (Environmental Systems Research Institute 2011). Our road variables can be interpreted as indirect surrogates of human development (Glennon and Porter 2005) and forest management intensity, in the absence of more direct variables like tree size and forest structure.

Existing Vegetation Type (EVT) at 30 m × 30 m cells across the study area was derived from the Landscape Fire and Resource Management Planning Tools Program (LANDFIRE; LANDFIRE 2001, 2008, Rollins 2009). Although LANDFIRE provides rather coarse land cover attributes, other available land cover datasets were either outdated or did not cover our entire study area. Again, we used the appropriate LANDFIRE EVT dataset that best matched the year during which a given bird study was conducted (e.g., we used LANDFIRE 1.1.0 for sites from the NNFBS). We reclassified the land cover pixels into four general categories (Gnass 2012) whose magnitude (positive or negative) is directly related to human disturbance: cultivated agriculture (e.g., row crop), developed lands (e.g., roads, urban/suburban areas), natural habitat (e.g., maple-basswood forest), and non-cultivated agriculture/silviculture (e.g., pasture, hay, tree plantation). This general scheme minimized potential land use misclassifications and provided direct evidence of human landscape modifications in the vicinity of the bird survey sites.

Percent area in each general land cover type and related fragmentation variables were calculated using the IAN image analysis program (DeZonia and Mladenoff 2004) developed at the University of Wisconsin-Madison (<http://forestandwildlifeecology.wisc.edu/staticsites/mladenofflab/Projects/IAN/index.htm>, 5 April

2012). To characterize habitat fragmentation in a primarily forest-dominated landscape, we calculated perimeter to area ratios (Baker and Cai 1992, DeZonia and Mladenoff 2004) and edge density (DeZonia and Mladenoff 2004) for natural habitat types. Perimeter to area ratios reflect the areas and shapes of class polygons and have been shown to be good predictors of habitat-specific bird species in grassland ecosystems (Helzer and Jelinski 1999). Large natural habitat patches, for example, receive lower perimeter to area ratios than small patches. We also calculated shared perimeters between developed lands and natural habitat and between non-cultivated agriculture/silviculture and natural habitat to capture ecologically relevant edge effects. Lastly, we calculated the core area of natural habitat, defined by an eight-neighbor rule in which one cell (in this case, 30 m × 30 m) is defined as core area if all of its surrounding cells are of the same class type as itself (DeZonia and Mladenoff 2004).

We used PC-ORD v5.19 (McCune and Mefford 2006) to calculate a principal components analysis (PCA) based on the correlation matrix of the 20 GIS/environmental variables; results enabled us to condense these variables into a few minimally correlated synthetic variables (component scores) that best differentiated the bird survey sites. If necessary, we reversed the sign of a PCA component so that the site-specific scores ranged from most impacted (low numbers) to least impacted (high numbers). Subsequently, we weighted the PCA scores of interpretable axes by the proportion of variance associated with the principal component; the weighted scores were summed and converted to a standardized (0–10) scale to yield a single index for each site. These indices define a reference gradient of environmental condition (C_{env}) that reflects the magnitude of human impacts or stress (the “human footprint”) on the landscape (Howe et al. 2007b). Sites with low values of environmental condition ($C_{env} = 0$), for example, are characterized by heavily managed land uses, highly reduced or fragmented natural habitats, or high densities of roads and buildings. In contrast, sites with high values of environmental condition ($C_{env} = 10$) are relatively pristine and non-fragmented, with little human disturbance and with low intensity (or no) active manage-

ment and development.

Biotic response functions

Biotic response (BR) functions describe the relationships between species’ occurrences or abundances and an environmental reference or stress gradient (Howe et al. 2007b). In our case, the y-axis represents the probability of a bird species being detected during a 10-min, unlimited-distance point count, and the x-axis represents a reference gradient of environmental stress or condition (C_{env}). Unlike the original formulation of BR functions (Howe et al. 2007b), which used a four parameter monotonically increasing or decreasing function to describe how species respond to the gradient of condition, we used a modified normal (Gaussian) distribution function (Bluman 2008):

$$P_i(C) = \frac{1}{\sigma\sqrt{2\pi}} e^{\left(-\frac{(C-\mu)^2}{2\sigma^2}\right)} h \quad (1)$$

where $P_i(C)$ represents the probability of detecting species i at a given value of condition, C ; μ and σ are the mean and standard deviation of the normal distribution respectively. The term, h , is a scaling factor that removes the normal distribution’s constraint that the area under the curve = 1. In order to find the best fit curve, we placed each of the 917 sites (removing 32 “reserved” sites for validation) into bins of environmental condition (C_{env}) representing intervals of 0.5 units. For example, we created bin 2.25 for sites with environmental condition values (C_{env}) greater than or equal to 2.0 but less than 2.5. Because we had fewer sites at lower values of environmental condition, we created the first two bins as bin 0.5 (sites with C_{env} values $0 \leq C_{env} < 1$) and bin 1.5 (sites with C_{env} values $1 \leq C_{env} < 2$); the remaining bins represented 0.5 unit intervals. Next, we calculated observed probabilities of occurrence (number of bird counts in which a species was observed/total number of counts) for each bin. The resulting probabilities and the corresponding values of C_{env} were used to estimate the three parameters, μ , σ , and h , defining the Gaussian function, Eq. 1. We used a PORT iterative algorithm (Gay 1990) calculated by the “nlminb” function of R (version 3.1.0, R Development Core Team 2014) to estimate these parameters by minimizing a lack-of-fit expression:

$$\sum_{j=1}^N \frac{(p_{ij} - P_i(C_{env,j}))^2}{P_i(C_{env,j})} \quad (2)$$

where N is the total number of bins, p_{ij} is the observed probability of detecting species i in bin j , and $P_i(C_{env,j})$ is the expected probability of detecting species i in bin j along the environmental stress or reference gradient given a set of species-specific parameters (μ , σ , and h) from Eq. 1. (Note that values of abundance or some other measure of response could be used in place of probabilities. In these cases, results from field observations do not need to be organized into bins.) During the iteration process, the parameters are varied until they converge on values that minimize Eq. 2 (Howe et al. 2007b). The mean of expression Eq. 1 (μ) was allowed to range beyond 0 and 10 (endpoints of the reference gradient) in order to permit a wide variety of BR functions, including unimodal (bell-shaped) curves as well as monotonically increasing or decreasing curves that exhibit only part of the bell-shaped Gaussian pattern. The parameter estimates were constrained by $-10.0 \leq \mu \leq 20.0$ and $0 < \sigma \leq 10.0$ to reduce computational time. At values beyond this range, the BR functions are generally “flat,” showing weak responses to the environmental gradient. We also constrained $h \geq 0$ to avoid convergence on a BR function that dips below 0 probability.

BR functions illustrate how species respond to environmental stressors. Some species might respond negatively to environmental stressors while others respond positively (Howe et al. 2007a). Still others might be most frequent or abundant at intermediate levels of stress. Consequently, BR functions can be used as tools for predicting the outcome of environmental degradation or improvement. As environmental quality (C_{env}) declines, species with monotonically increasing BR functions on our 0–10 scale will be expected to decline in frequency or abundance, while those with monotonically decreasing BR functions will be expected to increase in frequency or abundance.

Index of ecological condition.—Biotic response (BR) functions can be used further to develop a quantitative, multi-species index of ecological condition (IEC) following the general approach of Howe et al. (2007a, b). IEC values at individual

sites can be viewed as estimates of environmental condition (C_{env}) based on the species present at the site. Species composition likely provides additional information about environmental health beyond that conveyed by the originally defined reference gradient, however, so we assert that the biotic index estimates a more general value of condition, denoted as C . Two alternative approaches can be used to calculate IEC values for a single site or group of sites.

The *quantitative method* uses a weighted least squares lack-of-fit formula, Eq. 2, to find by iteration the value of condition (IEC) that minimizes the differences between observed (from field data) and expected (from BR function parameters) species response variables. Estimates of IEC, which can easily be calculated using the Solver tool of Microsoft Excel, typically converge on a single value, although multiple starting values should be used to avoid convergence on a suboptimal local stable point (Hilborn and Mangel 1997). We used probability of occurrence (=frequency) as the species response variable, but other quantitative variables (e.g., average abundance, density) can be used as long as they also were used to generate the BR functions.

An alternative *presence/absence method* calculates IEC values for individual sites by maximizing a likelihood function based on simple presence or absence of species at the site. Specifically, the iteration process (Howe et al. 2007a) maximizes the sum of the (log) probabilities of detecting the observed species plus the (log) probabilities of not detecting the unobserved species in a field sample, Eq. 3. Like the quantitative method, expected probabilities for a given value of condition (C) are given by the previously-derived BR functions. At this point, as well as in the calculation of IEC by the quantitative method, we make a rather subtle transition between the reference condition, C_{env} and the estimated ecological condition (IEC or, more generally, C). Whereas the BR functions relate directly to the pre-determined reference gradient, C_{env} species composition tells us more about the ecological health of a site. In other words, the reference gradient helps us identify sensitive species and provides a means to quantify the sensitivities of species to environmental stress; the species-based IEC values, however, provide additional information about

the condition of a site or group of sites because these species inevitably respond to multiple, interacting stressors and environmental influences. For the presence/absence method, we again used the R (version 3.1.0, R Development Core Team 2014) “nlminb” function (Gay 1990) to iteratively estimate the best-fit IEC values. In this case we maximized the following lack-of-fit expression:

$$\sum_{i=1}^M \log(P_i(C)) + \sum_{i=1}^N \log(1 - P_i(C)) \quad (3)$$

where M represents the total number of species that were detected at the site, N represents the total number of species that were not detected, and $P_i(C)$ is the expected probability of species i for $C = \text{IEC}$ given the previously determined BR function for that species. In both the quantitative and presence/absence methods, the same sampling protocol (in this case, unlimited-distance 10-min bird point counts) must be used for generating the BR functions and IEC scores.

We selected bird species for IEC calculations based on the goodness-of-fit of the BR functions and relevance of the species to forest habitat quality in northern Wisconsin. Bird species found mainly in non-forest habitats (e.g., open wetlands) or species that nest infrequently in northern Wisconsin were excluded. We also excluded bird species whose BR function showed little sensitivity (positively or negatively) to the environmental reference gradient of condition and species that were rarely detected at our sample sites. In order to differentiate highly impacted sites, we included several species characteristic of disturbed landscapes (e.g., Common Grackle [*Quiscalus quiscula*]) and invasive species (e.g., European Starling [*Sturnus vulgaris*]), even though they are not typical of natural forest landscapes in Wisconsin (Guth 1978).

We used BR functions of these selected species to calculate IEC values for sample sites in the Wild Rivers Legacy Forest (WRLF), a multi-million dollar conservation easement in northeastern Wisconsin involving The Nature Conservancy (TNC), the State of Wisconsin, and two private Timber Investment Management Organizations (TIMO). TNC staff biologists and volunteer ornithologists conducted point counts for birds at 200 locations throughout the WRLF in 2009, 2010, and 2011. Eighty sample sites were

established at the State lands, 80 at TIMO lands under easement, and 40 sites at TIMO lands not under easement. We used the presence/absence method to calculate IEC values for individual sites. These values were compared among management units and years using a mixed effects general linear model with management type and year as fixed effects and site as a random effect. Tukey's post hoc test was used to compare the three management prescriptions. Additionally, we used the quantitative method to estimate overall IEC values for the different management prescriptions during different years. This analysis illustrates how the IEC method can be applied at different scales, from individual sites to groups of many sites.

Model validation.—We validated the IEC model for individual sites, as recommended by Noss (1999) and illustrated by Howe et al. (2007b), by comparing the bird-based IEC values with the environmental reference values (C_{env}) for 32 randomly selected “reserved” sites that were not included in development of the species-specific BR functions. We used a stratified approach for selecting these reserved sites in order to account for the full range of environmental condition in our study region. We randomly removed one site from bins with 20 sites or less per bin and two sites from bins with more than 20 sites per bin, leaving a total of 917 sites for estimating the BR functions.

Except for the principal components analysis, all statistical tests used R statistical software (version 3.1.0, R Development Core Team 2014).

RESULTS

Environmental reference gradient

Principal components analysis (PCA) based on land use (GIS) variables and other measures of human impact yielded three interpretable and relevant components (axes), together explaining 79.3% of the variation in the 20 original landscape-level variables (Table 3). The first principal component accounted for 56.8% of the variation and was most highly correlated positively with core area of natural habitat within 500 m of the census site (500m_CA3, Fig. 2a). Other variables that were strongly positively correlated with component 1 included relative area of natural habitat (500m_RA3, 1km_RA3) and distance to

Table 3. Principal component analysis component loadings (eigenvectors scaled to unit length) of 20 variables used to generate the environmental gradient of condition ($n = 949$ sites).

Variable	Component 1	Component 2	Component 3
500m_RA4	-0.2608	0.0706	0.1409
1km_RA4	-0.2558	-0.0528	0.2752
1km_ED3	-0.2501	-0.2440	-0.0159
500m_ED3	-0.2446	-0.2026	-0.0853
RdDen1km	-0.2426	0.0771	-0.1815
500m_RA2	-0.2358	0.2015	-0.2585
RdDen500	-0.2357	0.1679	-0.2695
1km_RA2	-0.2348	0.1159	-0.1418
500mPA3	-0.2288	-0.1439	0.1633
500SP3_4	-0.2040	0.2258	0.3955
1km_PA3	-0.1944	-0.1638	0.3150
1kmSP3_4	-0.1850	0.2007	0.5124
HDen500m	-0.1823	-0.1939	-0.2264
1km_RA1	-0.1523	-0.3822	-0.1497
500SP2_3	-0.1463	0.4408	-0.1462
1kmSP2_3	-0.1247	0.4393	-0.0126
Dist2RdM	0.2227	-0.1567	0.2454
1km_RA3	0.2553	0.2212	-0.0003
500m_RA3	0.2688	0.0541	0.0627
500m_CA3	0.2694	0.1312	-0.0145

Note: Variable names are described in Table 2.

nearest road or railroad (Dist2RdM). Component 1 was strongly correlated negatively with the relative area of non-cultivated agricultural/silvicultural lands (500m_RA4 [Fig. 2b] and 1km_RA4), edge density of natural habitat (1km_ED3, 500m_ED3), and road density (RdDen1km), all characteristic of sites in fragmented, disturbed, or developed landscapes. The second component, accounting for 14.8% of the variation, was strongly correlated positively with the length of shared perimeter between developed lands and natural habitat (500SP2_3 [Fig. 2c] and 1kmSP2_3), as well as with shared perimeter of natural habitat and non-cultivated agricultural/silvicultural lands (500mSP3_4) and relative area of natural habitat within 1 km (1km_RA3). Component 2 was strongly correlated negatively with the relative area of cultivated agricultural lands (1km_RA1, Fig. 2d) and edge density of natural habitat within 1 km of the census site (1km_ED3). Component 3, accounting

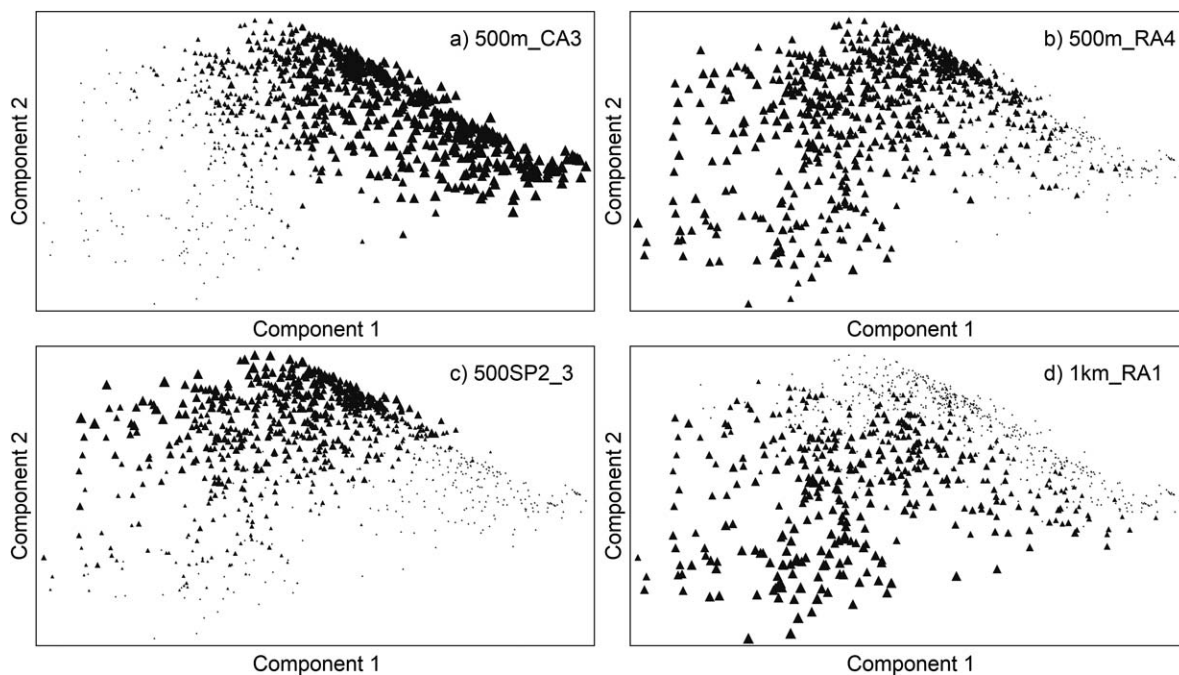


Fig. 2. Principal component analysis ordination plots of 949 bird survey sites (shown as triangles) based on 20 landscape environmental variables used to create an environmental reference gradient of condition. The size of the triangle represents the correlation with individual environmental variables: (a) core area of natural habitat in 500 m buffer (500m_CA3), (b) percent of non-cultivated agriculture/silviculture area in 500 m buffer (500m_RA4), (c) shared perimeter between developed lands and natural habitat in 500 m buffer (500SP2_3), and (d) percent of cultivated agriculture area in 1 km buffer (1km_RA1). Ordination plots were created using PC-ORD v5.19 (McCune and Mefford 2006).

for 7.7% of the inter-site variation, was strongly correlated positively with shared perimeter of natural habitat and non-cultivated agricultural/silvicultural lands (1kmSP3_4 and 500SP3_4), perimeter to area ratio of natural habitat (1km_PA3), and relative area of non-cultivated agricultural/silvicultural lands (1km_RA4), emphasizing sites with mosaics of natural habitat and non-cultivated agricultural/silvicultural lands. Component 3 was strongly correlated negatively with road density (RdDen500), relative area of developed lands (500m_RA2), and housing density (HDen500m). The remaining principal components were not interpretable in the context of human environmental impacts, so we did not include them in the development of the environmental gradient. The first three components clearly distinguished between highly disturbed and non-disturbed sites within the study area, providing a rigorous representation of the relative “human footprint” on the landscape.

Weighted PCA scores were combined and converted to a 0–10 scale, creating a standardized environmental gradient of condition (C_{env}) that was subsequently used to develop species-specific biotic response (BR) functions (Table 4, Fig. 3). Subjective analysis of satellite imagery confirmed that sites with high C_{env} values were characterized by extensive areas of contiguous forest, sometimes mixed with other natural habitats, but with little evidence of human impacts. Sites with low C_{env} values were invariably located in highly disturbed natural landscapes or in areas dominated by agriculture or urban/suburban development.

Biotic response functions

Observers identified 142 bird species at the 917 survey sites, excluding the 32 reserved sites. Many of these species were observed at only a few sites or were characteristic of non-forest habitats (e.g., Common Loon [*Gavia immer*] and Canada Goose [*Branta canadensis*]); these species were excluded from our analysis because they provided little information about forest condition. We selected 38 bird species (Table 4) of northern Wisconsin forested landscapes (including highly disturbed areas) that exhibited relatively strong sensitivity to our quantitative environmental gradient based on the lack-of-fit

calculation (LOF), Eq. 2 (Howe et al. 2007a). Nearly all of the biotic response (BR) curves of these species fit the observed data extremely well (LOF < 1.0), although four frequently observed species yielded slightly higher LOF values (Mourning Dove, LOF = 1.63; Common Grackle, LOF = 1.60; Ovenbird, LOF = 1.45; American Crow, LOF = 1.36). For each of the 38 selected species, we calculated the difference between the minimum and maximum expected probabilities of detection, P_{diff} , to describe the magnitude of the species’ sensitivity to the environmental gradient. European Starling (Fig. 3a), House Sparrow (Fig. 3b), Common Grackle, and Mourning Dove, for example, showed the strongest negative relationships with the environmental gradient, whereas, Ovenbird (Fig. 3c), Red-eyed Vireo (Fig. 3d), and Black-throated Green Warbler showed the strongest positive relationships. Species such as Chestnut-sided Warbler (Fig. 3e) and Indigo Bunting were found most commonly at intermediate values along the a priori environmental gradient. Ruffed Grouse (Fig. 3f), Black-throated Blue Warbler, and Blue-headed Vireo exemplified species that were uncommon ($P_{diff} < 0.1$) but were consistently associated with relatively undisturbed forest landscapes.

Index of ecological condition (IEC)

Bird-based index of ecological condition (IEC) values corresponded very closely to the a priori landscape/GIS-based environmental gradient of condition (C_{env} ; Fig. 4). IEC values for the validation sites ($n = 32$), withheld during the calculation of the BR functions, also were highly correlated with the corresponding C_{env} values (Spearman’s $\rho = 0.74$, $P < 0.0001$). This relationship resembled the pattern for all sites ($n = 949$; Spearman’s $\rho = 0.67$, $P < 0.0001$). Nevertheless, considerable scatter existed around the line where $IEC = C_{env}$. For example, some of the old growth sites (Howe and Mossman 1996) received IEC values of 10, while the corresponding landscape-based C_{env} values ranged from 7.97 to 9.91. Analysis of these deviations is beyond the scope of our study but may be of significant interest to forest managers. Sites where the bird-based IEC values were higher than the corresponding C_{env} values represented conditions that were particularly favorable for birds given the

Table 4. Bird species ($n = 38$) that exhibited strong responses (positive or negative) to a gradient of human impacts in local forest landscapes of northern Wisconsin and Michigan's Upper Peninsula.

Common name	Scientific name	μ	σ	h	LOF	P_{diff}^{\dagger}	R^2_{\ddagger}
European Starling	<i>Sturnus vulgaris</i>	-0.64	2.23	6.37	0.32	1.00	0.95
House Sparrow	<i>Passer domesticus</i>	-3.97	2.67	20.22	0.19	1.00	0.97
Ovenbird	<i>Seiurus aurocapilla</i>	7.93	3.29	7.96	1.45	0.91	0.91
Red-eyed Vireo	<i>Vireo olivaceus</i>	8.32	3.81	8.99	0.85	0.86	0.92
Common Grackle	<i>Quiscalus quiscula</i>	-10.00	5.89	50.36	1.60	0.80	0.78
Mourning Dove	<i>Zenaidura macroura</i>	-10.00	8.59	30.07	1.63	0.62	0.63
Black-throated Green Warbler	<i>Setophaga virens</i>	8.38	2.24	3.38	0.30	0.60	0.96
American Crow	<i>Corvus brachyrhynchos</i>	1.86	4.37	7.74	1.36	0.58	0.74
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	8.01	2.90	4.08	0.34	0.55	0.93
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	8.40	2.27	2.92	0.24	0.51	0.95
Hermit Thrush	<i>Catharus guttatus</i>	7.80	2.58	2.88	0.68	0.44	0.81
Least Flycatcher	<i>Empidonax minimus</i>	20.00	6.49	23.76	0.25	0.43	0.94
Blackburnian Warbler	<i>Setophaga fusca</i>	9.35	2.30	2.08	0.18	0.36	0.93
Mourning Warbler	<i>Geothlypis philadelphia</i>	8.82	2.82	2.44	0.67	0.34	0.74
Eastern Wood-Pewee	<i>Contopus virens</i>	7.11	3.99	3.46	0.89	0.28	0.42
Common Raven	<i>Corvus corax</i>	8.58	2.57	1.77	0.38	0.27	0.77
Scarlet Tanager	<i>Piranga olivacea</i>	8.27	2.54	1.67	0.29	0.26	0.86
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	5.95	2.63	1.78	0.84	0.25	0.46
Brown-headed Cowbird	<i>Molothrus ater</i>	-1.26	4.88	3.17	0.70	0.23	0.58
Veery	<i>Catharus fuscescens</i>	6.57	2.32	1.33	0.31	0.22	0.75
Blue Jay	<i>Cyanocitta cristata</i>	6.83	6.05	7.15	0.52	0.22	0.33
Black-capped Chickadee	<i>Poecile atricapillus</i>	4.15	4.19	3.45	0.40	0.20	0.54
House Wren	<i>Troglodytes aedon</i>	0.70	3.08	1.49	0.37	0.19	0.72
Winter Wren	<i>Troglodytes hiemalis</i>	8.85	1.96	0.94	0.16	0.19	0.86
Red-breasted Nuthatch	<i>Sitta canadensis</i>	9.08	3.64	1.79	0.26	0.19	0.74
Indigo Bunting	<i>Passerina cyanea</i>	4.11	3.20	1.80	0.66	0.18	0.38
Northern Parula	<i>Setophaga americana</i>	7.84	1.59	0.70	0.23	0.18	0.75
Baltimore Oriole	<i>Icterus galbula</i>	2.32	2.39	0.79	0.35	0.13	0.56
Hairy Woodpecker	<i>Picoides villosus</i>	17.90	6.40	4.71	0.23	0.13	0.75
Northern Flicker	<i>Colaptes auratus</i>	16.38	10.00	5.70	0.62	0.13	0.35
American Redstart	<i>Setophaga ruticilla</i>	5.25	1.87	0.57	0.46	0.12	0.57
Brown Creeper	<i>Certhia americana</i>	8.28	2.00	0.60	0.30	0.12	0.61
Pileated Woodpecker	<i>Dryocopus pileatus</i>	6.21	2.67	0.82	0.66	0.11	0.23
Black-and-white Warbler	<i>Mniotilta varia</i>	6.90	1.65	0.47	0.22	0.11	0.73
Yellow-rumped Warbler	<i>Setophaga coronata</i>	6.96	2.80	0.82	0.28	0.11	0.56
Ruffed Grouse	<i>Bonasa umbellus</i>	8.14	2.89	0.60	0.28	0.08	0.51
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	7.91	1.46	0.27	0.21	0.07	0.50
Blue-headed Vireo	<i>Vireo solitarius</i>	7.23	2.69	0.48	0.33	0.07	0.29

Notes: Common and scientific names of each bird species (Chesser et al. 2014) are listed with a species' biotic response (BR) function parameters, the mean (μ), standard deviation (σ), and height (h) scaling term, Eq. 1. Parameters describe the best-fit Gaussian function determined by iteration from 917 bird survey sites across the region. They were determined by minimizing a lack-of-fit (LOF) criteria, Eq. 2, and describe how each species responds along the environmental reference gradient of condition (C_{env}). Select BR function curves are as in Fig. 3. All BR function curves are available online (public communication, <http://www.uwgb.edu/biodiversity/forest-index/>).

† P_{diff} is the mathematical difference between the minimum and maximum expected probabilities of occurrence and describes a species' sensitivity to the gradient.

‡ R^2 is the goodness-of-fit for non-linear functions and was calculated as $R^2 = 1 - (SS_{reg}/SS_{tot})$.

corresponding "human footprint"; identification of forest attributes at these sites might illuminate beneficial bird habitat management practices. Likewise, sites where $IEC < C_{env}$ represented conditions that were particularly unfavorable for birds and may help identify harmful forest or land management practices.

Model application

We calculated index of ecological condition (IEC) values for the three different management treatments in the Wild Rivers Legacy Forest

(WRLF) based on three years of bird sampling (2009, 2010, and 2011). The quantitative method (with species-specific probabilities of detection as the response variable) showed clear differences among the treatments. In all three years, Timber Investment Management Organization (TIMO) lands under a working forest conservation easement and State of Wisconsin lands produced higher scores than TIMO lands not under a conservation easement (Table 5). Using the presence/absence method, we calculated IEC values for individual sites within the three forest

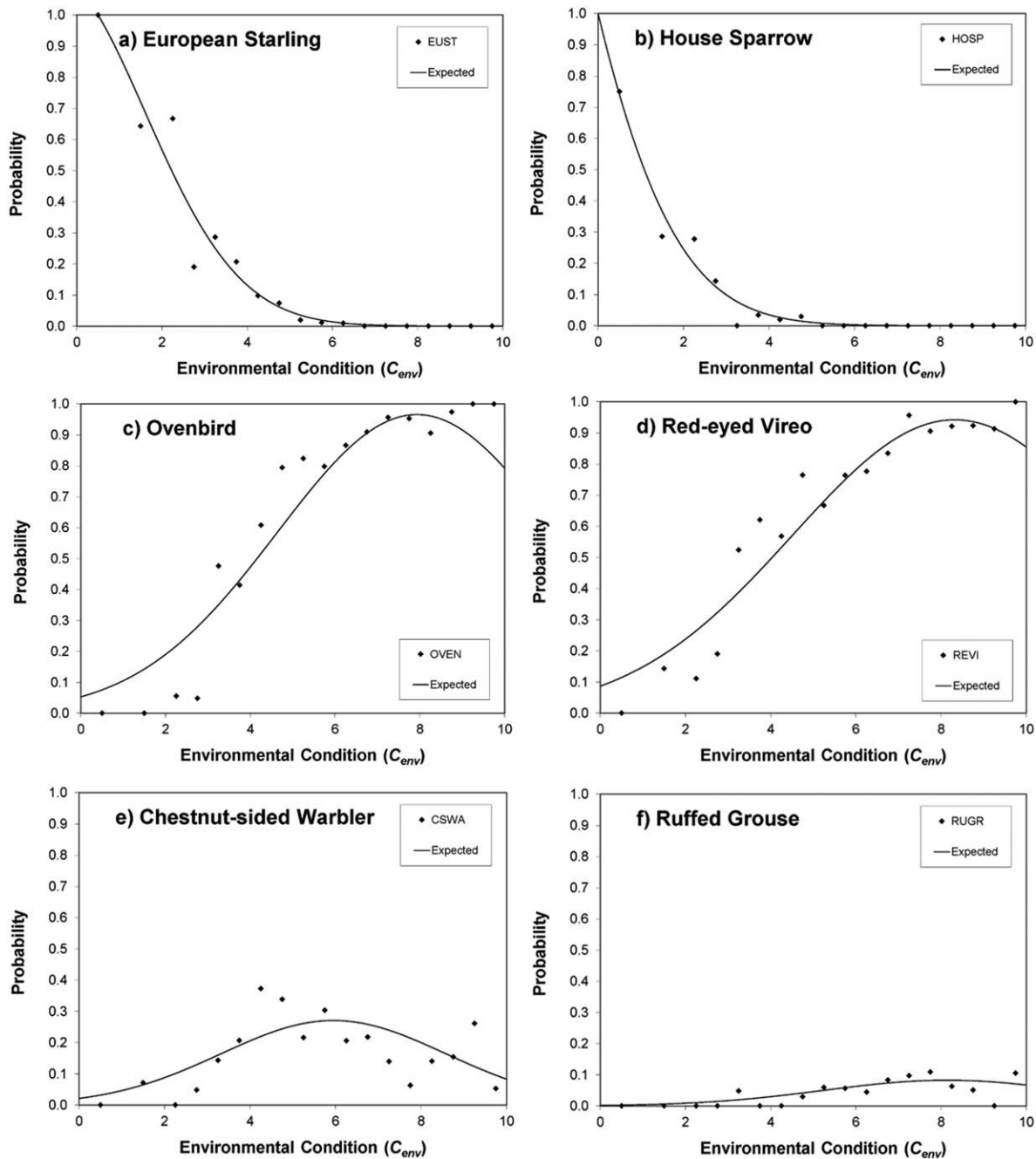


Fig. 3. Biotic response (BR) functions, Eq. 1, for six of the 38 bird species (Table 4) showing strong responses to the “human footprint” in forest landscapes of northern Wisconsin and Michigan’s Upper Peninsula. The x-axis is an environmental reference gradient of condition (C_{env}) created using a principal components analysis of landscape variables (Fig. 2). The gradient ranges from degraded forest condition ($C_{env}=0$) to relatively pristine forest condition ($C_{env}=10$), based on 18 C_{env} bins (e.g., bin 4.25 for $C_{env}=4.0$ to 4.5). The y-axis is the probability that a species occurs and is detected during an unlimited-distance 10-min bird point count at a given value of condition. Species shown are: (a) European Starling, (b) House Sparrow, (c) Ovenbird, (d) Red-eyed Vireo, (e) Chestnut-sided Warbler, and (f) Ruffed Grouse. Curves were created in Microsoft Excel 2013.

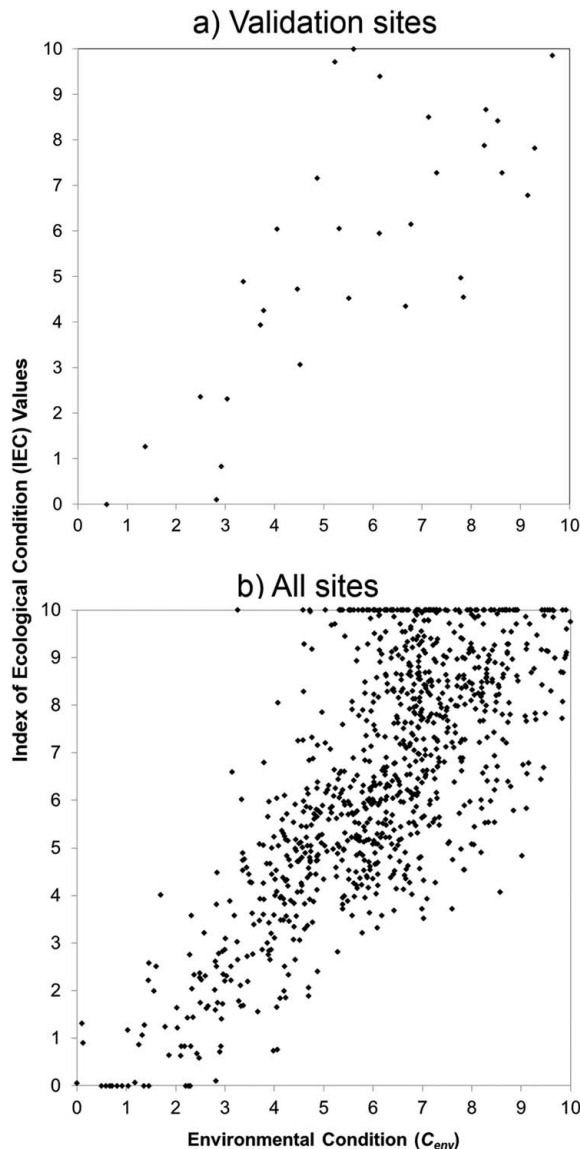


Fig. 4. Correlation between landscape/GIS-based environmental condition (C_{env}) values (x-axis) and bird-based index of ecological condition (IEC) values (y-axis) from bird survey sites for: (a) the validation set, or sites excluded from biotic response (BR) function derivation of the indicator species ($n = 32$; Spearman's $\rho = 0.74$, $P < 0.0001$), and (b) all sites ($n = 949$; Spearman's $\rho = 0.67$, $P < 0.0001$). IEC values were calculated using the presence/absence method in R (version 3.1.0, R Development Core Team 2014).

Table 5. Index of ecological condition (IEC) scores (quantitative method) of three land management treatments [Timber Investment Management Organizations (TIMO) lands under a working forest conservation easement ($n = 80$), State of Wisconsin lands ($n = 80$), and TIMO lands not under an easement ($n = 40$)] in the Wild Rivers Legacy Forest (WRLF) in northeastern Wisconsin based on 2009, 2010, and 2011 bird surveys.

Treatment	2009	2010	2011
TIMO lands under easement	8.84	8.88	8.81
State of Wisconsin lands	8.51	8.46	8.31
TIMO lands not under easement	7.35	6.83	6.70

management prescriptions. A linear mixed effects model with management strategy and year as fixed effects and site as a random effect (R function “lmer” from package lmerTest; Kuznetsova et al. 2013, Bates et al. 2014) yielded no significant interaction between management strategy and year, so the interaction term was excluded in the subsequent analysis. Management strategy exhibited a highly significant effect on mean IEC scores ($F = 48.36$; $df = 2, 197$; $P < 0.0001$; Fig. 5), while differences among years were not significant ($F = 1.60$; $df = 1, 399$; $P = 0.21$). IEC scores at TIMO lands under a conservation easement were significantly higher than IEC scores at State of Wisconsin lands (Tukey's HSD, $P < 0.0001$) and significantly higher than those at TIMO lands not under easement (Tukey's HSD, $P < 0.0001$). IEC scores at TIMO lands not under a working forest conservation easement were significantly lower than those at State of Wisconsin lands (Tukey's HSD, $P < 0.0001$).

In order to better understand the biological significance of these differences, we compared the bird species composition of protected forest lands (TIMO lands under conservation easement + State lands) with TIMO lands not under conservation easement using simple species-by-species t tests with Holm-Bonferroni correction for multiple comparisons (Holm 1979). Twelve species differed significantly (adjusted $P < 0.05$) between the two management groups. Black-capped Chickadee ($\mu = 4.15$), Blue-headed Vireo ($\mu = 7.23$), Blackburnian Warbler ($\mu = 9.35$), Brown Creeper ($\mu = 8.28$), Common Raven ($\mu = 8.58$), Mourning Warbler ($\mu = 8.82$), Northern Parula ($\mu = 7.84$), Rose-breasted Grosbeak ($\mu =$

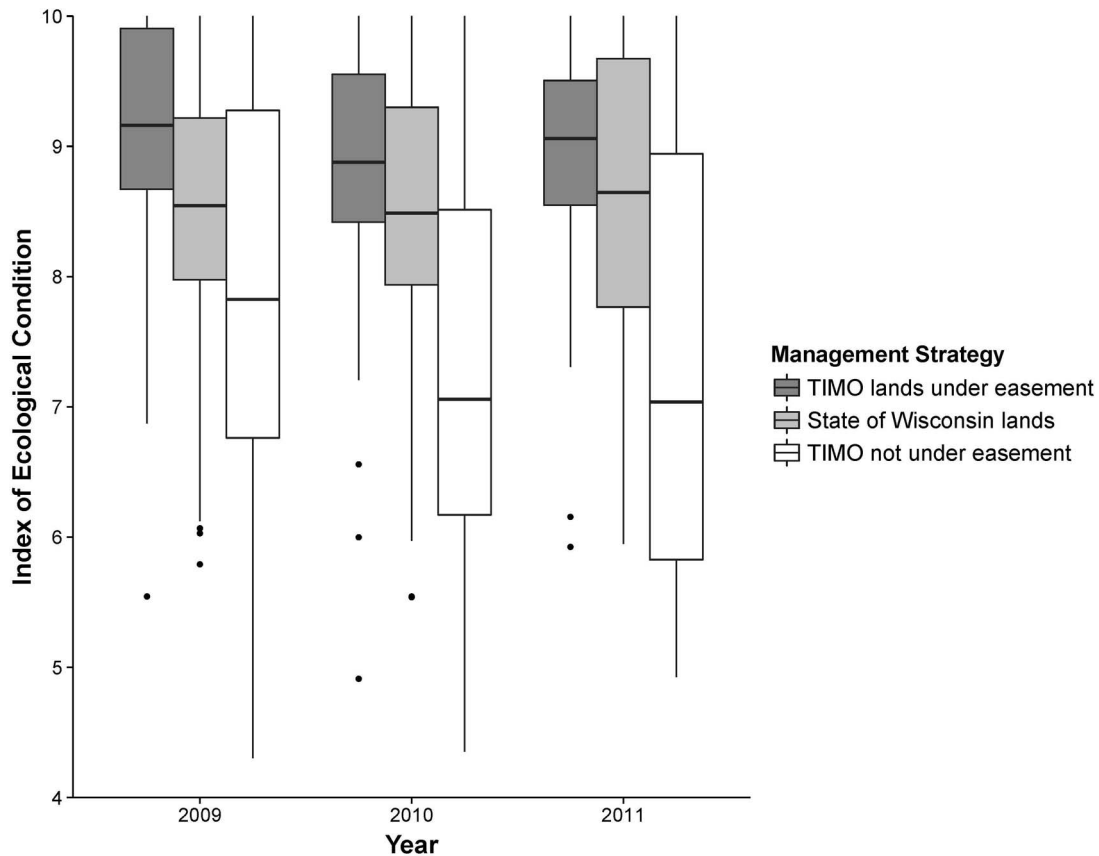


Fig. 5. Box and whisker plots display the index of ecological condition (IEC; presence/absence method) of three management strategies in the Wild Rivers Legacy Forest in northeastern Wisconsin based on 200 bird surveys each conducted in 2009, 2010, and 2011. Management strategies include Timber Investment Management Organization (TIMO) lands under a working forest conservation easement ($n = 80$), State of Wisconsin lands ($n = 80$), and TIMO lands not under an easement ($n = 40$). The difference among the three management strategies was statistically significant ($P < 0.0001$). The interaction term (year \times management strategy) and year were not statistically significant factors.

8.01), and Winter Wren ($\mu = 8.85$) were significantly more frequent at protected forest sites (conservation easement or State owned), whereas American Crow ($\mu = 1.86$), Eastern Wood-Pewee ($\mu = 7.11$), and Veery ($\mu = 6.57$) were more common at sites with no conservation easement. Except for Black-capped Chickadee (whose distribution in more urbanized areas is likely affected by bird feeding), these results are consistent with the previously calculated responses to the “human footprint” (Table 4). Forests within the conservation easement or State ownership tended to be characterized by species whose BR functions exhibited a high mean (μ), while unprotected sites with lower IEC scores

tended to be inhabited by species whose BR functions exhibited lower means. Smaller but statistically significant differences in IEC scores between the TIMO easement sites and State-owned lands were mainly attributable to differences in Blackburnian Warbler, which was significantly more frequent at sites in the TIMO easement lands, and American Crow, Mourning Dove ($\mu = -10.0$), and Veery, which were more frequent in State-owned lands.

DISCUSSION

Species responses to environmental gradients have been analyzed by many researchers follow-

ing Robert Whittaker's classic work (Whittaker 1956, 1967), although direct field studies have lagged behind theoretical applications. Excellent examples of environmental gradient analysis include quantitative studies of birds (Terborgh 1977), trees (Austin et al. 1985), old field plants (Tilman 1987), diatoms (Oksanen et al. 1988), and the general analysis of community and environmental variables (canonical correspondence analysis) developed by Ter Braak (1986).

One of the most important applications of gradient analysis has been the analysis of species' responses to environmental degradation. For example, small mammal diversity was found to be negatively associated with human development within 500 m of forest remnants in Australia (Brady et al. 2009, Brady et al. 2011). Bird species composition has been shown by multiple studies to vary significantly across gradients of urban/suburban development (Crooks et al. 2004, Miller et al. 2007). Effects of anthropogenic development on native arthropods, plants, and amphibians have been documented recently by Sattler et al. (2010), Vallet et al. (2010), and Hamer and Parris (2011), respectively. Indeed, urbanization has been characterized as a "massive unplanned experiment" (McDonnell and Pickett 1990), providing an opportunity for ecologists to explore both theoretical and applied questions about ecosystem structure and function. Ecological studies of these developed landscapes can be vitally important in guiding successful ecological planning and restoration efforts (Ramalho and Hobbs 2012).

Anthropogenic landscape degradation can be inferred by remotely-sensed land cover variables, fragmentation metrics, and other measures of human activity (e.g., road density), similar to the approach of Bryce et al. (2002) and Browder et al. (2002). We used principal components analysis to reduce a relatively uncorrelated subset of these variables to a single axis of condition scaled from 0 (maximally disturbed) to 10 (minimally disturbed). Many forest bird species in our study area were sensitive (either positively or negatively) to this landscape disturbance gradient (Table 4), a result that is consistent with findings of Blair (1996), Howe et al. (2007a), Minor and Urban (2010), and others. For example, researchers have found that Blackburnian Warbler, Black-throated

Green Warbler, Least Flycatcher, Mourning Warbler, Red-breasted Nuthatch, Red-eyed Vireo, Ovenbird, and Yellow-bellied Sapsucker responded negatively to landscape disturbance (Miller et al. 2007), just as we did. Like us, they also found that Brown-headed Cowbird, Common Grackle, European Starling, House Sparrow, and Mourning Dove responded positively to disturbance (Miller et al. 2007). These parallels suggest that breeding birds are robust indicators of at least some elements of forest landscape integrity.

Biotic response (BR) functions (Table 4, Fig. 3) help identify sensitive species and provide quantitative information about the nature of these sensitivities; many bird species in our study area exhibited negative responses, while fewer numbers of species showed positive responses to the collective "human footprint." Among the 38 bird species with the strongest BR functions, 28 (74%) yielded estimates of μ greater than 5.0, indicating a negative response to the local "human footprint." Local populations of breeding birds and other species must integrate many complex dimensions of environmental quality, including food web dynamics, legacy effects of past events (Foster et al. 2003), and altered disturbance regimes (Pickett and Thompson 1978, Ramalho and Hobbs 2012). Our results suggest that human activities in Wisconsin forest landscapes influence these and other drivers of environmental quality for birds; in most cases the influence is negative.

The explicit estimation of BR functions enables us to predict the effects of changes in the environmental condition of forests, as measured by the environmental reference (stress) gradient (C_{env}) used to generate quantitative species response patterns. For example, an increase in forest fragmentation (one of the influential variables in our calculation of C_{env}) will be expected to cause population declines in Ovenbird, Red-eyed Vireo, Black-throated Green Warbler, and other species that showed a strong response to our reference gradient (Table 4). We could dissect this gradient into more specific environmental variables (e.g., habitat fragmentation metrics) to further explore species' responses to environmental stress. The BR functions also help make the index of ecological condition (IEC) calculations more transparent. Differences

among management treatments at the Wild Rivers Legacy Forest in Wisconsin, for example, can be attributed to differences in the occurrences of species that have been explicitly shown to respond positively or negatively to our quantitative “human footprint.”

Today, virtually every effective, long-range approach to natural resource management requires some type of systematic monitoring (Nichols and Williams 2006). Indeed, long-term monitoring is central to widely embraced approaches like adaptive management (Walters 1986, McCarthy and Possingham 2007) and integrated pest management (Hobbs and Humphries 1995, Cumming and Spiesman 2006). Given ongoing and potentially accelerating threats such as the spread of invasive species (Holdsworth et al. 2007, Corio et al. 2009), climate change (Scheller and Mladenoff 2005, Jones et al. 2012), and habitat or landscape degradation (Radeloff et al. 2005, Hawbaker et al. 2006), the need for effective monitoring of forest ecosystems is widely recognized (Riitters et al. 1992, Failing and Gregory 2003, Woodall et al. 2011). Our analysis of breeding bird assemblages in northern Wisconsin demonstrates a novel approach to ecological monitoring of managed forest landscapes. Our goal was to develop a monitoring framework that is scientifically rigorous, transparent, and cost-effective.

Species-based (biotic) metrics like the IEC are advantageous over physical (abiotic) measurements of environmental quality (e.g., habitat fragmentation) because (1) abiotic environmental measurements are often highly variable over time, (2) species distributions reflect many ecologically relevant but, in some cases, unmeasured environmental stressors, (3) species responses incorporate interactions among environmental variables, and (4) species distributions reflect biologically meaningful responses to environmental stressors, whereas environmental variables might be just surrogates of critical stressors (Karr and Chu 1999, Niemi and McDonald 2004).

By including multiple indicator species in the calculation of IEC values, we inherently address multiple functions of a forest ecosystem or landscape (Carignan and Villard 2002). The value of species assemblages as indicators of ecosystem health has been recognized by many other

researchers (Karr and Chu 1997, Bradford et al. 1998, Brooks et al. 1998, O’Connell et al. 1998, Canterbury et al. 2000, O’Connell et al. 2000, Browder et al. 2002, Bryce et al. 2002, Glennon and Porter 2005, Howe et al. 2007a, b). In this analysis we used all bird species that were adequately abundant and showed consistent responses to environmental disturbance. A more strategic ecosystem function approach to selecting indicator assemblages (e.g., Karr 1981) can easily be incorporated into the IEC framework. For example, weakly documented biotic response (BR) functions of rare species might be replaced by more robust BR functions describing the probability of occurrence of at least one individual from a functional group or a suite of rare species. Uncommon diurnal raptor species such as Broad-winged Hawk (*Buteo platypterus*), Northern Goshawk (*Accipiter gentilis*), and Red-shouldered Hawk (*Buteo lineatus*) might be combined into a single category, where the BR function quantifies the probability of finding an individual of any one of these three species. In order to identify and address the key components of biological integrity for forest ecosystems on a large geographic scale, we suggest classifying indicator bird species into guild types, as defined by O’Connell et al. (2000) and applied by Glennon and Porter (2005). For example, one could classify species into general bird guild types such as compositional (e.g., origin), structural (e.g., nest placement), and functional (e.g., trophic) guilds (O’Connell et al. 2000). In the absence of region-specific BR functions, a forest IEC model derived from one area could be applied to forested regions with different bird community composition by substituting species according to guild classifications (e.g., substituting a ground forager common in one region [Hermit Thrush] with a ground forager common to another region [Wood Thrush, *Hylocichla ustulata*]). This approach might be especially important in light of regional climate change (Scheller and Mladenoff 2005). For example, species whose geographic ranges shift northward from the western Great Lakes region might need to be replaced with ecologically similar species exhibiting similar patterns of sensitivity to environmental stress. Although our analysis focused on bird assemblages in northern Wisconsin, the method that we have described is

both flexible and portable. Calculation of a site-specific IEC can combine information from multiple taxonomic groups as long as quantitative BR functions are explicitly described in advance (Howe et al. 2007a).

In summary, we have demonstrated that breeding bird assemblages are remarkably sensitive to the “human footprint” in a forest-dominated region of northern Wisconsin. Other researchers (O’Connell et al. 2000, Bryce et al. 2002, Glennon and Porter 2005) using different methods and at different places have reached similar conclusions. Bird assemblages represent only part of an area’s ecological condition, but because birds are generally diverse and can be reliably sampled, they provide a cost-effective means of assessing spatial and temporal variation in environmental quality. The BR functions and IEC framework that we present here provide a basis for numerous forest inventory and monitoring applications, including identification of priority conservation areas and certifying sustainable forestry management practices. Demands for rigorous, cost-effective methods of monitoring environmental quality in forests and other habitats are greater than ever today. Thanks to the availability of high speed computers for iteratively estimating model parameters, the method presented here is both practical and easily generalized to other systems and taxa. The IEC approach serves a dual purpose by (1) explicitly identifying species’ responses to environmental stressors and (2) providing a tool for quantifying spatial and temporal variation in ecological condition based on the composition of biotic assemblages.

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