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One Hundred Fifty Years of Change in Forest Bird Breeding Habitat: Estimates of Species Distributions

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Abstract

Evaluating bird population trends requires baseline data. In North America the earliest population data available are those from the late 1960s. Forest conditions in the northern Great Lake states (U.S.A.), however, have undergone succession since the region was originally cut over around the turn of the twentieth century, and it is expected that bird populations have undergone concomitant change. We propose pre-Euro-American settlement as an alternative baseline for assessing changes in bird populations. We evaluated the amount, quality, and distribution of breeding bird habitat during the mid-1800s and early 1990s for three forest birds: the Pine Warbler (Dendroica pinus), Blackburnian Warbler (D. fusca), and Black-throated Green Warbler (D. virens). We constructed models of bird and habitat relationships based on literature review and regional data sets of bird abundance and applied these models to widely available vegetation data. Original public-land survey records represented historical habitat conditions, and a combination of forest inventory and national land-cover data represented current conditions. We assessed model robustness by comparing current habitat distribution to actual breeding bird locations from the Wisconsin Breeding Bird Atlas. The model showed little change in the overall amount of Pine Warbler habitat, whereas both the Blackburnian Warber and the Black-throated Green Warbler have experienced substantial habitat losses. For the species we examined, habitat quality has degraded since presettlement and the spatial distribution of habitat shifted among ecoregions, with range expansion accompanying forest incursion into previously open habitats or the replacement of native forests with pine plantations. Sources of habitat loss and degradation include loss of conifers and loss of large trees. Using widely available data sources in a habitat suitability model framework, our method provides a long-term analysis of change in bird habitat and a presettlement baseline for assessing current conservation priority.

One Hundred Fifty Years of Change in Forest Bird Breeding Habitat: Estimates of Species Distributions

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Abstract: *Evaluating bird population trends requires baseline data. In North America the earliest population data available are those from the late 1960s. Forest conditions in the northern Great Lake states (U.S.A.), however, have undergone succession since the region was originally cut over around the turn of the twentieth century, and it is expected that bird populations have undergone concomitant change. We propose pre-Euro-American settlement as an alternative baseline for assessing changes in bird populations. We evaluated the amount, quality, and distribution of breeding bird habitat during the mid-1800s and early 1990s for three forest birds: the Pine Warbler (*Dendroica pinus*), Blackburnian Warbler (*D. fusca*), and Black-throated Green Warbler (*D. virens*). We constructed models of bird and habitat relationships based on literature review and regional data sets of bird abundance and applied these models to widely available vegetation data. Original public-land survey records represented historical habitat conditions, and a combination of forest inventory and national land-cover data represented current conditions. We assessed model robustness by comparing current habitat distribution to actual breeding bird locations from the Wisconsin Breeding Bird Atlas. The model showed little change in the overall amount of Pine Warbler habitat, whereas both the Blackburnian Warber and the Black-throated Green Warbler have experienced substantial habitat losses. For the species we examined, habitat quality has degraded since presettlement and the spatial distribution of habitat shifted among ecoregions, with range expansion accompanying forest incursion into previously open habitats or the replacement of native forests with pine plantations. Sources of habitat loss and degradation include loss of conifers and loss of large trees. Using widely available data sources in a habitat suitability model framework, our method provides a long-term analysis of change in bird habitat and a presettlement baseline for assessing current conservation priority.*

Key Words: avian ecology, conservation planning, habitat suitability modeling, historical range of variability, landscape ecology, pre-Euro-American settlement, Wisconsin

Ciento Cincuenta Años de Cambios en el Hábitat para Reproducción de Aves de Bosque: Estimación de la Distribución de Especies

Resumen: *La evaluación de tendencias de las poblaciones de aves requiere de datos de referencia. En Norte América, los primeros datos disponibles de poblaciones son del final de la década de 1960. Sin embargo, las condiciones de los bosques en los estados de los Grandes Lagos (E.U.A.) han experimentado sucesión desde que la región fue talada en los inicios del siglo veinte, y se espera que las poblaciones de aves hayan experimentado cambios concomitantes. Proponemos que se considere al período previo a la colonización euro americana como referencia alternativa para evaluar los cambios en las poblaciones de aves. Evaluamos la cantidad, calidad y distribución del hábitat para reproducción de tres especies de aves de bosque (*Dendroica pinus*, D. fusca y D. virens) a mediados del siglo XIX e inicios del XX. Construimos modelos de las relaciones entre las aves y el hábitat con base en la literatura y conjuntos de datos de abundancia de aves y los aplicamos a los datos*

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de vegetación ampliamente disponibles. Los registros topográficos de tierras públicas originales representaron las condiciones históricas del hábitat, y una combinación de datos del inventario forestal y de cobertura de suelo representaron las condiciones actuales. Evaluamos la robustez del modelo mediante la comparación de la distribución de hábitat actual con sitios de reproducción de aves registrados en el Wisconsin Breeding Bird Atlas. El modelo mostró poco cambio en la cantidad total de hábitat de Dendroica pinus, *mientras que tanto* D. fusca *como* D. virens *han experimentado pérdidas sustanciales de hábitat. Para las especies examinadas, la calidad del hábitat se ha degradado desde antes de la colonización y la distribución espacial del hábitat cambió entre ecoregiones, con la expansión del rango acompañando la incursión de bosques en hábitats anteriormente abiertos o el reemplazo de bosques nativos con plantaciones de pinos. Las fuentes de pérdida y degradación de hábitats incluyen la pérdida de coníferas y de árboles grandes. Mediante la utilización de fuentes de datos ampliamente disponibles en un modelo de aptitud de hábitat, nuestro método proporciona un análisis a largo plazo de los cambios en el hábitat de aves y una referencia precolonización para evaluar prioridades de conservación actuales.*

Palabras Clave: aptitud del hábitat, ecología aviar, ecología de paisaje, planificación de conservación

Introduction

Choosing appropriate baseline ecological conditions is critical for quantifying change (Stohlgren et al. 1995; Arcese & Sinclair 1997; Moore et al. 1999), but conservationists struggle to identify baselines because of contrasting notions of what constitutes a useful reference and a lack of data from critical time periods. North American landscapes have changed significantly in recent decades because of change in land-use practices, alteration of disturbance regimes, and introduction of alien species (Palmer et al. 2004). One anticipated consequence of such change is loss of native biodiversity (Theobald et al. 1997). Understanding a species' status just before rapid change provides land managers with a benchmark against which to measure its present distribution and abundance, which facilitates the prioritization and evaluation of conservation practices.

One approach to understanding change in populations has been to use long-term data sets. For example, the Breeding Bird Survey (BBS) was designed to monitor the status and trends of breeding bird populations across North America (Robbins et al. 1986). Available since the late 1960s, BBS data are extremely valuable for assessing avian population trends and have been instrumental in quantifying the decline of songbirds in North America (Flather & Sauer 1996; Sauer et al. 2003). What is lacking, however, is a way to estimate baseline species population levels before anthropogenic land-use and land-cover change was widespread.

The period just before Euro-American settlement (hereafter, presettlement) has been used as an alternative baseline for assessing trends in North American plants and animals. Conditions before settlement have been used to establish reference conditions in old-growth forests of the Pacific Northwest (Cissel et al. 1994), floodplain forests of the upper Mississippi River (Knutson & Klass 1998), and the heathlands of Martha's Vineyard (Motzkin & Foster

2002). Presettlement records have been used to identify likely changes in avian trends in abundance and distribution in Missouri River woodlands (Rumble & Gobeille 1998) and the Chihuahuan Desert (Pidgeon et al. 2001). This period represents ecological conditions before the extensive and rapid changes in land use, alteration of disturbance regimes, and introduction of alien species associated with the shift to Euro-American land tenure.

In Wisconsin the mid-1800s provide a reasonable baseline for estimating change associated with Euro-American settlement. Northern Wisconsin was dominated by extensive mature conifer and mixed-hardwood forest (Schulte et al. 2002), and the predominant oak savannas of southern Wisconsin were interspersed with tallgrass prairies, oak (*Quercus*) and maple-basswood (*Acer-Tilia*) forests, and wetlands (Bolliger et al. 2004). The extent and arrangement of these land-cover types have changed greatly in the 150 years since Wisconsin became a state (Radeloff et al. 1999; Bolliger et al. 2004)—vegetation change during this period exceeded that of the previous 850 years by 2.4 times (Cole et al. 1998). More recent baseline ecological data do not take into account the effects of the sweeping change in land use around the turn of the twentieth century (Fries 1951), thus providing a snapshot of habitat, and probably populations, in flux due to succession. More recent baseline data are valuable, but the presettlement period is critical for understanding comprehensive change due to anthropogenic causes.

Using presettlement conditions as a baseline, we developed a method for assessing changes in forest bird habitat and, by inference, changes in the populations of three avian species. The Pine Warbler (*Dendroica pinus*) has a strong association with mature pines (Morse 1989; Niemi et al. 1997), a relationship that facilitated our initial development of methodology (Pidgeon et al. 2005). Here we expand the technique to the Blackburnian (*D. fusca*) and Black-throated Green Warblers (*D. virens*), species with habitat associations that are fairly well known and

that are of management concern in the Boreal Hardwood Transition Zone, which includes Wisconsin (Matteson et al. 2003). Our objectives were to quantify changes in the amount, quality, and distribution of habitat for these bird species; locate present-day conservation areas of priority for forest birds; and broaden the temporal perspective considered in biodiversity conservation planning to include the presettlement period.

Methods

We developed models of habitat suitability for each bird species based on published habitat associations, existing regional bird monitoring data sets, and expert knowledge (Table 1). Because of variation in vegetation and habitat associations over the species' ranges, data on habitat use from the Great Lake states generally, and Wisconsin specifically, were given stronger consideration in our model development than data from elsewhere. We assumed that the habitat relationships of these species and the set of factors driving regional bird abundance have not changed between presettlement and today.

Data on habitat distribution were derived from a variety of sources. Presettlement habitat was based on U.S. General Land Office original public land survey (PLS) records (Stewart 1935). These records were collected between 1832 and 1866 in Wisconsin and provide spatially explicit data on land-cover characteristics before the late 1800s, when widespread land-cover change occurred (Fries 1951). Data on current habitat was derived from a combination of U.S. Department of Agriculture Forest Service forest inventory and analysis (FIA) data and national land cover data (NLCD). The FIA is a national plot-based survey designed to assess changes in timber resources (Miles et al. 2001), and early 1990s FIA data were used to estimate stand-level habitat characteristics (Schmidt 1997). The NLCD is derived from 1992 Landsat Thematic Mapper satellite imagery (Vogelmann et al. 2001) and was used to estimate landscape-scale forest fragmentation (Riitters et al. 2002).

We summarized all habitat data by land type association (LTA) polygons (Fig. 1), one level of ecoregional patterning in a hierarchical ecoregion classification (WI DNR 1999). The LTA ecoregions correspond to patterns in geomorphology, surficial geology, elevation, soil, local climate, and potential natural vegetation (Cleland et al. 1997). In Wisconsin LTAs vary between 12.2 and 3,847.3 km^2, with a mean of 499.1 km^2 (WI DNR 1999).

Presettlement Habitat Data

We used bearing-tree data from the PLS to estimate forest composition and stand- and landscape-level structural habitat characteristics by ecoregion. Bearing-tree data

Table 1. Criteria used to model pre-Euro-American settlement habitat distribution for three wood warblers (*Dendroica* spp.), and data sources from which they were derived.

| Habitat category	Criteria	Sources
All three species		
tree density	forest (>47 trees/ha)	Morse 1993, 1994; Rodewald et al. 1999
Pine Warbler		
pine dominance	>10% pine species	Robbins et al. 1989; Hoffman & Mossman 1990
tree composition	(white pine = red pine) > jack pine > all else	Hanowski & Niemi 1991*a*, 1991*b*; Howe & Roberts 2005
stand age	mature > nonmature (≥50 cm dbh > 40–49 cm > 30–39 cm > all else)	Collins et al. 1982; Hoffman & Mossman 1990; Rodewald et al. 1999
Blackburnian Warbler		
conifer dominance	>10% conifer species	Holmes & Robinson 1981; Doepker et al. 1992
tree composition	(% hemlock; high > low) >(% conifer; high > low) > all else	Martin 1960; Hanowski & Niemi 1991*a*, 1991*b*; Collins et al. 1982; Morse 1994; Howe & Mossman 1995; Howe & Roberts 2005
stand age	mature > nonmature (≥50 cm dbh > 40–49 cm > 30–39 cm > all else)	Webb et al. 1977; Titterington et al. 1979; Collins et al. 1982; Hanowski & Niemi 1991*a*, 1991*b*
landscape context	more contiguous > less contiguous forest (≥50% contiguous forest > 30–50%; else, nonhabitat)	R. Howe, personal communication
Black-throated Green Warbler		
conifer dominance	>10% conifer species	Morse 1993; Robichaud & Villard 1999
tree composition	hemlock > (northern hardwood = white pine = red pine) > (lowland hardwood = white birch)	Collins et al. 1982; Morse 1993; Howe & Mossman 1995; Davis 1996; Howe & Roberts 2005
stand age	mature > nonmature (≥ 50 cm dbh > 40–49 cm > 30–39 cm > all else)	Morse 1976; Holmes & Sherry 2001
landscape context	>25% contiguous forest	R. Howe, personal communication; Freedman et al. 1981; Holmes & Sherry 2001
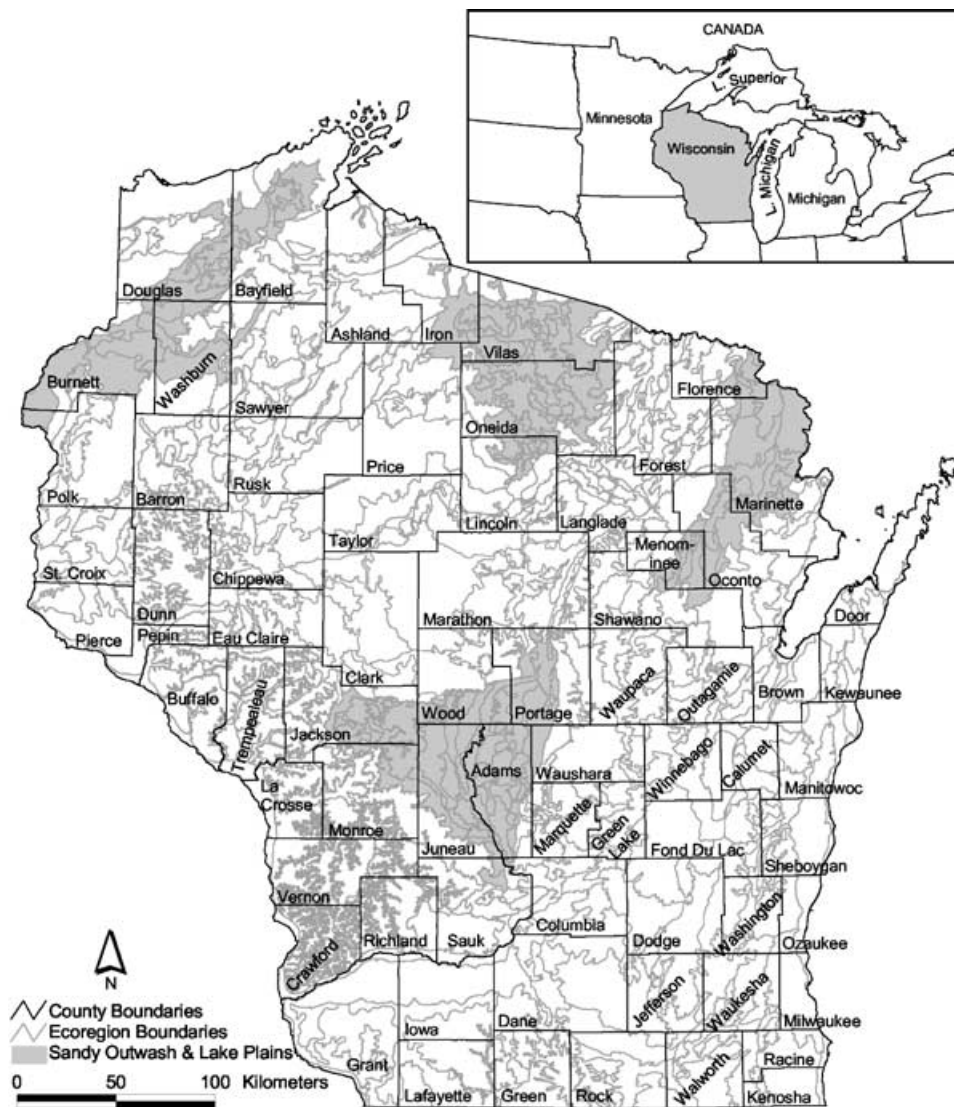
Figure 1. Study area with county and ecoregion boundaries shown; ecoregions dominated by sandy glacial outwash shown in gray.

were collected at survey section and quarter corners, located at 0.8-km (0.5-mi) intervals along the 2.6-km^2 (1-mi^2) PLS grid framework covering the entire state. (See Stewart [1935] for a full description of the PLS and Manies et al. [2001] for an evaluation of its advantages and limitations.) Section corners are located where gridlines intersect and quarter corners are located halfway between these intersections. At survey corners, surveyors recorded information on up to four bearing trees, including their species, diameter, azimuth, and the distance between the bearing tree and the corner. The density of PLS corners contained within an ecoregion varies between 1.0 and 1.3/km^2. We used bearing-tree diameters and distances to estimate stand-scale forest structure.

We estimated relative forest fragmentation by comparing tree density, as derived from bearing-tree distances (Cottam & Curtis 1956; Anderson & Anderson 1975), at each survey corner to tree densities at neighboring survey corners. For section corners the neighborhood consisted

of the four closest quarter corners, each 0.8 km away. For quarter corners the neighborhood consisted of the two nearest section corners, 0.8 km away, and a random draw of two of the four nearest quarter corners, 1.1 km away. Unequal distances for nearest neighbors is an artifact of the PLS sampling design, which cannot be modified; randomly drawing two of the four nearest quarter corners in defining quarter-corner neighborhoods, however, created a sample as similar as possible to that of the section corners. If a survey corner was defined as "forested" (=100 trees/ha) and one of its neighboring corners was defined as "open" (=47 trees/ha; Anderson & Anderson 1975), then that corner was considered fragmented. Because we assumed the bird species in question would not respond to subtle density differences, only gross differences in tree densities were considered (i.e., = 100 trees/ha and = 47 trees/ha). The proportion of all corners within an ecoregion characterized as fragmented constituted the landscape-level fragmentation estimate.

Current Habitat Data

We used early 1990s FIA data to capture stand-level composition and structure for the current period (Schmidt 1997). Tree species, size, and density data from FIA plots were summarized by ecoregion. The density of FIA plots contained within an ecoregion averages $1/13.9$ km^2 and varies between $1/6.7$ and $1/105.4$ km^2. Forest fragmentation estimates for the current period were obtained from a national analysis of the NLCD (Riitters et al. 2002). A square analysis window of 9×9 pixels (7.29 ha) was iteratively centered on each subject forest pixel (coniferous, deciduous, mixed, and wetland forest classes combined). We defined the subject pixel as interior forest if it and all other pixels within the analysis window were in forest land cover. The fragmentation index was then based on the proportion of interior forest pixels within the ecoregion.

Habitat Suitability Modeling

We developed models of habitat suitability in Excel 2003 (Microsoft, Seattle, Washington) and linked models with ecoregion data in ArcView (ESRI 1999) to obtain spatial estimates. Habitat relationships were first developed and applied to current vegetation data sources and then, as a measure of model performance, we compared the current habitat suitability map with current known bird distributions from the Wisconsin Breeding Bird Atlas (WSO 2002) through spatial overlays in ArcView (ESRI 1999; Table 2). We calculated omission error, commission error, and KHAT (estimate of the Kappa coefficient) (Landis & Koch 1977) as measures of model accuracy.

Pine Warblers have the narrowest breeding habitat criteria of the three species we modeled—they are strongly associated with mature pine forests (Green 1992; Niemi et al. 1997). In Wisconsin, Pine Warblers show near equal preference for white and red pine (*Pinus resinosa* Ait.) and lower preference for jack pine (*P. banksiana* Lamb; Hoffman & Mossman 1990; Hanowski & Niemi 1991*a*, 1991*b*; Howe & Roberts 2005). A positive relationship with stand age also has been documented (Collins et al. 1982; Rodewald et al. 1999). Our habitat suitability model for the Pine Warbler (HS$_{PIWA}$) was based on these criteria and took the form of

$$HS_{PIWA} = \text{forest cutoff} * \text{pine cutoff}$$
$$* (\text{white pine dominance} + \text{red pine dominance})$$
$$* (\text{jack pine dominance}/2),$$

where "cutoff" denotes a cutoff point between habitat and nonhabitat (see Table 1 for numeric criteria).

The Blackburnian Warbler breeds in forests extending from the northeastern United States and adjacent Canada to Saskatchewan south through the Appalachian Mountains (Morse 1994). It is closely associated with conifer in the northern part of its range, and forests with greater proportions of conifer generally provide more suitable

Table 2. A comparison of the number of land-type-association ecoregions designated as habitat or nonhabitat for three bird species during the current period based on habitat suitability models and Wisconsin Breeding Bird Atlas data (WBBA; WSO 2002).

	Modeled habitat	Modeled nonhabitat	Total
Pine Warbler			
WBBA habitat	110	63	173
WBBA nonhabitat	29	230	259
total	139	293	432
omission error			36.4%
commission error			20.9%
KHAT*			0.54
Blackburnian Warbler			
WBBA habitat	111	28	139
WBBA nonhabitat	40	253	293
total	151	281	432
omission error			20.1%
commission error			26.5%
KHAT*			0.65
Black-throated Green Warbler			
WBBA habitat	150	56	206
WBBA nonhabitat	24	202	226
total	174	258	432
omission error			27.2%
commission error			13.8%
KHAT*			0.63

*Estimate of the Kappa coefficient. The KHAT values of >0.8 represent strong agreement; 0.4–0.8 moderate agreement; and <0.4 poor agreement (Landis & Koch 1977).

habitat (Doepker et al. 1992; Morse 1994). Although the species uses northern deciduous forest for foraging, it is generally absent in areas without conifers (Holmes & Robinson 1981). In the western part of its range, the Blackburnian Warbler prefers eastern hemlock (*Tsuga canadensis* [L.] Carr.; Martin 1960; Howe & Mossman 1995) and eastern white pine (*P. strobus* L.; Howe & Roberts 2005). Mature forests with large-diameter trees are preferred to young forests (Titterington et al. 1979; Collins et al. 1982; Doepker et al. 1992), and local population declines may follow removal of large trees (Webb et al. 1977). In Canada Blackburnian Warblers are virtually absent from forests fragmented by agriculture but are common in contiguous forest (Hobson & Bayne 2000). Using these criteria, the Blackburnian Warbler habitat suitability model (HS$_{BLBW}$) took the form of

$$HS_{BLBW} = \text{forest cutoff} * \text{pine cutoff}$$
$$* \text{tree diameter class} * \text{fragmentation cutoff}$$
$$* (\text{hemlock dominance} + \text{percent conifer}),$$

where "cutoff" denotes a cutoff point between habitat and nonhabitat and "tree diameter class" is a weighting based on the average size of trees in the ecoregion (Table 1).

The Black-throated Green Warbler has a large breeding range encompassing a wide variety of forest types (Morse

1993). The species is generally associated with coniferous forest (Morse 1993; Robichaud & Villard 1999); it also breeds, however, in mixed deciduous-conifer forest or even exclusively in deciduous forest (Morse 1993; Davis 1996). In Minnesota the Black-throated Green Warbler occurs primarily in mature, undisturbed forest containing conifers (Collins et al. 1982). Hemlock is a preferred species in northern Wisconsin (Howe & Mossman 1995), but in locations where hemlock density is low northern hardwoods and aspen-conifer forests are preferred to lowland hardwood and ash-aspen forests (Davis 1996; Howe & Roberts 2005). The Black-throated Green Warbler prefers mature forest to young forest and contiguously forested landscapes to fragmented ones (Robichaud & Villard 1999; Hobson & Bayne 2000). Our habitat suitability model (HS_{BTNW}) for the Black-throated Green Warbler consisted of

$$
\begin{aligned}
HS_{BTNW} = {} & \text{forest cutoff} * \text{pine cutoff} \\
& * \text{tree diameter class} * \text{fragmentation cutoff} \\
& * (\text{hemlock dominance} * 2 \\
& + \text{northern hardwoods} \\
& + \text{white pine} + \text{red pine} \\
& + \text{lowland hardwoods}/5).
\end{aligned}
$$

Northern hardwoods included American beech (*Fagus americana* Ehrh.), sugar maple (*Acer saccharum* Marsh.), American basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britton), and white ash (*Fraxinus americana* L.). Lowland hardwoods included silver maple (*A. saccharinum* L.), river birch (*B. nigra* L.), eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.), American elm (*Ulmus americana* L.), slippery elm (*U. rubra* Muhl.), and black ash (*F. nigra* Marsh.).

These models—developed based on current vegetation data and evaluated using current Wisconsin Breeding Bird Atlas data—were then applied to the historical vegetation data. For mapping we grouped habitat suitability into six categories, defined by percentage of the maximum habitat suitability value for each species across the two periods. The zero category was considered unsuitable.

Results

Pine Warbler

A comparison of the model of current habitat with the distribution of breeding Pine Warblers revealed moderately good model fit (Landis & Koch 1977), although our predictive ability for this species was poorest overall (Table 2; Figs. 2a & 2b). The areas of suitable habitat corresponded to the geographic distribution of the pineries in Wisconsin (Bolliger et al. 2004). Minor discrepancies between the two maps included an area of west-central Wisconsin, where the model may have erroneously predicted habitat (La Crosse County; Fig. 1), and scattered areas

where the model failed to identify suitable habitat (Douglas and Door counties and isolated forests in the south).

Habitat location and overall quality changed (Figs. 2b & 2c). There was no appreciable net gain or loss in the overall extent of habitat between the two periods (Table 3; 0.5%); the range of suitable habitat, however, expanded in some locations and contracted in others. Changes in habitat quality included a 10.2% increase in the number of ecoregions within the lowest suitability category and decreases in all higher suitability categories (Table 3). The mean value of change in habitat suitability among ecoregions experiencing changes was −11.6%. Positive changes in habitat suitability occurred in 22.2% of ecoregions and averaged 10.0%. Negative changes occurred in 30.5% of all ecoregions and 92.1% of ecoregions that historically provided habitat and averaged −27.7%. The proportion of white and red pine decreased in 75% of ecoregions (Table 4).

Blackburnian Warbler

The modeled habitat distribution for the current period captured the distribution of breeding Blackburnian Warblers with moderately good fit (Landis & Koch 1977; Table 2; Figs. 3a & 3b). Small discrepancies included failure of the model to identify areas of breeding activity on the northernmost portion of the Door Peninsula and in two isolated forested ecoregions in southern Wisconsin. The model may have overpredicted habitat in the central portion of the state in ecoregions straddling the Wisconsin River (Juneau and Adams counties).

Changes in both habitat distribution and suitability between the current and presettlement periods were substantial (Figs. 3b & c.). The range of suitable habitat contracted northward, and entire counties that were highly suitable historically and made up the southern border of habitat in the state are now unsuitable or minimally suitable habitat. Approximately 15% fewer ecoregions were classed as habitat at present (Table 3). In presettlement times 32% of the state was classed as ≥20% suitability, whereas < 2% of the current area fell into these categories. Reasons for the decline in habitat quality include a decrease in the proportion of hemlock in 94% of ecoregions and a reduction of forest age in up to 62% of ecoregions (Table 4). Blackburnian Warbler habitat degradation or loss occurred in 47.8% of all ecoregions and 95.3% of ecoregions that historically provided habitat, with an average decline in habitat suitability of 23.3%.

Black-Throated Green Warbler

Correspondence between the current modeled habitat distribution and the location of breeding Black-throated Green Warblers was moderately good (Table 2; Figs. 4a & 4b). Our model captured the spatial distribution of birds,
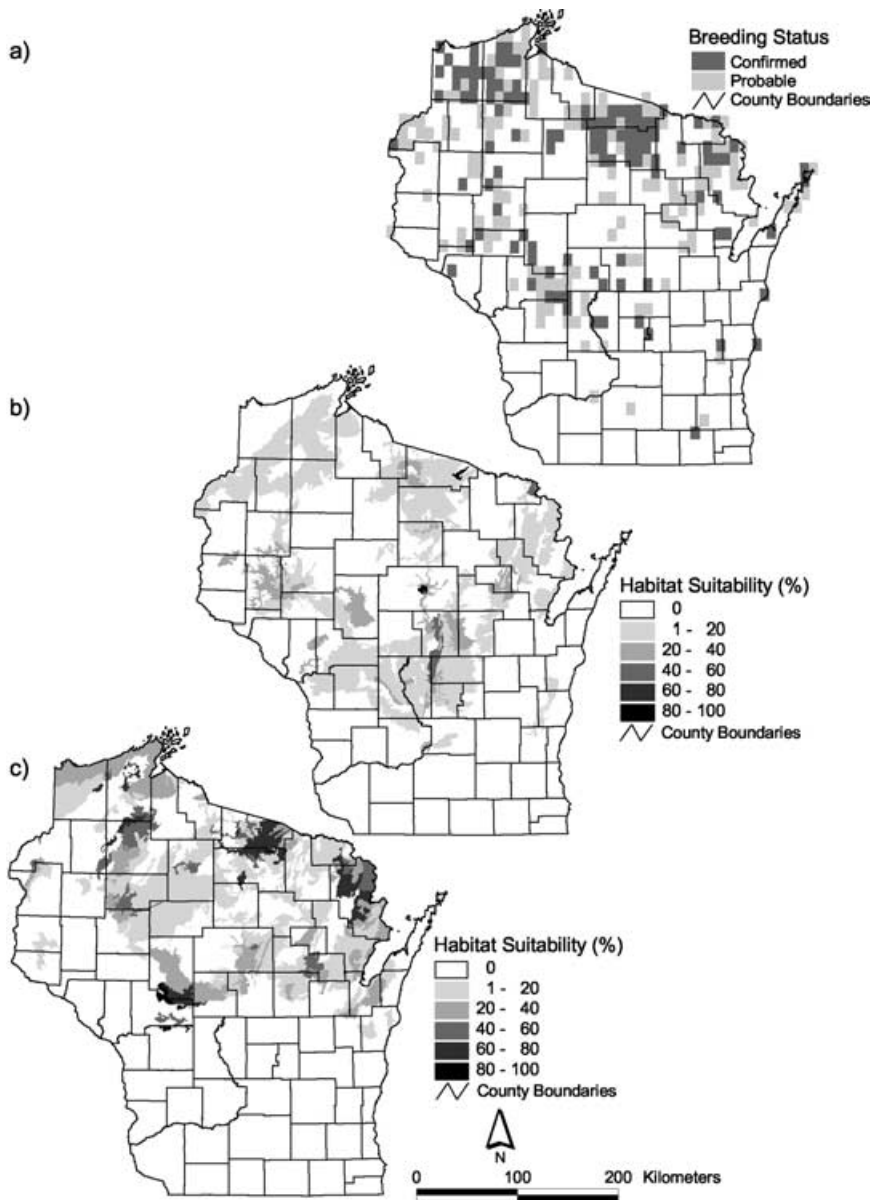
Figure 2. Pine Warbler (a) breeding bird locations (WSO 2002), (b) current habitat, and (c) presettlement habitat.

Table 3. Number (and percentage[a]) of land-type-association ecoregions within habitat suitability categories for three bird species during presettlement and current periods.

	Habitat suitability categories[b]					
	0%	*1–20%*	*20–40%*	*40–60%*	*60–80%*	*80–100%*
Pine Warbler						
presettlement	292 (67.6[b])	72 (16.7)	31 (7.2)	17 (3.9)	16 (3.7)	4 (0.9)
current	294 (68.1)	116 (26.9)	18 (4.2)	2 (0.5)	0 (0)	2 (0.5)
Blackburnian Warbler						
presettlement	220 (50.9)	74 (17.1)	60 (13.9)	64 (14.8)	13 (3.0)	1 (0.2)
current	285 (66.0)	141 (32.6)	3 (0.74)	2 (0.5)	1 (0.2)	0 (0)
Black-throated Green Warbler						
presettlement	216 (50.0)	4 (0.9)	43 (10.0)	87 (20.1)	66 (15.3)	16 (3.7)
current	260 (60.2)	103 (23.8)	54 (12.5)	12 (2.8)	3 (0.7)	0 (0)

[a]*Percentages based on proportion of maximally suitable habitat for each species as derived from model.*
[b]*These percentages based on proportion of total ecoregions within given habitat suitability category; rows sum to 100.*

Table 4. The percentage of ecoregions with changes in habitat elements between presettlement and current periods.

Change in habitat element	Contiguous forest	White & red pine	Hemlock	Trees > 38 cm dbh	Trees > 49 cm dbh
Increase > 75%	1.0	0.3	0	0	0
Increase 50–75%	0.6	1.0	0.4	0	0
Increase 25–50%	1.7	3.6	0.4	0.8	0.5
Increase up to 25%	2.9	20.3	4.7	1.6	2.2
Overall increase	6.2	25.2	5.5	2.4	2.7
Decrease up to 25%	19.	49.6	66.0	90.0	96.4
Decrease 25–50%	18.3	17.4	23.0	7.2	0.9
Decrease 50–75%	34.6	7.3	5.1	0.4	0
Decrease >75%	21.9	0.5	0	0	0
Overall decrease	93.9	74.8	94.0	97.6	97.3

with the exception of northern Door Peninsula and intermittent patches in eastern Wisconsin.

As with the Blackburnian Warbler, habitat range and quality for Black-throated Green Warbler decreased overall between time periods (Figs. 4b & 4c.). Habitat was eliminated from 10% of the ecoregions in Wisconsin (Table 3), with the majority of this range contraction occurring in the eastern and central portion of the state.
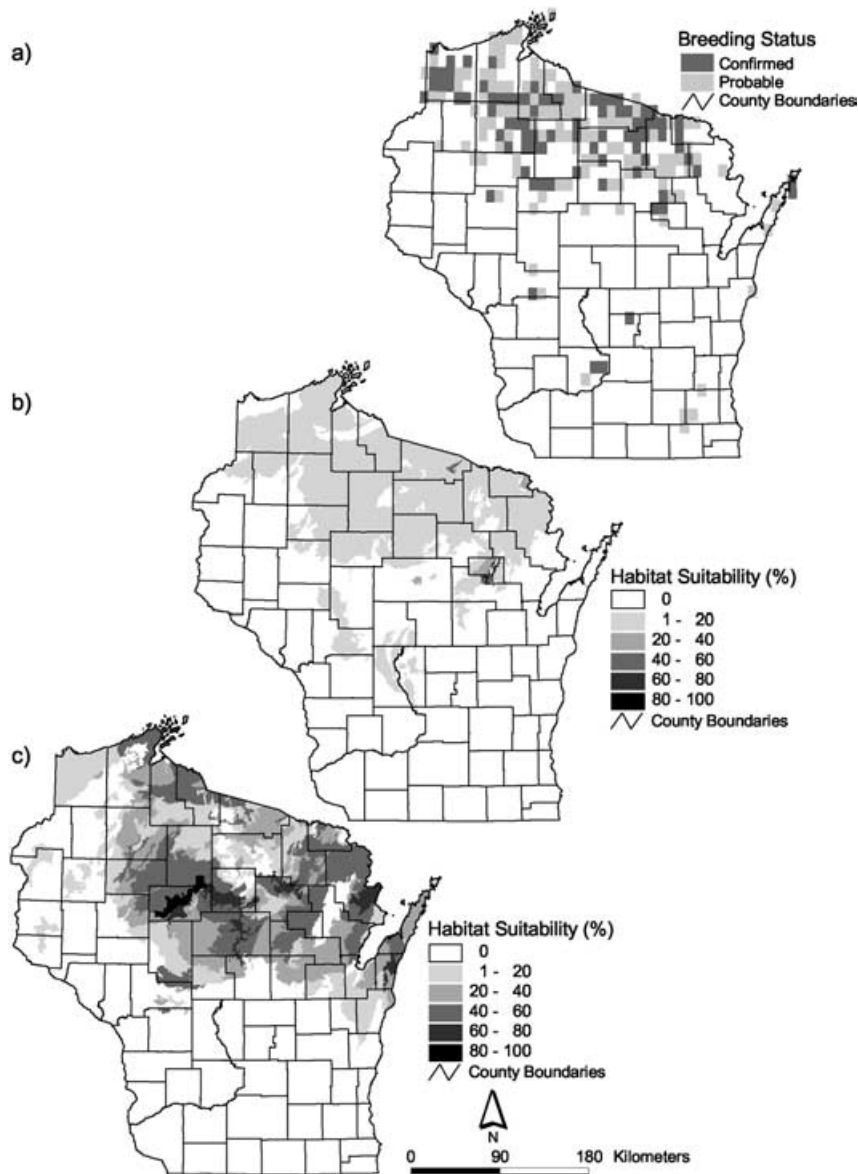

Figure 3. Blackburnian Warbler (a) breeding bird locations (WSO 2002), (b) current habitat, and (c) presettlement habitat.
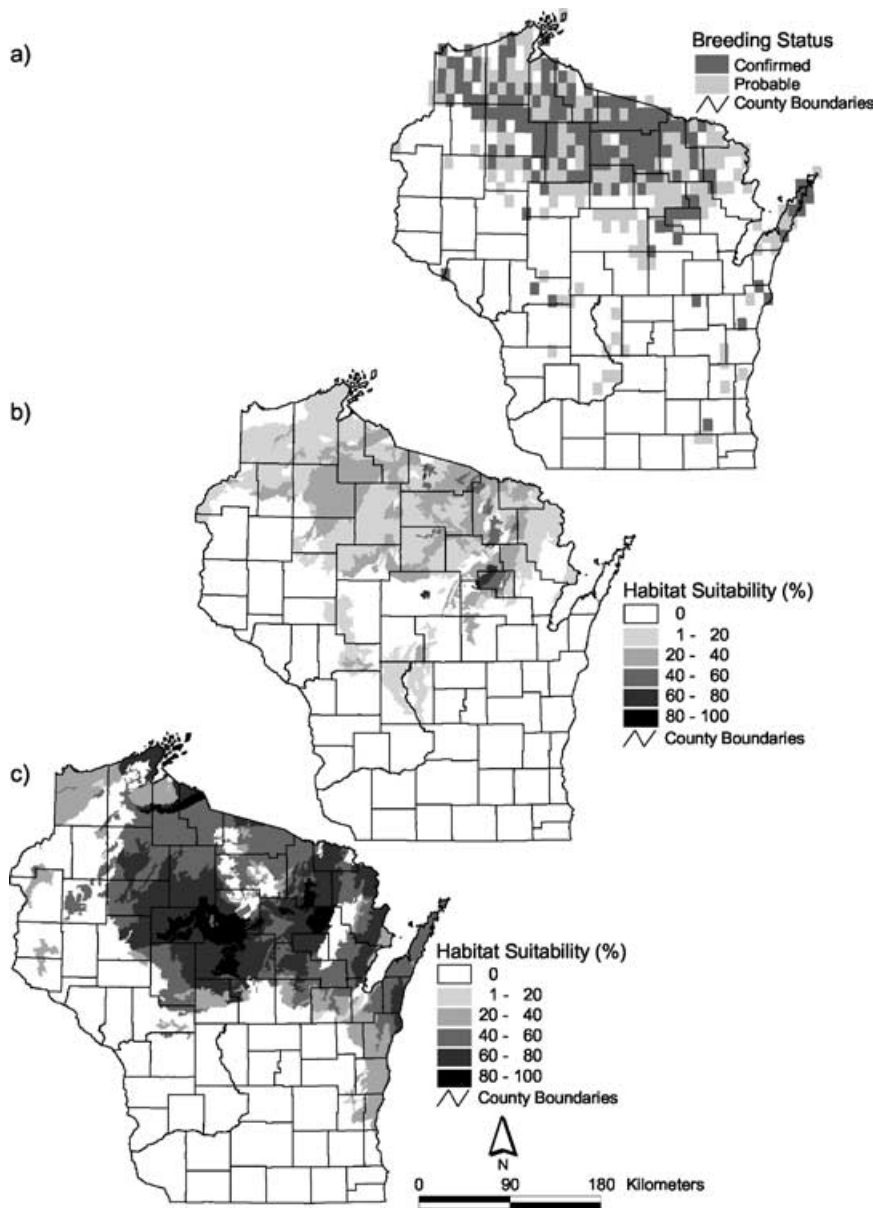
Figure 4. Black-throated Green Warbler (a) breeding bird locations (WSO 2002), (b) current habitat, and (c) presettlement habitat.

Like the Pine Warbler, however, this species has also seen an expansion in Bayfield, Washburn, Juneau, and Adams counties. Historically, 49.1% of ecoregions were in more highly suitable conditions ($\geq$20%), compared with 16.0% today (Table 3). The mean value of habitat suitability change among those ecoregions experiencing change was −31.5%. Positive changes in habitat suitability occurred in 13.2% of ecoregions with an average of 11.4%. Degradation of habitat suitability occurred in 49.9% of total ecoregions and 97.7% of the historical habitat, and averaged −43.2%.

Overall Change

The models for each species emphasized different habitat elements of mature coniferous forest and revealed some new patterns when taken together. Areas of habitat ex-

pansion for all three species occurred in small patches in northern and central Wisconsin; the primary trend in habitat change, however, was one of loss and degradation. At the stand level this results primarily from the loss of hemlock, white pine, and large-diameter conifers (Table 4). Fragmentation of current-day forest at the landscape scale also contributes substantially to degradation (Table 4).

Discussion

We quantified changes in the amount, quality, and distribution of forest bird habitat between presettlement times and today, thus evaluating wildlife response to a period of historically unprecedented landscape change. Our approach strikes a balance between describing bird habitat

over broad temporal and geographic scales, scales significant to biodiversity conservation planning, and captures the details in forest-habitat parameters necessary to guide forest management practices.

Bird Habitat Conservation

The distribution of bird species and their breeding success are affected by both the amount (Fahrig 1997; Trzcinski et al. 1999) and spatial pattern of habitat (Donovan et al. 1995; Flather & Sauer 1996). Mapping population distributions and densities is an important tool for conservation planning because it (1) reveals relationships between species abundance and geographic range (Linder et al. 2000); (2) identifies potential suitable habitat, gaps in habitat protection, and multiple species hotspots of vulnerability (Scott et al. 1993; Abbitt et al. 2000; Pidgeon et al. 2003); and (3) documents change (Donald & Fuller 1998; Sauer et al. 2003). Our maps provide a powerful tool for assessing changes in suitable habitat in Wisconsin over relatively broad spatial and temporal scales; by inference, they also suggest how population levels may have experienced concomitant change. The models provide strong evidence of widespread shifts in habitat range and degradation in habitat suitability since presettlement. The Blackburnian and Black-throated Green Warblers have also experienced substantial losses in the overall amount of suitable habitat.

Because regional variation in population processes may have important consequences for species as a whole (Donovan & Flather 2002), the conservation implications of range contraction in Wisconsin should be considered in the context of the species' continent-wide breeding range. The breeding range of the Pine Warbler is fragmented and discontinuous (Rodewald et al. 1999), whereas breeding ranges for both Blackburnian and Black-throated Green Warblers center on northeastern North America (Morse 1993, 1994). Taken as an isolated occurrence, the observed contraction in Wisconsin does not represent a significant proportion of the range of any of the species; yet, it is likely that the pattern identified in Wisconsin is similar to the patterns occurring elsewhere within their range, particularly in the northern United States and southern Canada, where similar forces have influenced land-cover change (Whitney 1987; Simard & Bouchard 1996).

Although habitat loss is the dominant trend, range expansion has occurred with forest incursion into previously open habitats or the replacement of native forests with pine plantations. This habitat expansion seems to benefit the Pine Warbler most (Fig. 2). Before Euro-American settlement, glacial sandy outwash plains in the state were largely dominated by pine barrens and savannas (Fig. 1; Bolliger et al. 2004). Because of fire suppression, pine plantation establishment, and modern forestry

practices (Radeloff et al. 1999), these formerly open areas currently provide habitat for forest songbirds (Figs. 2–4).

The degradation in habitat suitability since presettlement has been most substantial for the Blackburnian and Black-throated Green Warblers (Table 3; Figs. 3 & 4). Sources of degradation include loss of hemlock, white pine, and red pine from northern forests and loss of large trees in all regions (Bolliger et al. 2004; L.A.S., unpublished data). For Blackburnian and Black-throated Green Warblers, which respond to forest fragmentation (Hobson & Bayne 2000; Holmes & Sherry 2001), reductions in forest patch size and replacement of the forest matrix by agriculture and urban lands, particularly across central Wisconsin and on the Door Peninsula (L.A.S. unpublished data), have contributed to habitat degradation. The Pine Warbler may exhibit region-specific area sensitivity (Whitcomb et al. 1981; Freemark & Collins 1992), but we found that addition of a fragmentation index did not improve model fit for this species.

Although widespread loss and degradation of habitat are predominant, one area of the state is a notable exception. Habitat suitability in Menomonee County, which includes the 88,000 ha Menominee Indian Reservation, has been maintained at presettlement levels (Figs. 2–4). Forests of the reservation largely escaped the harvesting and wildfires associated with the cutover period around the turn of the twentieth century, which removed the old-growth forests in the majority of northern Wisconsin (Fries 1951).

Methodological Considerations

Because birds respond to vegetation patterning at continental, regional, and local scales, bird population trends observed at a local scale often differ from those at broader scales (Holmes & Sherry 1988). Through our focus on stand- to landscape-level habitat factors, we were able to tailor model parameters to observed responses of our focal bird species at the scale of the state of Wisconsin, as indicated by current breeding-activity maps. Advantages of this approach include use of widely available data and methodological ease and robustness, an approach that lends itself to the pressing needs of conservation organizations (Groves 2003).

The historical PLS data are available for most of the United States (Ohio to the Pacific coast), FIA and NLCD data are available nationwide, and bird atlas data are available for many states. This broad-scale availability, plus the fact that all four of these data sets were collected using standardized methodology, makes them useful for regional- to continental-scale ecological investigations and conservation planning.

Parameterization of our models resulted from the synthesis of range-wide, species-specific data from published accounts, two local surveys (Hanowski & Niemi 1991*a*,

1991*b*; Howe & Roberts 2005), and expert opinion. Because bird-habitat relationships were built from these widely varying sources, our model parameters are robust to interannual variation, site-specific response, and the biases of a single collection method.

We validated the present-day model with Breeding Bird Atlas data, which confirm breeding activity based on physical or behavioral evidence and are compiled over six breeding seasons (WSO 2002). In some cases our models predicted suitable habitat at present in locations where no activity has been reported (Table 2; Figs. 2–4). It is difficult to be certain whether these are failures of the model or whether they represent suitable but uncolonized habitat (sensu Wiens 1989) or locations where observers failed to detect the presence of breeding birds.

Of more concern are areas where our models failed to predict habitat in known bird locations (Table 2; Figs. 2–4), especially given the moderate predictive power of our models (Table 2). Failures to predict suitable habitat may be due to inaccurate data (either habitat or bird data), regional variation in bird response (birds may have more flexible requirements than elsewhere), or issues of scale (averaging of more local nonhabitat and habitat conditions over the ecoregion). All these factors most likely contributed to our failure to predict suitable habitat, but we expect that the last factor is key in Door County (Fig. 1), where our models consistently failed to predict habitat. Because this peninsula is mostly one large ecoregion, forested areas in the north and along the coastline were averaged with agricultural areas to the south and in the center of the peninsula. The scale of available habitat data also most likely played a role in our ability to predict Pine Warbler habitat, the species for which we obtained the poorest fit (Table 2). The current distribution of Pine Warblers is more spatially dispersed than the other two species we considered (Fig. 2a), and Pine Warblers are most likely responding to small patches of pine habitat within a generally unsuitable matrix. The lack of data to validate the presettlement models is a limitation for which we have no direct solution; circumstantial evidence from accounts of late eighteenth-century naturalists, however, suggests that species-habitat relationships are generally stable (Wetmore & Seeley 1901; Grinnell 1917; Bailey 1928).

Although the maps we produced are powerful conservation tools, our conclusions must be interpreted cautiously. The plasticity of bird-habitat relationships such as those modeled here is unknown, and although available data suggest a linear relationship between habitat suitability and bird density (Webb et al. 1977; Conner et al. 1979; Hobson & Bayne 2000), our focal species' fitness responses to habitat quality differences are also unknown. For example, conservation implications of a linear relationship between habitat suitability and fitness are different if the response is nonlinear—there may be a threshold in habitat suitability below which species' populations

sink into an extinction vortex. A simulation modeling approach such as performed by Hansen and Rotella (2002) could account for individual-level habitat plasticity and more robust population-based measures but would be much more resource intensive in terms of data, time, and funding. Our approach is based on widely available data sources and is relatively straightforward, but it can be applied only to species with fairly well-established habitat relationships and that respond to fairly coarse forest vegetation attributes (e.g., attributes in Table 1).

Conclusions

Our method provides a powerful tool for biodiversity conservation planning, revealing statewide changes since presettlement times in habitat distribution, area, and quality for the species we examined. These changes are not likely isolated occurrences because similar land-use changes have occurred elsewhere in the species' ranges. We urge caution, however, in interpreting our maps in terms of species fitness or as a broad indication of habitat quality for forest wildlife. Habitat trends as opposed to population-level trends are addressed, although future efforts may achieve population-level estimates of change through a simulation modeling approach.

Acknowledgments

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