Comparison of statistical and theoretical habitat models for conservation planning: the benefit of ensemble prediction

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Abstract. Selection of a modeling approach is an important step in the conservation planning process, but little guidance is available. We compared two statistical and three theoretical habitat modeling approaches representing those currently being used for avian conservation planning at landscape and regional scales: hierarchical spatial count (HSC), classification and regression tree (CRT), habitat suitability index (HSI), forest structure database (FS), and habitat association database (HA). We focused our comparison on models for five priority forest-breeding species in the Central Hardwoods Bird Conservation Region: Acadian Flycatcher, Cerulean Warbler, Prairie Warbler, Red-headed Woodpecker, and Worm-eating Warbler. Lacking complete knowledge on the distribution and abundance of each species with which we could illuminate differences between approaches and provide strong grounds for recommending one approach over another, we used two approaches to compare models: rank correlations among model outputs and comparison of spatial correspondence. In general, rank correlations were significantly positive among models for each species, indicating general agreement among the models. Worm-eating Warblers had the highest pairwise correlations, all of which were significant ($P < 0.05$). Red-headed Woodpeckers had the lowest agreement among models, suggesting greater uncertainty in the relative conservation value of areas within the region. We assessed model uncertainty by mapping the spatial congruence in priorities (i.e., top ranks) resulting from each model for each species and calculating the coefficient of variation across model ranks for each location. This allowed identification of areas more likely to be good targets of conservation effort for a species, those areas that were least likely, and those in between where uncertainty is higher and thus conservation action incorporates more risk. Based on our results, models developed independently for the same purpose (conservation planning for a particular species in a particular geography) yield different answers and thus different conservation strategies. We assert that using only one habitat model (even if validated) as the foundation of a conservation plan is risky. Using multiple models (i.e., ensemble prediction) can reduce uncertainty and increase efficacy of conservation action when models corroborate one another and increase understanding of the system when they do not.

Key words: Bayesian hierarchical model; Breeding Bird Survey; classification and regression tree; forest inventory and analysis; habitat suitability index; model uncertainty; species distribution model.

Introduction

Habitat models are a vital component of the conservation planning process (Will et al. 2005) because they tie populations to landscape conditions, formalize uncertainties as testable assumptions, and create a direct link between management and research (National Ecological Assessment Team 2006). Researchers have generally employed two main classes of wildlife–habitat models to link avian populations to estimates of habitat (Millspaugh and Thompson 2009). Statistical models (i.e., inductive approaches) use empirical data to

quantify patterns of coincidence between population characteristics and habitat conditions (Morrison et al. 1998). Techniques within this class of models include regression techniques (e.g., Jones et al. 2002), hierarchical models (e.g., Thogmartin and Knutson 2007), and machine learning techniques such as neural networks (e.g., Lusk et al. 2002). Alternatively, theoretical models (i.e., deductive approaches) rely on literature and/or expert opinion to identify relationships between populations and habitat condition (Morrison et al. 1998). Techniques within this class of models include expert systems (e.g., Lower Mississippi Valley Joint Venture Forest Resource Conservation Working Group 2007), database models (e.g., Thogmartin et al. 2006a), and index models (e.g., Dijak and Rittenhouse 2009).

The different basis of these models may affect their utility for ecoregional-scale planning for a variety of species. The statistical approach provides a more objective assessment of current bird-habitat relationships; however, it typically requires large amounts of data collected with an appropriate experimental design (Millspaugh and Thompson 2009). Therefore, species whose abundance is poorly known (e.g., nocturnal or rare species) may be poorly modeled statistically (McPherson and Jetz 2007) or there may be a mismatch between the scope of inference of the available data and the question being asked. Additionally, by failing to consider the underlying processes explicitly (Peterjohn 2001), statistical patterns in the data may be artifactual, reducing the portability of these models beyond the regions and times in which they were developed. Further, statistical approaches tend to work better for specialists than for generalists (Thuiller et al. 2004, Hernandez et al. 2006). The theoretical approach may overcome these issues by relying less on raw data and more on a priori knowledge of the putative relationships between a species and its habitat (Fitzgerald et al. 2009). However, a theoretical approach may introduce bias into the models (e.g., biases associated with expert opinion) or overlook important but unidentified habitat cues.

With an increasing arsenal of analytical tools at our disposal (Guisan and Zimmermann 2000, Elith and Graham 2009, Millspaugh and Thompson 2009), the crisis is not the lack of an available method but the selection of an appropriate one. The growing body of literature on species distribution models (e.g., habitat models, ecological niche models) does not provide clear guidance for selecting appropriate methods (Elith and Graham 2009). Further, studies comparing modeling techniques have largely been academic exercises focused on comparing statistical methods (e.g., Marmion et al. 2009, Murtaugh 2009, Thuiller et al. 2009), despite the fact that theoretical models are widely used in conservation planning (Brooks 1997). Statistical and theoretical approaches have not been directly compared and the relative efficacy of each to facilitate bird conservation planning at multiple spatial scales (local, regional, national, or continental) remains unknown.

Our objective was to compare five habitat modeling approaches that are being used to assess avian habitat at the scale of a bird conservation region (BCR). Two approaches were classified as statistical modeling approaches because they were developed using Breeding Bird Survey (BBS) data: hierarchical spatial count (HSC; Thogmartin et al. 2004, 2006b) and classification and regression tree (CRT; Fearer et al. 2007). Three approaches were classified as theoretical modeling approaches because they were based on literature reviews or expert opinion: habitat suitability index (HSI; Tirpak et al. 2009a, b, c), forest structure database (FS), and habitat association database (HA). The HSC, CRT, and HSI methodologies utilize nationally available land cover data to assess the effects of habitat configuration and composition on avian presence and abundance. All five approaches used here incorporate Forest Inventory and Analysis (FIA) data to assess the effects of forest age and structure, which has been lacking in previous large-scale models. We developed the two database approaches (FS and HA) because they represent a spatially inexplicit alternative to the other models that could be quickly estimated without complex spatial analyses, and because they are similar to database approaches being used in some western BCRs (Fitzgerald et al. 2009). We assessed how well these approaches agreed with each other and how well they captured conditions in the field. We believed such comparison would provide important insights to conservation planners who rely on these models to guide their planning for habitat restoration and management efforts.

METHODS

We focused our comparison on models for five priority (Rich et al. 2004, Panjabi et al. 2005) forest-breeding species in the Central Hardwoods (CH) BCR: Acadian Flycatcher (*Empidonax virescens*), Cerulean Warbler (*Dendroica cerulea*), Prairie Warbler (*Dendroica discolor*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), and Worm-eating Warbler (*Helmitheros vermivorus*). The CH BCR is centrally located on the North American continent, encompassing a 30-million-ha area that straddles the Mississippi River (Fig. 1). The mixed mesophytic and oak (*Quercus* spp.)–hickory (*Carya* spp.) forests of the BCR provide habitat for many high-priority bird species (U.S. North American Bird Conservation Initiative Committee 2000), including these focal species.

Statistical models

Bayesian hierarchical spatial count models have been used to model patterns in the predicted relative abundance for more than two dozen species of conservation concern in eastern and central North America (Thogmartin et al. 2004, Thogmartin and
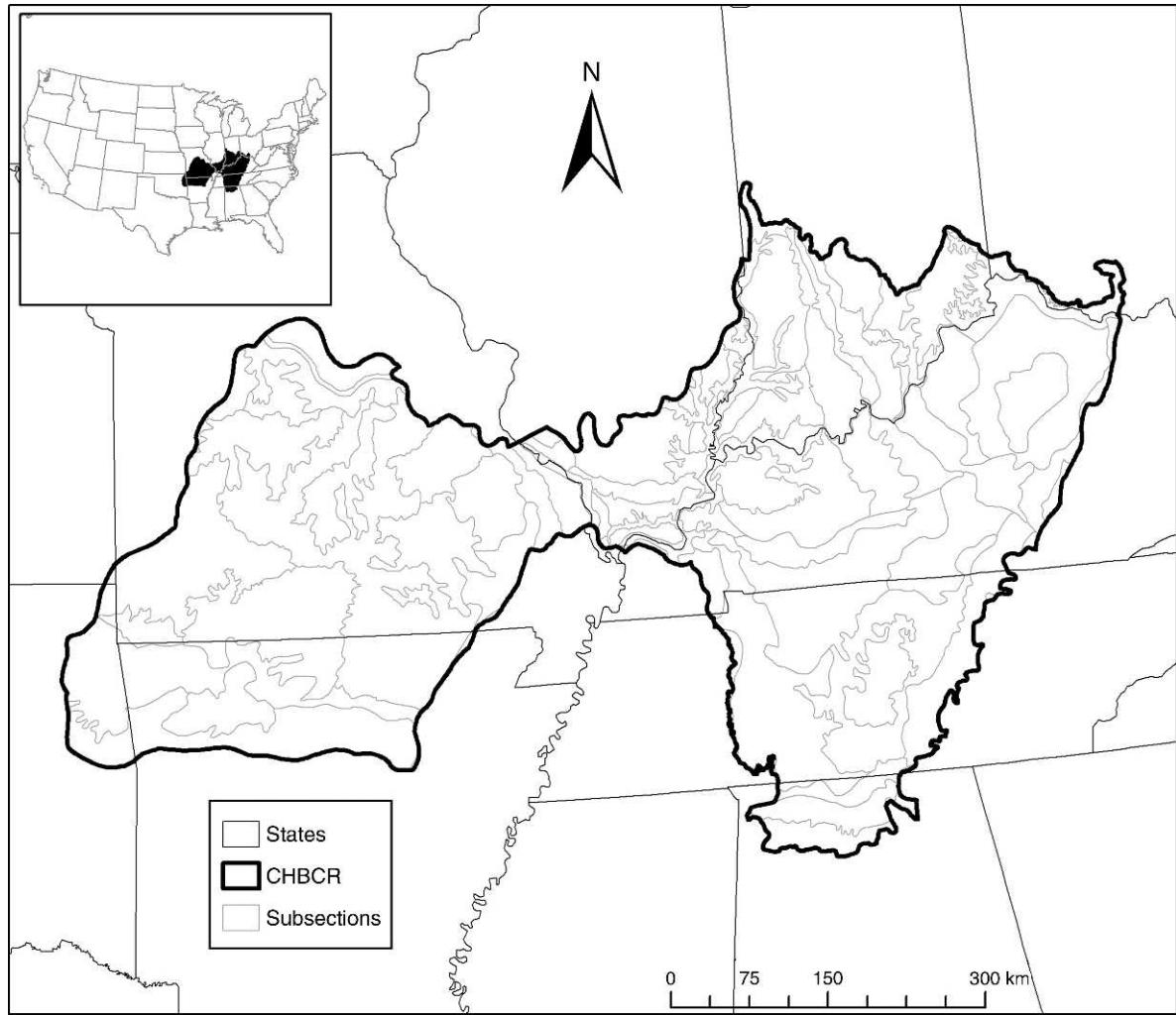
FIG. 1. Location of the Central Hardwoods Bird Conservation Region (CHBCR) in the central United States and the boundaries of ecological subsections used as planning units within the region.

Knutson 2004, 2006b, 2007, Forcey et al. 2007). These methods were used to develop HSC models from data in the BBS, the National Land Cover Database (NLCD), the National Elevation Dataset (NED), and the Forest Inventory and Analysis (FIA) database. Models for all five species examined the same variables (Table 1). This assumes that the distribution and abundance of each species are limited by the same set of factors, though each factor can have different degrees of influence on each species. BBS data provided the response variable (birds/route) for the models, as well as several predictor variables. We built the models based on annual data for 177 routes within and around (100-km buffer) the CH BCR during the 11-year period centered on the nominal date of the 2001 NLCD (1995–2005); we conducted an internal validation (Table 2) using data from within the period for which the models were built and for the two years following the model building period (2006 and 2007). Predictor variables were generated from the

NLCD using Fragstats software or statistical analysis (software *available online*).[10] The FIA program provided summary statistics of forest structure from the first annual cycle for each state covered by the BCR (i.e., data closest to 2001) within tessellation polygons around each route (Thogmartin et al. 2004). Although models were developed using estimates of the predictor variables within nested buffers (100 m, 1 km, and 10 km) around each BBS route, only models based on the 100-m buffer were used in this analysis because of similarity in model composition and parameter estimates across scales (W. E. Thogmartin, *unpublished data*; also see Laurent et al. 2005). These HSC models do not have a well-defined resolution, but outputs were mapped across the BCR at an ad hoc resolution of 100 × 100 m pixels. Thus, outputs are interpreted as the predicted number of

[10] ⟨http://www.umass.edu/landeco/research/fragstats/fragstats.html⟩

birds per route that could be expected if a route was centered on that cell and run in average conditions (observer, year, temperature, etc.).

Similar to the HSC approach, CRT models were developed from BBS, NLCD, and FIA data. Abundance data (2000–2005) were gathered for each BBS route within the CH BCR and average abundance was calculated for each route separately by state using a 3-year (Cerulean Warbler only) or 4-year window concluding the same year as the most recent 5-year annual FIA cycle (2004 or 2005) for that state. We excluded routes not having acceptable runs (e.g., conducted during poor weather, exceeded time limitations) as defined by the BBS (Sauer et al. 2008) for any of the years within their given window. Based on these criteria, 62 routes were suitable for analyses for four of the five species; 82 routes were suitable for the Cerulean Warbler because of the smaller time window. Fifty FIA variables (see Table 2 in Fearer et al. 2007) were aggregated from the plot level to county level using expansion factors and algorithms as described in the FIA database user's guide (U.S. Department of Agriculture Forest Service 2010). We focused on variables that described forest structural attributes as many studies have demonstrated the importance of microhabitat structure to habitat suitability (Hagan and Meehan 2002, Lichstein et al. 2002, MacFaden and Capen 2002). We used Fragstats software to generate landscape-level predictor variables from the NLCD, developing 14 metrics at the forest cover class level and 15 metrics for the landscape as a whole (see Table 3 in Fearer et al. 2007). Models were developed using estimates of predictor variables at three logarithmically related buffer distances (i.e., landscapes) around each route (100 m, 1 km, and 10 km). Fragstats metrics were calculated directly for each buffer; values of FIA variables were calculated as area-weighted averages from the county-level estimates, with the weights calculated as the proportional area a given county composed within the buffer (Fearer et al. 2007). Unlike the HSC approach, CRT models were more exploratory, allowing the inclusion of variables in the models to vary according to species and landscape. This assumes that the distribution and abundance of individual species are controlled by different factors. Models were developed using S-PLUS version 7 (Insightful Corporation, Seattle, Washington, USA) with the rpart library (Therneau and Atkinson 2000) and were pruned to avoid overfitting using 10-fold cross-validation subsets of the original BBS data set. For this analysis, we used the best model (100 m, 1 km, 10 km, or multiscale) for each species (Table 1) based on a measure of the amount of variation explained by the model (Table 2). The CRT models make county-level predictions of (1) the probability of presence under average conditions and (2) the number of birds per route that could be expected if a route existed in that county under average conditions.

Theoretical models

The HSI models for the five focal species were developed through a literature review identifying important components of habitat structure at the site and landscape scales that could be mapped from NLCD, FIA, or other national geospatial data sets (Tirpak et al. 2009*a*, *b*). To the extent possible, we restricted our review to studies done within the central and southcentral United States. Our review focused on variables thought to limit abundance or density of the species (e.g., percent canopy cover). Thus, we assumed that each species could be limited by a unique set of variables and that each limiting factor was necessary in the model (i.e., no alternative candidate models were considered). Once we selected the variables and identified data points representing the relative abundance or density of a species at different levels of each habitat component, we fit equations using CurveExpert 1.38 software that output values between 0 and 1 representing the suitability (i.e., index of relative abundance or density) expected for a particular value of a variable (software *available online*).[11] We supplemented reported data with hypothesized data based on generalizations from the literature when we found fewer than three data points with which to fit a curve. Final HSI values for each species were calculated as a three-step process: the geometric mean of the site-scale variables, the geometric mean of the landscape-scale variables, and then the geometric mean of the site and landscape means. This approach assumes that each variable is equally important to the species and that if any model variable is absent or does not have a value in the suitable range for the species (i.e., received a suitability value of 0) then the location is unsuitable (i.e., HSI value is 0). We sent the models to two to five experts on each species for review, and models were revised based on their comments (Tirpak et al. 2009*b*). The models were applied to NLCD, FIA, NED, and ecological subsection boundary (Cleland et al. 1997) data sets to depict the spatial configuration of suitable habitats (Table 1). To map HSI values across the CH BCR, we developed an ecologically stratified randomization process in cooperation with staff at FIA Spatial Data Services to interpolate FIA plot data at the resolution of the NLCD (30-m pixel) (Tirpak et al. 2009*a*). Initially, this was accomplished using the 1992 NLCD and associated periodic FIA surveys. These model outputs were validated against BBS data (Table 2; Tirpak et al. 2009*c*). We later applied the HSI models to the 2001 NLCD and the first annual 5-year cycle of FIA surveys for each state (1999–2005). For this analysis, we used model outputs associated with the later time period. The HSI models predict the relative suitability of habitat on a scale from 0 (non-habitat) to 1 (optimal habitat). Although the model outputs are mapped at a 30-m resolution, the interpolation of FIA data used here

[11] ⟨http://curveexpert.webhop.biz⟩

TABLE 1. Variables included for each species model under each modeling approach, by data source.

Approach and species‡,§	Model type and output	Data source† BBS	Data source† FIA
HSC			
All five	abundance	year, day of year, start temperature, easting, northing	mean live basal area, density of trees ≥12 inches dbh, % forest in oak–hickory
CRT			
ACFL	presence–absence	na	na
	abundance	na	na
CERW	presence–absence	na	understory dbh CV
	abundance	na	stand size, understory dbh CV
PRAW	presence–absence	na	density of all trees
	abundance	na	na
RHWO	presence–absence	na	understory height CV
	abundance	na	density of understory trees
WEWA	presence–absence	na	na
	abundance	na	na
HSI			
ACFL	suitability	na	overstory canopy cover
CERW	suitability	na	density of trees >30 inches dbh, overstory canopy cover
PRAW	suitability	na	overstory canopy cover, density of trees <1 inch dbh
RHWO	suitability	na	density of all snags, density of snags >12 inches dbh, density of trees >11 inches dbh
WEWA	suitability	na	density of trees <1 inch dbh
FS			
All five	suitability	na	same as HSI
HA			
All five	suitability	na	forest type, stand size class

Notes: Data sources not used in a model are identified with "na." For variables in the FIA, note that 1 inch = 2.54 cm.

† Data source codes: BBS, Breeding Bird Survey; FIA, Forest Inventory and Analysis; NLCD, National Land Cover Database; NED, National Elevation Dataset.

‡ Modeling approach codes: HSC, hierarchical spatial count model; CRT, classification and regression tree models; HSI, habitat suitability index model; FS, forest structure database model; HA, habitat association database model.

§ American Ornithological Union species codes (Pyle and DeSante 2003): ACFL, Acadian Flycatcher; CERW, Cerulean Warbler; PRAW, Prairie Warbler; RHWO, Red-headed Woodpecker; WEWA, Worm-eating Warbler.

TABLE 2. Evaluation statistics for species–habitat relationship models for five species in the Central Hardwoods Bird Conservation Region.

Model type	Evaluation method	Acadian Flycatcher	Cerulean Warbler	Prairie Warbler	Red-headed Woodpecker	Worm-eating Warbler
HSC†	coefficient of determination (R^2)	0.43	0.62	0.78	0.38	0.49
HSC†	coefficient of variation in the root mean squared error (CV[RMSE])	2.30	2.97	0.89	1.26	1.30
CRTp‡	relative error explained	0.77	0.81	0.56	0.50	0.65
CRTa‡	relative error explained	0.62	0.68	0.56	0.55	0.68
HSI§	Spearman rank correlation, r	0.47 (<0.001)	0.44 (<0.001)	0.41 (<0.001)	0.11 (0.308)	0.66 (<0.001)
HSI§	GLM models predicting abundance from HSI scores, R^2	0.05 (0.095)	0.21 (<0.001)	0.12 (0.005)	0.23 (<0.001)	0.41 (<0.001)
HSI§	HSI parameter, β	4.25 (0.043)	0.63 (0.023)	15.32 (<0.001)	−3.36 (0.827)	1.80 (<0.001)

Notes: The forest structure and habitat association models were not evaluated. Values in parentheses are P values.

† For hierarchical spatial count (HSC) models, R^2 provides a relative measure of predictive accuracy on a scale from 0 to 1 (higher better); CV[RMSE] provides a measure of bias with higher values indicating more bias.

‡ CRTp is a classification tree model predicting presence/absence; CRTa is a regression tree model predicting relative abundance. Relative error explained denotes the proportional reduction in error (PRE) of the given model compared to a null model and is analogous to R^2.

§ HSI stands for habitat suitability index model. Results are for HSI models taken from Tirpak et al. (2009c: Tables 1 and 2). Models were considered validated for use if there was a significant ($P < 0.10$) correlation of HSI score to abundance, linear model including HSI predicted abundance better ($P < 0.10$) than an intercept-only model, and the coefficient on HSI variable in the linear model was significantly >0 ($P < 0.10$).

TABLE 1. Extended.

	Data source†	
NLCD	NED	Other
% forest land (within 100 m), residual of developed index, forest interspersion/juxtaposition index	residual of wetness index	spatial autocorrelation, 100-m buffer, interaction of %forest and wetness residual
largest patch index, area-weighted mean shape index	na	multi-scale buffer
forest patch density, area-weighted forest core area index, core % of landscape	na	multi-scale buffer
% core forest	na	physiographic region, 1-km buffer
na	na	100-m buffer
na	na	100-m buffer
largest patch index, mean shape index CV	na	multi-scale buffer
% core forest	na	1-km buffer
total edge contrast index, largest patch index	na	100-m buffer
area-weighted forest core area index	na	1-km buffer
forest core % of landscape, forest largest patch index	na	100-m buffer
forest type, patch size, % forest land (1 km)	landform	subsection boundaries, distance to stream
forest type, patch size, % forest land (1 km)	landform	subsection boundaries
forest type, patch size, % forest land (1 km)	landform	subsection boundaries
forest type	landform	subsection boundaries
forest type, patch size, % forest land (1 km)	landform, slope	subsection boundaries
na	na	na
na	na	na

makes the forest structure variables spatially representative only at broader scales such as ecological subsection (portions of multiple counties, 70 000 to 2.6 million ha). Thus, the models are most appropriately interpreted at that scale; the utility of these model outputs at finer resolutions is unknown.

In addition to the HSI models, we developed two database models for each species (Table 1) because this type of approach is being used for some BCR-scale conservation planning. The forest structure (FS) database approach assumed that the forest structure variables in the HSI models were sufficient to accurately depict variation in habitat suitability across the BCR (i.e., site-scale factors are influenced by and adequately capture landscape processes). We used the FS models to calculate habitat suitability for each species on each FIA plot. To estimate habitat suitability we assembled FIA data tables for each state within Microsoft Access (Microsoft, Redmond, Washington, USA) and (1) derived forest structure variables for each FIA plot condition , (2) applied suitability relationship equations developed for those variables in the HSI model building process (above and Tirpak et al. 2009b), (3) calculated the geometric mean of resulting suitability values across model variables for a species for each condition on each plot, and (4) used FIA area expansion factors (U.S. Department of Agriculture Forest Service 2010) to calculate an area-weighted relative suitability value across all plot conditions for counties and subsections. As with the HSI models, the FS models predict the relative suitability of habitat on a scale from 0 (nonhabitat) to 1 (optimal habitat).

The habitat association (HA) database approach assumed that the relative suitability scores assigned to combinations of forest type and successional stage described in Hamel (1992) were sufficient to accurately depict variation in habitat suitability across the BCR (i.e., complex models are not any better than simple ones). We generated model outputs for this approach using a similar method to the one used for the FS database approach. First, we converted the categorical rankings of habitat associations used by Hamel (1992) to numerical values (unsuitable = 0.000, marginal = 0.333, suitable = 0.667, and optimal = 1.000). Next we assigned these values to combinations of forest type and successional age class for each condition on each FIA plot. We then used the area expansion factors to calculate an area-weighted relative suitability value across all plot conditions for counties and subsections. As with the HSI models, the HA models predict the relative suitability of habitat on a scale from 0 (nonhabitat) to 1 (optimal habitat).

Model evaluation

Because we do not know the true distribution of these species and were not working solely with presence–

absence data, most objective techniques for comparing model predictions (Fielding and Bell 1997, Guisan and Zimmermann 2000) were not available to us. We attempted to use a collection of available point count data sets as an independent evaluation of predictions across the models (Guisan and Zimmermann 2000, Thuillier 2009) to illuminate differences between approaches and to provide strong grounds for recommending one approach over another. Unfortunately, point count data available to us were spatially restricted and at scales of organization different than the BBS data used in the HSC and CRT modeling approaches. Further, due to differences in methodologies of each approach (e.g., categorical vs. continuous data), no single approach to estimating the variance explained (e.g., R^2) exists for direct comparison of model performance. Therefore, for three of the five modeling approaches we used internal measures of performance (Table 2). We evaluated the HSC approach by comparing predicted to observed abundance (R^2 and coefficient of variation in the root mean squared error, CV[RMSE]). We evaluated the CRT approach by examining the variability in the data explained (proportional reduction in error) by the model (Table 2). We evaluated the HSI approach evaluated model fit by examining the relationship between model outputs and BBS data (i.e., independent evaluation data set) using three criteria: rank correlation (r), fit of a regression model (R^2) predicting subsection-level abundance as a function of average HSI values, and the direction and significance of the HSI parameter in the regression model (Table 2; Tirpak et al. 2009c).

Model comparison

Ideally, we would compare the models based on the known distribution and abundance of each species. Lacking such knowledge, we used two approaches to compare models – rank correlations among model outputs and comparison of spatial correspondence.

Rank correlation analysis.—We compared model outputs using rank correlations in SAS (SAS Institute 2004) because each approach predicted different quantities (birds per route vs. relative suitability). The models were developed for different resolutions (HSC, township; CRT, county; HSI, ecological subsection; FS and HA, FIA plot), so we first needed to summarize the model outputs for each species such that they were directly comparable across modeling approaches. We opted to summarize outputs at two resolutions, county ($n = 204$) and ecological subsection ($n = 59$), because they represent the finest and broadest resolutions at which the model outputs can be appropriately interpreted based on the resolution of their input data sets.

We calculated rank correlations separately for each resolution. For analysis of county-level model outputs, we only considered counties completely within the BCR because the HSI approach truncated model outputs at the BCR boundary (truncated or not). For the CRT

models, we used model outputs directly for determining the county-level ranks and calculated area-weighted averages of the model outputs for determining the subsection-level ranks. The HSC and HSI approaches were mapped at scales finer than a county, so we calculated the mean of cells encompassed by a county or subsection using the zonal statistics tool in ArcGIS 9.2 (ESRI, Redlands, California, USA) to determine ranks for each resolution. Habitat suitability estimates from the FS and HA model approaches were produced for counties and subsections directly based on plot membership reported in the FIA database. Because the FIA program limits their forest estimates to areas that have a minimum of 12 plots, counties with <12 plots were combined with other counties as needed based on adjacency and the number of data points. Grouped counties received identical model outputs and ranks.

Spatial correspondence.—We examined correspondence of mapped outputs from each modeling approach in two ways. First, we assessed model congruence by simply counting the number of models that ranked a particular location (i.e., county or subsection) in the top 10% of locations at that resolution. Second we assessed confidence in our rankings by assessing the variability in predicted ranks for each location. To assess variability, we calculated the coefficient of variability (%CV) across rank values provided by each modeling approach at each location. Locations with lower %CV values indicate areas with higher agreement among models (and thus higher confidence) regardless of relative rank.

As an example of how ensemble prediction might be used, we mapped the combination of congruence and confidence values at the subsection resolution to define the areas most likely to be high quality for each species (Fig. 2). Lacking an objective function to rank one model better than another (see *Model evaluation*), we created our ensemble predictions by combining outputs equally from all five models for each species. For simplicity, we divided congruence values into two ranges ad hoc: low (zero to one models) and high (two to six models). Similarly, we divided the range of %CV values into high and low confidence ranges using a threshold value of 50%. The resulting four categories (high congruence, high confidence; high congruence, low confidence; low congruence, low confidence; and low congruence, high confidence) represent a continuum of conservation value from highest value to lowest. Risk associated with conservation decisions is lowest for the first and last categories and highest for the middle two categories. Given space restrictions, we chose to present only subsection-level results because this resolution was most appropriate for interpretation across all modeling approaches; county-level results can be derived from the Appendices.

RESULTS

Hierarchical spatial count models for Cerulean Warbler and Prairie Warbler were relatively accurate in predicting patterns in relative abundance, with
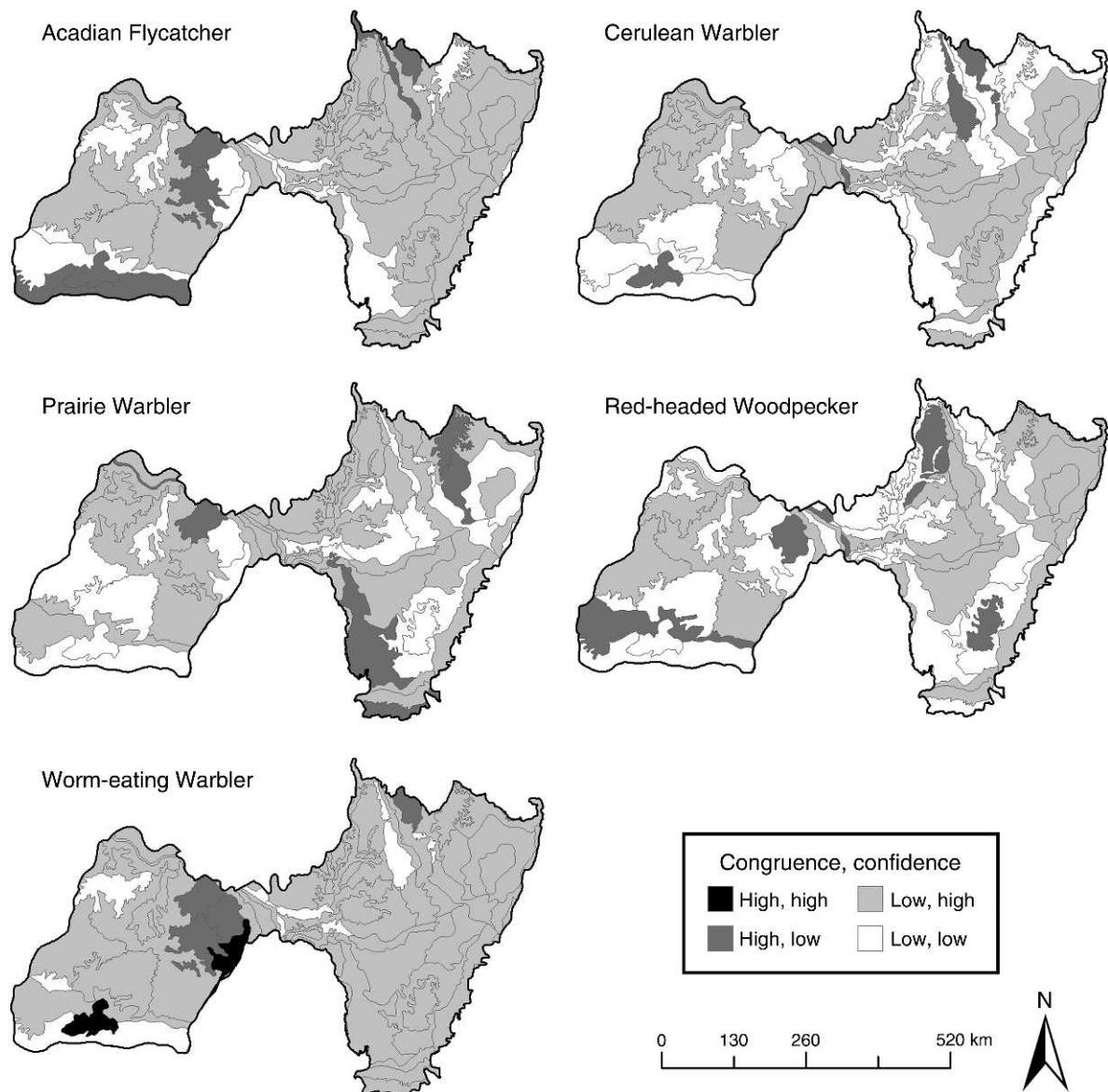
FIG. 2. Congruence-confidence maps for five focal species showing model congruence (i.e., number of models ranking the subsection in the top 10%) and ranking confidence (i.e., inverse of variability in ranking score across models). High model congruence indicates that 2–6 models ranked the subsection in the top 10%, and low congruence indicates that zero or one model ranked it that high. High model confidence indicates a low range of variability (<50% coefficient of variation) in rank values for the location.

predictions for Prairie Warblers less biased (i.e., lower coefficient of variation in the root mean squared error) than those for Cerulean Warblers (Table 2). Predictions from HSC models for Red-headed Woodpeckers were the least accurate but were among the least biased of the five species modeled. The performance of CRT results varied slightly by model type with classification trees (presence–absence) outperforming regression trees (abundance) for Cerulean Warblers and Acadian Flycatchers but not for the other species; overall the Prairie Warbler and Red-headed Woodpecker models explained less variation in presence and abundance than

CRT models for other species (Table 2). All species passed the evaluation tests for the HSI approach, with the exception of the Red-headed Woodpecker model which did not show significant rank correlation between HSI value and BBS abundance or have a significant and positive HSI parameter in the regression model (Table 2; Tirpak et al. 2009c).

Correlation analysis

Pairwise comparisons of ranked outputs from each modeling approach indicated congruity in predictions, with most rank correlations as significant (*P* values <

TABLE 3. Summary of rank correlations among pairs of model outputs across five focal species.

Correlations	Modeling approach					
	CRTp	CRTa	HSC	HSI	FS	HA
County-level resolution						
Positive	16 (0.64)	18 (0.72)	19 (0.76)	21 (0.84)	19 (0.76)	21 (0.84)
Significant	13 (0.52)	12 (0.48)	17 (0.68)	19 (0.76)	15 (0.60)	16 (0.64)
Subsection-level resolution						
Positive	20 (0.80)	19 (0.76)	20 (0.80)	22 (0.88)	21 (0.84)	22 (0.88)
Significant	14 (0.56)	14 (0.56)	16 (0.64)	17 (0.68)	15 (0.60)	14 (0.56)

Note: For each modeling approach, we report the total number of positive correlations with the other modeling approaches, the number of significant positive correlations ($P < 0.05$), and the proportion (in parentheses) of all combinations ($n = 25$) that each represents at the county ($n = 204$) and subsection ($n = 59$) resolutions.

0.05) and positive (Table 3). Model correspondence was highest for the Worm-eating Warbler where all pairwise comparisons were significant and positive (Appendix A: Tables A.9 and A.10). Model correspondence was lowest for the Red-headed Woodpecker where most rank correlations between the theoretical models and the statistical models were significant and negative (Appendix A: Tables A.7 and A.8). For three of the five species we examined (Acadian Flycatcher, Cerulean Warbler, and Worm-eating Warbler) outputs from the HSC models were more highly correlated with the theoretical models than with the abundance outputs from the CRT models (Appendix A).

Spatial correspondence

Model congruence ranged from zero (i.e., no model ranked a county or subsection in the top 10% of locations at that resolution) to five at the county resolution and six at the subsection resolution. Confidence (%CV) values ranged from 2% to 178% across species at the county resolution and 5% to 133% at the subsection resolution. Maps showing ranks of model outputs under each modeling approach individually and combined are available in Appendix B. Ensemble predictions (Fig. 2) reflect the uncertainty across models in predictions of the best places to focus conservation efforts. Worm-eating Warbler is the only species for which any subsection showed both high congruence (i.e., more than one model ranked the subsection in the top 10%) and high confidence (i.e., <50% CV across model ranks). For all species, most subsections fell in the low congruence, high confidence category indicating these areas are not likely good places for conservation effort because they do not contain a high abundance of birds or high quantity of suitable habitat.

DISCUSSION

Selection of a modeling approach is an important step in the conservation planning process (Will et al. 2005, National Ecological Assessment Team 2006), but little guidance is available to assist planners (Elith and Graham 2009). In our experience, planners select a single modeling approach because they (or the researchers they employ) are familiar with it or because it is the latest technique. Frequently more than one suitable technique is available (Murtaugh 2009, Thuiller et al. 2009). Whereas it is widely recognized that different modeling approaches have their own set of benefits and drawbacks (Segurado and Araujo 2004, Elith and Graham 2009, Fitzgerald et al. 2009), different models may imply different conservation strategies (Hauser et al. 2007) and little attention is paid to the potential consequences of choosing a particular modeling approach (Langford et al. 2009). By choosing a single modeling approach, planners are essentially formulating a problem in one of many possible ways and accepting its objectives, constraints and assumptions as the only ones applicable (Wilson et al. 2005).

The modeling approaches we examined represent the broad array of approaches currently used for avian conservation planning at landscape and regional scales. They reflect the different philosophies (statistical vs. theoretical) and constraints (e.g., technical expertise, data availability) of the planners who employ them. By comparing these methods for the same species in the same geography, we illuminated the different conservation priorities each approach would suggest to landscape and regional conservation planners. Although each approach was based on a similar set of spatial data, direct comparison was complicated by differences in response variables (abundance vs. suitability), data processing techniques, predictor variables, and mapping resolutions. Thus, we conducted a real-world comparison of these modeling approaches that reveals the complexity and potential consequences of implementing uncoordinated conservation planning.

Although most conservation planning for birds in North America now occurs under the auspices of a Joint Venture (e.g., Loesch et al. 1995) or similar partnership, not all organizations within a geography are a part of the partnership and existing partnerships frequently bisect administrative boundaries (e.g., states or provinces may be part of multiple Joint Ventures; see description *available online*).[12] If individual planning groups use different modeling approaches (formal or not) as the basis for their planning, conservation efforts may be at odds, as was often

[12] ⟨www.fws.gov/birdhabitat/jointventures/index.shtm⟩

observed, for instance, in early attempts at regionalizing state-level GAP (Crist and Jennings 1997).

Despite differences in methods and data, the various models we developed generally ranked locations (i.e., counties or subsections) in the Central Hardwoods similarly, resulting in significantly positive pairwise correlations. This might suggest that the choice of modeling approach is relatively inconsequential to the planning process, especially at broader spatial scales where we tended to observe larger correlation coefficients. However, differences among ranks at specific locations reveal uncertainty in model outputs and subsequent planning decisions. One way to address this dilemma is to combine model predictions. Sometimes called ensemble classifiers or consensus models, combined models are akin to multi-model inference (Burnham and Anderson 2002) and are used in remote sensing applications as a way to assess uncertainty when ground truth data are sparse or impractical to collect (e.g., Liu et al. 2004) and in climate change (e.g., Tebaldi and Knutti 2007) or other applications whose primary purpose is projection of future conditions. Combining model predictions by simple averaging or by using some sort of weighting system (Liu et al. 2004, Araujo and New 2007, Marmion et al. 2009) provides an alternative to selecting a "best" model (Thuiller et al. 2009) and produces robust predictions (Marmion et al. 2009). Of course, the accuracy of combined predictions is dependent upon the accuracy of the underlying individual model predictions (Araujo and New 2007).

We believe ensemble prediction provides stronger justification for conservation action when models corroborate with one another. Where different modeling approaches identify the same counties or subsections as high priorities (i.e., high ranks), the risks associated with conducting conservation in these priority areas should be lower (i.e., greater confidence that the models are correct). Relying on the predictions of a single model incorporates an unknown amount of risk that is difficult to quantify. Visual inspection of our output maps (Fig. 2) revealed different conservation priorities presented by each model (i.e., all models did not highlight the same subsections as highest ranks), even for Worm-eating Warbler where correlations among models were strongest. Models that produce conflicting predictions, as observed for the Red-headed Woodpecker, are still valuable in that they can shed light on the sources of error and may provide improved understanding of spatial patterns and processes (Liu et al. 2004), especially when the discrepancies are examined in light of their ecological context (e.g., unsaturated habitat, competition, conspecifics, historical context; Fielding and Bell 1997).

Congruence-confidence mapping

We created ensemble predictions using a method that combined similarity of model predictions and their variability (i.e., congruence-confidence). We turned to this approach for two reasons. First, a simple average of ranked outputs tended to produce maps where few if any locations were ranked high, masking model congruence. At the county resolution, this resulted in part because the CRT approach produces a limited number of discrete outputs (two to four terminal nodes for models in this study), which produced many tied ranks that were assigned a value at the midpoint of the range by SAS. This problem was alleviated to some extent at the subsection resolution by the area-weighted averaging of county values. Another issue with simple averaging was that the failure of the independent evaluation analysis left us without an objective method to determine if a model approach should be included in the average (i.e., was a given model accurate?). We expected modeling approaches that incorporated landscape characteristics (HSC, CRT, and HSI) to perform better, but we observed high rank correlations with the spatially implicit database approaches (FS and HA). One might also expect that statistical models should have more predictive power than models based on theory or expert opinion. The high correlations between the statistical and theoretical models did not support that expectation either, likely because the BBS was designed to detect population trends over large regions (Sauer et al. 2003) not to inform landscape-scale habitat modeling (Bart et al. 1995, Lawler and O'Connor 2004, Harris and Haskell 2007). Thus, we used all five model outputs and did not examine how results might differ by using different subsets of the models to produce the ensemble predictions. Second, we could not produce a weighted average of scores because there were no consistent measures of accuracy across all modeling approaches. The congruence-confidence method allowed identification of the extent to which models were in agreement about what areas likely contained abundant populations in good quality habitat (i.e., received high ranks from multiple models with low variation across ranks) in contrast to areas that did not (i.e., low ranks with low variation). Areas that did not fall in these classifications represent areas where conservation action incorporates more risk due to greater uncertainty.

The conservation implications of the congruence-confidence maps are most illustrative for the Worm-eating Warbler, where the modeling approaches we examined were in greatest agreement. Of the six subsections where congruence was high, three were prioritized (i.e., ranked in the top 10%) by four models, one was prioritized by three models, and two were prioritized by two models (see Appendix B: Fig. B.10). Although there was relatively high variability in model ranks for four of these subsections (i.e., low confidence), they are likely to be the best locations for conservation actions to conserve abundant populations (as predicted by the statistical models) in abundant habitat (as predicted by the theoretical models). The 44 subsections that models consistently did not prioritize (i.e., no congruence and high confidence) are less likely to be strategic locations for conservation efforts for this species.

The conservation implications of this analysis are much less clear for the Red-headed Woodpecker. No subsections were prioritized by more than two models and 37 subsections had low confidence, indicating there was considerable disagreement among the models. This disagreement between models is nonetheless informative, with at least two potential explanations. The first possible explanation is that one or several of the models are bad. The HSI model for this species did not pass all evaluation tests (Tirpak et al. 2009c) suggesting that it poorly depicts the habitat relationships of this bird because of poorly parameterized functions, improperly weighted functions, or the absence of key limiting factors from the model. As the FS and HA database models were based on similar relationships (with minor modifications) underlying the HSI model, it was not surprising that all three were positively correlated with each other and negatively correlated with the statistical models. However, the fact that no subsection was prioritized by more than two models indicates there was little congruence among the theoretical models or the statistical models. Thus, developing conservation plans based on any of these models by itself is likely to entail substantial risk.

Another possible explanation is that all the models are missing some key component of the species-habitat relationship for the Red-headed Woodpecker, a contention supported by the fact that this species had the least accurate HSC model and the poorest fit CRT models among the species we examined. This species uses forests and woodlands in open landscapes such as orchards, parks, open agricultural country, savanna-like grasslands with scattered trees, and forest edge in addition to more forested areas such as bottomland forests (Smith et al. 2000 and references therein). The statistical models contained different variables that might capture this open landscape component (HSC, forest interspersion/juxtaposition index; CRT, total edge contrast index), but the theoretical models did not. In the absence of a good independent evaluation data set, it is difficult to say which, if either, statistical model better captures this component of Red-headed Woodpecker habitat use. Despite the confusion about where conservation priorities are for this species, there was agreement across the models about where they are not. All eight of the subsections where confidence in ranks was high received low priority ranks. Thus, even in this extreme case, combining models provided useful information for conservation planning. Developing and testing hypotheses about the causes underlying the different prioritizations can further our understanding of habitat relationships for this species and help us generate more useful models in the future.

CONCLUSIONS

Species habitat models are a simplification of a complex biological system (Laurent et al. 2010). This simplification means species habitat models cannot be perfectly explanatory or predictive (Van Horne 2002). They are, in essence, wrong, but they can provide useful inference despite their errors (Starfield 1997) and inability to capture all sources of variance in species abundance (Cushman et al. 2008). As Van Horne (2002) suggested, the modeling techniques biogeographers employ are closely tied to their modeling objectives. Thus, to properly evaluate the utility of these different modeling approaches, we need an explicit characterization of how the model parameters and mapped products are to be used. In conservation design, maps of species–habitat predictions are used to identify where regional resources may be devoted to provide the most efficient and effective return on the investment ("bang for the buck"). This return on investment comes in terms of increased population size or stability or decreased risk of extinction.

This comparison of independently generated species-habitat models implied that the choice of modeling approach may be less a function of predictive accuracy and more a function of needs, abilities, and ease of use and interpretation. All approaches tended to concur on the relative spatial distribution of abundance and quality habitats in the BCR for each species. That said, each modeling approach implied a different conservation design, even for the species with the most congruence among model outputs. Under the business model of strategic habitat conservation (National Ecological Assessment Team 2006), the true efficacy of a model built and tested in the biological planning phase is not known until the conservation design and conservation delivery phases are complete and the project is in the monitoring and evaluation phase. Thus, reliance on a single modeling approach as the basis for conservation planning is risky because a great deal of resources can be invested and the return (e.g., population stability) may not materialize for years (i.e., it will be a long time before you know how wrong your model is). Most of the models we compared here passed evaluation tests, yet there were important discrepancies among model predictions and the conservation design they implied.

Assessing uncertainty is important for assessing the tradeoffs inherent in conservation planning (Langford et al. 2009). Developing multiple habitat models is one way to assess the uncertainty within these biological planning tools. This approach avoids the trap of thinking that one modeling approach or set of approaches (e.g., statistical models) will consistently perform better. We encourage conservation planners to adopt an "all the tools in the toolbox" mindset and base their decisions upon a critical, objective evaluation of each model's output that includes an assessment of why it might yield the answer it does (i.e., know thy model). Although developing multiple models may mean more work, lengthen the conservation planning process, and slow initial progress, it will reduce uncertainty thereby helping us make more effective progress. Conservation

action occurs at the intersection of programmatic opportunities, habitat suitability, and land use opportunities (J. L. Burger, Jr., and R. Hamrick, oral presentation, summarized in Thogmartin et al. 2009). We need to minimize uncertainty on the habitat side of this equation to the greatest extent possible so that we may be strategic about the opportunities we seize.

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APPENDIX A

Rank correlations among models for each species at county and subsection scales (*Ecological Archives* A021-102-A1).

APPENDIX B

Maps of ranked model outputs from each modeling approach (*Ecological Archives* A021-102-A2).