

Change in avian abundance predicted from regional forest inventory data

Daniel J. Twedt^{a,*}, John M. Tirpak^b, D. Todd Jones-Farrand^b, Frank R. Thompson III^c,
William B. Uihlein III^d, Jane A. Fitzgerald^e

^a United States Geological Survey, Patuxent Wildlife Research Center, 2524 South Frontage Road, Vicksburg, MS 39180, USA

^b Department of Fisheries and Wildlife Sciences, 302 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211, USA

^c United States Forest Service, Northern Research Station, 202 Anheuser-Busch Natural Resources Building, University of Missouri-Columbia, Columbia, MO 65211, USA

^d Lower Mississippi Valley Joint Venture, U.S. Fish and Wildlife Service, 2524 South Frontage Road, Vicksburg, MS 39180, USA

^e Central Hardwoods Joint Venture, American Bird Conservancy, 8816 Manchester, Suite 135, Brentwood, MO 63144, USA

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ABSTRACT

An inability to predict population response to future habitat projections is a shortcoming in bird conservation planning. We sought to predict avian response to projections of future forest conditions that were developed from nationwide forest surveys within the Forest Inventory and Analysis (FIA) program. To accomplish this, we evaluated the historical relationship between silvicolous bird populations and FIA-derived forest conditions within 25 ecoregions that comprise the southeastern United States. We aggregated forest area by forest ownership, forest type, and tree size-class categories in county-based ecoregions for 5 time periods spanning 1963–2008. We assessed the relationship of forest data with contemporaneous indices of abundance for 24 silvicolous bird species that were obtained from Breeding Bird Surveys. Relationships between bird abundance and forest inventory data for 18 species were deemed sufficient as predictive models. We used these empirically derived relationships between regional forest conditions and bird populations to predict relative changes in abundance of these species within ecoregions that are anticipated to coincide with projected changes in forest variables through 2040. Predicted abundances of these 18 species are expected to remain relatively stable in over a quarter (27%) of the ecoregions. However, change in forest area and redistribution of forest types will likely result in changed abundance of some species within many ecosystems. For example, abundances of 11 species, including pine warbler (*Dendroica pinus*), brown-headed nuthatch (*Sitta pusilla*), and chuck-wills-widow (*Caprimulgus carolinensis*), are projected to increase within more ecoregions than ecoregions where they will decrease. For 6 other species, such as blue-winged warbler (*Vermivora pinus*), Carolina wren (*Thryothorus ludovicianus*), and indigo bunting (*Passerina cyanea*), we projected abundances will decrease within more ecoregions than ecoregions where they will increase.

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1. Introduction

Predicting bird population response to future habitat projections is a critical shortcoming in current bird conservation planning. Conservation planners have been challenged to predict current bird distributions (Beard et al., 1999; Thogmartin et al., 2004) and to assess avian response to historical change in habitat (Boren et al., 1999; Blackwell and Dolbeer, 2001; Cumming et al., 2001), although Matthews et al. (2004) forecast bird distributions based on presumed future climate conditions in the eastern United States. Even so, because silvicolous bird populations likely respond to changes in forest habitat, it may be possible to exploit projections

of future forest conditions to forecast avian species response to changed forest conditions.

Various studies have used econometric models and landscape simulators to predict future habitat conditions. For example, the Subregional Timber Supply Model uses Forest Inventory and Analysis (FIA) data to predict timber supply trends based on current forest conditions and the economic forces acting on the timber market (Abt et al., 2000). Similarly, as part of the Southern Forest Resource Assessment (Wear and Greis, 2002), the U.S. Forest Service projected significant changes in the extent, condition, and distribution of forest types across 13 states within the southeastern United States (Prestemon and Abt, 2002). In another study, the Resource Planning Act Assessment of Forest and Range Lands predicted the area of forestland to decline by 3.6 million acres in the southeastern United States in the next half-century (USDA Forest Service, 2000). Moreover, within this region of the United States,

* Corresponding author. Tel.: +1 601 629 6605; fax: +1 601 636 9541.

E-mail address: dtwedt@usgs.gov (D.J. Twedt).

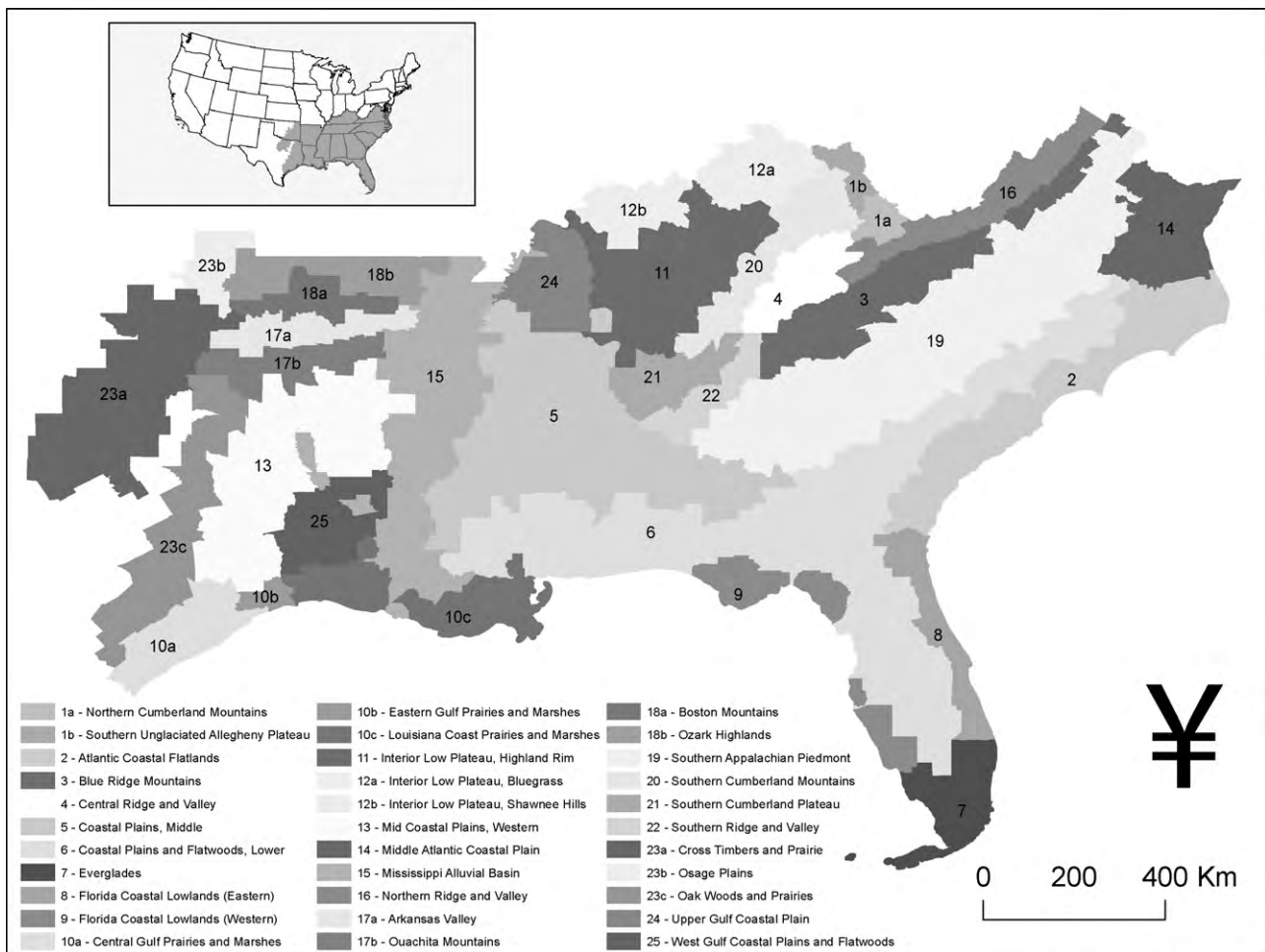


Fig. 1. County-based ecoregions, representing level III ecoregions (Omernik, 1987) of the southeastern United States, within which historical forest conditions were characterized from Forest Inventory and Analysis (FIA) data and related to contemporaneous avian abundance on Breeding Birds Survey (BBS) routes. Due to small area or paucity of Breeding Bird Survey routes within their borders, 8 of the 33 areas identified as Forest Inventory and Analysis survey units were combined with adjacent areas resulting in 25 ecoregions used for our analyses.

softwood prices are projected to increase 29–39% while hardwood prices are expected to double. Using the Subregional Timber Supply Model and assumed market demands, projections of forest area and timber supply within the southeastern United States have been made through 2040 (Prestemon and Abt, 2002).

FIA data have been used to assess statewide trends in forest area, volume, growth, mortality, and removals between 1953 and 1999 within 13 southeastern states (Conner and Hartsell, 2002). Because FIA data provide detailed information on the status, trends, and projections of the area and condition of forestlands within the United States, these data are particularly well suited for modeling change in forest habitat and avian population response to habitat change. The value and utility of FIA data for ecological assessments, such as wildlife monitoring and conservation planning, are increasingly recognized (Fearer et al., 2007; Welsh et al., 2006; Zielinski et al., 2006; Tirpak et al., 2009).

Authorized by Congress in 1928, FIA (aka, Forest Survey) began in the Mississippi Delta in 1932 with all 13 southeastern states completing their initial inventory by 1950 (Frayer and Furnival, 1999). Subsequent surveys followed at approximately 10-year intervals with every southeastern state, except Kentucky, inventoried at least six times. Within the past decade, FIA sampling within most states has moved from a single decadal sample to annual sampling of a subset of plots locations (Gillespie, 1999). These data are intended to be used to annually update 20-year projections of forest resource attributes (Reams et al., 1999).

Analogous to FIA monitoring of forests, a long-term, large-scale, roadside avian monitoring program known as the Breeding Bird Survey (BBS) was initiated in 1966 to track the status and trends of North American bird populations (Robbins and Van Velzen, 1967). Resultant data have been used to assess historical trends in populations of breeding birds (Sauer and Link, 1999; Link and Sauer, 2002) as well as to predict historical abundance and distribution of some species (Twedt et al., 2007). However, forecasts of future avian populations have generally not been developed.

An assumption fundamental to bird conservation is that population changes are a function of changes in the extent and condition of habitats (e.g., Hansen et al., 1995). Specifically, we assumed that changes in abundance of silvicolous bird species are directly related to changes in forest area and condition. This assumption, however, is rarely testable at landscape or ecoregional scales. Fortunately, the relatively long-term continuity of FIA and BBS data make possible an assessment of the historical relationship between forest condition and avian abundance. To conduct such an assessment, we used a retrospective analysis to relate species-specific avian abundance, based on detections during Breeding Bird Surveys, with forest area and condition as derived from FIA data.

We believe these historical relationships provide a basis for prediction of changes in avian populations associated with projected change in forest habitat within the southeastern United States. Our objectives were (1) to assess the historical relationships of populations of silvicolous bird species with forest area, forest

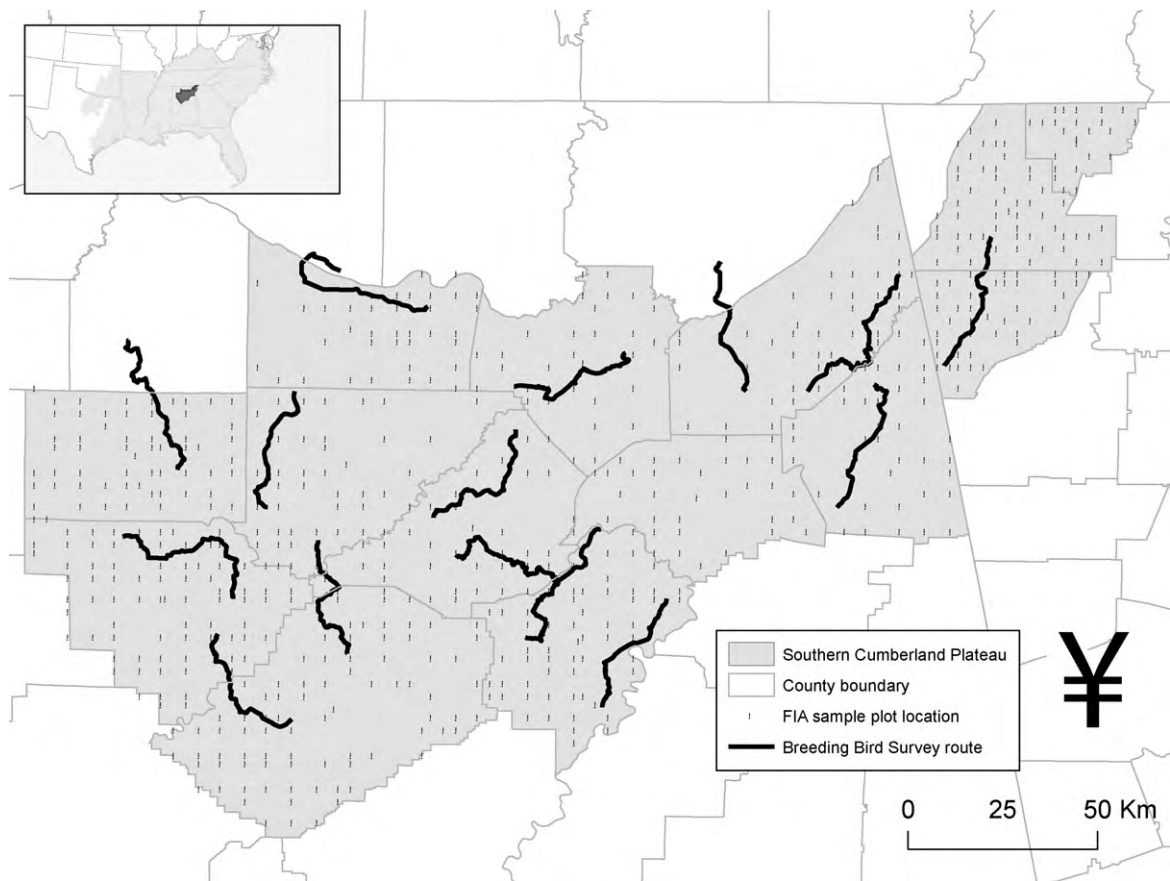


Fig. 2. Locations of Forest Inventory and Analysis (FIA) plots and Breeding Bird Survey (BBS) routes within the Southern Cumberland Plateau ecoregion of Alabama and Georgia in the southeastern United States.

composition, tree size-class, and land ownership within the southeastern United States and (2) to predict future populations of these same bird species based on their empirically derived relationship with regional forest conditions.

2. Methods

2.1. Study area

Our assessment was made within the 13 southeastern United States, albeit only the eastern forested biomes of Texas (44 counties) and Oklahoma (18 counties) were included in our analyses (Fig. 1). We amalgamated countywide forest projections derived from FIA data on forest area to 33 FIA survey units (ecoregions; Fig. 1) that were county-based surrogates of level III ecoregions of the southeastern United States (Omernik, 1987).

2.2. Data sources

The FIA program surveys forest using a three phase systematic sample of sites located across all forested lands in the United States. These phases determine (1) location of forested lands using remotely sensed data, (2) land ownership, forest type, tree species, tree size, tree condition, and site attributes from sample plots distributed approximately 1 plot for every 2428 ha (6000 acres) of forested land (Fig. 2), and (3) a broader suite of forest health attributes at a 1:16 subset of these sample plots.

Forest statistics, based on FIA data, were projected for each county within each state at each of 5 time periods from 1963 to 2006. Time periods reflected dates of statewide periodic FIA sur-

veys (Table 1). County projections for years after 1983 (except where noted, Table 1), were obtained online via the USDA forest inventory Mapmaker web-application (Miles, 2008). County projections before 1983 were extracted from standard reporting tables within hardcopy USDA publications ($n=34$) associated with each statewide periodic inventory (e.g., Hedlund and Earles, 1969).

Breeding Bird Survey routes were randomly located along secondary roads and were assumed to be representative of their surrounding landscape (Fig. 2). Each route consisted of 50 survey stops located at 0.8-km intervals. At each stop an observer recorded for 3-min all birds heard or seen within 0.4 km. Within 13 southeastern states, 752 different BBS routes have been surveyed, though not all routes were surveyed each year.

We obtained bird abundance data (i.e., number of detections of each species per BBS route) for all BBS routes within our study area that were surveyed between 1966 and 2008 (<http://www.pwrc.usgs.gov/BBS/retrieval/menu.cfm>). Using a geographic information system (ArcMap 9.2) we linked data for each BBS route to the ecoregion that encompassed the majority of the route. When fewer than five BBS routes were linked to an ecoregion, we subjectively combined adjacent ecoregions so as to achieve a more representative sample of the avian community. Combining ecoregions reduced their number from 33 to 25 that we used for analyses (Fig. 1).

2.3. Model development

Forest statistics obtained for each county within each time period included total forest area, and forest area by ownership, forest type, and tree size-class categories. Forestlands (commer-

Table 1
Allocation among time periods of statewide Forest Inventory and Analysis (FIA) data and Breeding Bird Survey data used to assess historical relationship between avian abundance and forest condition within ecoregions of the southeastern United States.

	Period 1 ^a	Period 2 ^a	Period 3	Period 4	Period 5
BBS	1966–1972	1973–1982	1983–1989	1990–1999	2000–2008
Alabama	1963, 1972	1982	1990	2000	2005
Arkansas	1969	1978	1988 ^a	1995	2005
Florida	1969	1980	1987	1995	2005
Georgia	1971	1982	1989	1997	2004
Kentucky	1963 ^b	1975	1988	1996 ^c	2004
Louisiana	1964	1974	1984 ^a	1991	2005
Mississippi	1967	1977	1987 ^a	1994	2006
North Carolina	1964 ^b	1974	1984	1990	2002, 2005
Oklahoma	1966	1976	1986 ^a	1993	2004 ^d
South Carolina	1968	1978	1986	1993	2001, 2005
Tennessee	1971	1980	1989	1999	2004
Texas	1965	1975	1986 ^a	1992	2006
Virginia	1966	1976	1984	1992	2005

^a Data were extracted from hardcopy USDA Forest Service publications.

^b Incomplete county data, county estimates extrapolated from state or multi-county areas.

^c FIA survey data do not exist, data estimated as mid-point between 1988 and 2004.

^d FIA survey data do not exist, data estimated via linear regression projection.

cial and reserved) were lands $\geq 16.7\%$ stocked by forest trees of any size, or formerly having such tree cover and not developed for non-forest use. The minimum area considered for forest classification was 0.4 ha and ≥ 36 m wide. Forest ownership categories included National Forests, other public ownerships (federal, state, or local), and private ownership. Forest type was based on the species forming a plurality of live stocking. The most common forest types in the southeastern United States, as defined by FIA (USDA Forest Service, 2007), were: longleaf-slash pine, loblolly-shortleaf pine, other softwoods (e.g., white-red-jack pine, spruce-fir), oak-pine (forests in which hardwoods constitute a plurality of the stocking but pines account for 25–50% of stocking), oak-hickory, oak-gum-cypress (bottomland forests in which tupelo, blackgum, sweetgum, oaks, or cypress are a plurality of stocking), elm-ash-cottonwood, and other hardwoods (e.g., maple-beech-birch).

Tree size-class was based on stands $\geq 10\%$ stocked with live trees whereas stands $< 10\%$ stocked were considered nonstocked. Stands with half or more of total stocking in sawtimber and poletimber trees were considered large-diameter size-class stands when sawtimber exceeded poletimber or they were considered medium-diameter size-class stands when poletimber exceeded sawtimber. Small-diameter size-class stands had more than half of total stocking as saplings and seedlings. May (1991) provides detailed methods for determining forest stocking, tree size-class, and forest type from FIA data.

We combined county estimates of FIA data within each ecoregion to derive 7 measures of forest condition (Table 2) that we believed to be relevant to silvicolous bird distribution and abundance. These measures within each ecoregion were: proportion of total area in forest (FOREST), proportion of forest land in each of two forest type classes (HARDWOOD and PINE), proportion of forest land in each of two tree size-class categories (large diameter [MATURE] and small diameter [YOUNG]), and proportion of hardwood forest that was predominately bottomland species (BLH). We also included the proportion of total forest area that was in public ownership (PUBLIC) because public lands are often not subject to the same management regimes and economic pressures as are private lands. We transformed the square root of all these proportions to their arcsine before analyses.

We allocated each statewide FIA survey effort to 1 of 5 time periods: 1966–1972, 1973–1982, 1983–1989, 1990–1999, and 2000–2006. Because FIA data were historically collected within statewide periodic (10-year) survey efforts and some ecoregions encompassed multiple states, allocation of data within these sub-decade intervals was problematic. Thus, FIA data within some

ecoregions spanned or exceeded the breadth of these time intervals (Table 1).

We selected for evaluation 24 bird species which were widely distributed among the ecoregions of the southeastern United States and that were designated as either a Continental Stewardship Species or listed on the Partners in Flight Continental Watch List for North America in 2004 (Panjabi et al., 2005). Continental Stewardship Species were those with a high proportion of their global population or range within one of seven Avifaunal Biomes identified by Rich et al. (2004). Continental Watch List species were species deemed vulnerable due to small and declining populations, limited distributions, and high threats throughout their ranges.

Because the proportion of birds detected on BBS routes varied among observers and there is evidence of a temporal trend in detection among years of service of an observer (Sauer et al., 1994), we used hierarchical models employing Markov chain Monte Carlo (MCMC) sampling to estimate annual abundance of a species within each ecoregion. To accomplish this we used BBS data for each

Table 2

Models used to assess relationship between avian detections along Breeding Bird Surveys and forest conditions derived from Forest Inventory and Analysis data for 5 time periods spanning 1963–2006 within 25 ecoregions in the southeastern United States.

NULL [Intercept only]
FOREST ^a
FOREST – PUBLIC ^b
FOREST – Type ^c (either HARDWOOD or PINE)
FOREST – Age ^d (either YOUNG or MATURE)
FOREST – HARDWOOD – BLH
FOREST – Age – Type
FOREST – PUBLIC – Type
FOREST – Age – PUBLIC
FOREST – PUBLIC – Type – BLH
FOREST – Age – HARDWOOD – BLH
FOREST – Age – HARDWOOD – PUBLIC
FOREST – Age – HARDWOOD – BLH – PUBLIC
Saturated (FOREST – YOUNG – MATURE – HARDWOOD – PINE – BLH – PUBLIC) ^e

^a Proportion of forest within ecoregion (forest area/total area).

^b Proportion of public ownership (area of public forest (federal, state, and local)/forest area).

^c Proportion of forest type: HARDWOOD is the proportion of forest area in hardwoods (sum of hardwood forest types/forest area), PINE is the proportion of forest area in softwoods (sum of softwood forest types/forest area), and BLH is the proportion of hardwood forest comprised of bottomland species (area of oak-gum-cypress forest/area of hardwood forest).

^d Proportion of forest area in large-diameter (MATURE, sawtimber) or early-successional (YOUNG, sapling-seedling and nonstocked) tree size-classes.

^e Used only for calculation of R^2_{DEV} .

species from all routes surveyed in our study area between 1966 and 2008. We constructed overdispersed Poisson regression models that incorporated covariates for observers and first year of survey by an observer (Link and Sauer, 2002) using the BRugs package within R (the R Project for Statistical Computing; URL: <http://www.r-project.org/>) to access OpenBUGS (Bayesian Inference Using Gibbs Sampling, Release 3.0.3) and estimate annual abundance (i.e., number of detections per BBS route) of each species in an ecoregion.

For each species, we allocated the resultant median annual abundance estimate within each ecoregion among the 5 time periods associated with FIA data. The measure of avian abundance used for analysis of each species was the mean of annual abundance estimates for all years in a time period within an ecoregion. We assumed detections of each species at count locations along a BBS route were Poisson distributed with mean λ , and that λ (expressed as number of detections per BBS route per year) was a random variable that was Gamma distributed. We used a Gamma distribution because it can take a variety of shapes, from Exponential to a Normal, so random variations in λ from a Poisson distribution can be well approximated by a Gamma distribution.

We evaluated each species' response to forest conditions based on a common set of 24 *a priori* models that incorporated 7 measures of historical forest condition within 25 ecoregions of the southeastern United States (Table 2). We did not include highly correlated ($r \geq |0.6|$) variables, such as the proportions of forest type classes (HARDWOOD and PINE; $r = -0.68$) or the proportions of tree size-class categories (YOUNG and MATURE; $r = -0.82$), within the same model. An exception was a saturated model which included all seven measures of forest condition that was used only to aid in assessment of performance of models under evaluation.

We used generalized linear regression, PROC GENMOD (SAS Institute, Cary, North Carolina), to fit mean estimated avian abundance on BBS routes to contemporaneous forest conditions based on an assumed gamma distribution of avian detections using a log link function and repeated measurements (time periods) within ecoregions. We evaluated model performance within an information-theoretic framework (Burnham and Anderson, 2002) using Akaike information criteria adjusted for small sample sizes (AIC_c) as a measure of support among competing models (Hurvich and Tsai, 1995). When multiple models had strong support (i.e., $\Delta AIC_c < 2$) we used model averaging of the most-supported models to obtain model-averaged coefficients (Burnham and Anderson, 2002).

Performance of the most-supported models assessing avian response to forest conditions was evaluated based on the models' goodness of fit R^2 defined as:

$$R^2 = 1 - \exp \left\{ \frac{2[\log L(M) - \log L(0)]}{n} \right\},$$

where $\log L(M)$ and $\log L(0)$ are the maximized log likelihood for the fitted model and the null model with only the intercept term, respectively, and n is the sample size. This statistic is a measure of the ability of the model variables to account for variation in the data beyond that accounted for by the null model. Additionally, we evaluated model performance using the deviance R^2 , adjusted for bias due to small sample sizes and model complexity, defined as:

$$R^2_{DEV} = \left[\frac{[(\log L(M) - \log L(0)) - (k(M) + 1) \times (n - 1)/(n - k(M) - 1)]}{[(\log L(S) - \log L(0)) - 1]} \right],$$

where $\log L(M)$, $\log L(0)$, and $\log L(S)$ are the maximized log likelihoods for the fitted, null, and saturated models, respectively (Hosmer and Lemeshow, 1989; Menard, 1995), n is the sample size, and $k(M)$ is the number of covariates in the fitted model. This statistic provides a re-scaled measure of variation that is a com-

parison between two models – the fitted and the reference models (Shtatland et al., 2000).

Quality of variables included in the most-supported model(s) was assessed by examination of 95% confidence intervals (CI) on model coefficients and their odds ratios. Model parameters were deemed to have strong support if we had confidence in the direction (positive or negative) of the effect coefficient, as evidenced by a CI that did not span zero, and better than equal odds of effecting model prediction (i.e., CI on odds ratio did not include 1).

2.4. Model predictions

We used data on change in percentage of forest land within counties (Southern Forest Resource Assessment; <http://www.srs.fs.fed.us/sustain/data/dataset=socio1f11>) that were generated for 2020 and 2040 under an urban-growth scenario forecasting model (Hardie et al., 2000). Projected forest area by forest type classes (PINE, HARDWOOD, and BLH) for these same years were developed using the Subregional Timber Supply Model under 4 projection scenarios (Prestemon and Abt, 2002) within FIA survey units (Southern Forest Resource Assessment; <http://www.srs.fs.fed.us/sustain/data/dataset=area2>). These area projections for the southeastern United States showed little loss of forestland (1–3%) over the coming decades, but marked increase in the area of pine plantations at the expense of other forest management types. Using projections from the scenario that assumed elastic (price-sensitive) demand for forest products and high productivity associated with increased plantation forestry (Prestemon and Abt, 2002), we used county-based, proportional allocation of these projections to forecast forest area by management type within each of our ecoregional study units.

Unfortunately, the Southern Forest Resource Assessment (Wear and Greis, 2002) did not forecast change in area of public land or tree size-class. However, a region-wide forecast of timber volume by age class developed using the Subregional Timber Supply Model was provided for 1995, 2020 and 2040 (Southern Forest Resource Assessment; <http://www.srs.fs.fed.us/sustain/data/dataset=volage>). Based on the projected ratio of younger age-class (≤ 15 years) to older age-class (≥ 45 years) stands, we projected a region-wide 7% and 11% increase in area of early-successional forest (YOUNG) by 2020 and 2040, respectively, with a concomitant decrease in area of large-diameter forest stands (MATURE). We assumed the area of public land remained unchanged from the most recent FIA-based estimates. Using projected forest habitat conditions and each species' most-supported forest habitat model(s), we forecast abundance (mean number of detections per BBS route) within ecoregions for 2020 and 2040. Because forecasting population response to future habitat conditions is speculative, we chose a response threshold of >25% change within an ecoregion as indicative of marked population change.

3. Results

3.1. Resources

Avian survey data were distributed relatively evenly among time periods, although the initial period averaged fewer BBS routes surveyed (81 BBS surveys/ecoregion) compared to the other 4 periods (range: 108–213 BBS surveys/ecoregion). Conversely, avian survey effort varied among ecoregions proportional to their area: the Allegheny Plateau, at 1.3 million ha, averaged only 26 BBS routes surveyed per time period whereas the 24.2 million ha East Gulf Coastal Plain averaged 551 BBS routes surveyed per time period. Because we were able to use hierarchical modeling to esti-

Table 3
Measures of quality (R^2 and R^2_{DEV}) for the most-supported model(s) of the relationship between seven forest variables derived from Forest Inventory and Analysis (FIA) data and mean detections on Breeding Bird Survey (BBS) routes from 1966 to 2008, and the number of ecoregions within which the mean number of detections is predicted to increase by >25% (Gain), decrease by >25% (Loss), or remain within 25% (Same) of period 5 (circa 2005) detections by year 2040.

Species	R^2 ^a	R^2_{DEV} ^b	Loss ^c	Same ^c	Gain ^c
Acadian flycatcher, <i>Empidonax vireescens</i>	0.36	0.75	5	5	13
Blue-winged warbler, <i>Vermivora pinus</i>	0.80	0.75	6	0	3
Brown-headed nuthatch, <i>Sitta pusilla</i>	0.63	0.81	5	1	10
Brown thrasher, <i>Toxostoma rufum</i>	0.29	0.45	– ^d	– ^d	– ^d
Carolina wren, <i>Thryothorus ludovicianus</i>	0.51	0.74	8	12	5
Cerulean warbler, <i>Dendroica cerulea</i>	0.58	0.53	2	0	5
Chuck-wills-widow, <i>Caprimulgus carolinensis</i>	0.47	0.78	2	7	14
Eastern towhee, <i>Pipilo chlorurus</i>	0.37	0.75	4	7	11
Hooded warbler, <i>Wilsonia citrina</i>	0.43	0.86	7	4	10
Indigo bunting, <i>Passerina cyanea</i>	0.67	0.88	11	6	7
Kentucky warbler, <i>Oporornis formosus</i>	0.42	0.83	10	6	8
Louisiana waterthrush, <i>Seiurus motacilla</i>	0.51	0.82	4	6	11
Pine warbler, <i>Dendroica pinus</i>	0.72	0.75	8	6	10
Prairie warbler, <i>Dendroica discolor</i>	0.27	0.67	– ^d	– ^d	– ^d
Prothonotary warbler, <i>Protonotaria citrea</i>	0.56	0.85	3	7	12
Red-bellied woodpecker, <i>Melanerpes carolinus</i>	0.25	0.67	– ^d	– ^d	– ^d
Red-headed woodpecker, <i>Melanerpes erythrocephalus</i>	0.31	0.56	– ^d	– ^d	– ^d
Red-shouldered hawk, <i>Buteo lineatus</i>	0.71	0.91	5	12	7
Swainson's warbler, <i>Limnithlypis swainsonii</i>	0.25	0.40	– ^d	– ^d	– ^d
White-eyed vireo, <i>Vireo griseus</i>	0.39	0.77	10	6	9
Wood thrush, <i>Hylocichla mustelina</i>	0.54	0.83	10	4	10
Worm-eating warbler, <i>Helmitheros vermivorum</i>	0.20	0.45	– ^d	– ^d	– ^d
Yellow-throated vireo, <i>Vireo flavifrons</i>	0.53	0.89	7	12	5
Yellow-throated warbler, <i>Dendroica dominica</i>	0.41	0.81	8	3	12

^a Goodness of fit $R^2 = 1 - \exp\{2[\log L(M) - \log L(0)]/n\}$.

^b Deviance $R^2 = [(\log L(M) - \log L(0)) - (k(M) + 1) \times (n - 1) / (n - k(M) - 1)] / [(\log L(S) - \log L(0)) - 1]$.

^c Ecoregions with insufficient detections of a species on BBS routes to estimate historical detection rate per survey route using MCMC simulations via program BUGS were not included in model projections for that species.

^d Species lacking a historical relationship between avian abundance and forest condition ($R^2 < 0.32$) were not included in model projections.

mate avian abundance only within ecoregions where a species was detected on >5 BBS routes, the number of ecoregions used to develop relationships between avian abundance and forest conditions varied among species. Although >21 ecoregions were used for 19 of the 24 species we evaluated, data from only 7 ecoregions were used for cerulean warbler (*Dendroica cerulea*) and data for blue-winged warbler (*Vermivora pinus*) were available for only 9 ecoregions (Table 3).

3.2. Model assessment

The most-supported models for six species, brown thrasher (*Toxostoma rufum*), prairie warbler (*Dendroica discolor*), red-bellied woodpecker (*Melanerpes carolinus*), red-headed woodpecker (*Melanerpes erythrocephalus*), Swainson's warbler (*Limnithlypis swainsonii*), and worm-eating warbler (*Helmitheros vermivorum*) provided only slight improvement over a null (intercept only) model as evidenced by an $R^2 \leq 0.31$ (Table 3). The most-supported models for three additional species, Acadian flycatcher (*Empidonax vireescens*), eastern towhee (*Pipilo chlorurus*), and white-eyed vireo (*Vireo griseus*), had relatively modest predictive ability ($R^2 < 0.40$) yet, with $R^2_{DEV} \geq 0.75$, these models explained a high proportion of the variability within the seven measurements of forest condition we used to model avian abundance (Table 3). The most-supported models for the remaining 15 species suggested a substantial relationship between forest variables and avian abundance ($R^2 > 0.40$) and, except for Cerulean warbler, each model accounted for a high proportion of the total variability ($R^2_{DEV} \geq 0.74$) within these data (Table 3).

Forest area was included in the most-supported models for all 18 species for which we established useful relationships ($R^2 > 0.36$) between avian abundance on BBS routes and FIA-derived forest conditions. Increased forest area was a strong predictor of increased bird abundance for 13 of these species (Table 4). Public ownership was included in the most-supported models for 12 species

but was a strong predictor of avian abundance for only 4 species: 3 of these species exhibited decreased abundance with increased public ownership of forest lands (Table 4).

Forest type class was also an important predictor of bird detections with some combination of hardwood, bottomland hardwood, or pine included in the most-supported models for all but two of these species (Table 4). Although hardwood was included in the most-supported model for more species than were models that included either pine or bottomland hardwood, these latter forest types were more often strong predictors of avian abundance than was hardwood (Table 4).

Finally, tree size-class was included in the most-supported models for 11 of these species, with the abundance of 8 species positively related to area of mature forest or negatively related to area of early-successional forest (Table 4). An increased proportion of large-diameter-class forest or a decreased proportion of small-diameter-class forest was strongly associated with increased avian abundance of four species. Conversely, a decreased proportion of large-diameter-class forest was associated with increased abundance of chuck-wills-widow (*Caprimulgus carolinensis*) and eastern towhee (Table 4).

3.3. Model predictions

Projected change in forest area (Fig. 3) and other forest condition variables over the next 40 years within the southeastern United States influenced predicted avian populations. Even so, predicted change in mean abundance on BBS routes varied widely among ecoregions and among species (Appendix A). For all species, predicted abundance was projected to increase in 42% of ecoregions, decrease in 30% of ecoregions, and remain unchanged in 27% of ecoregions. However, 11 of 18 species for which we developed predictive models were projected to have >25% increase in abundance within more ecoregions than the number of ecoregions wherein abundance was projected to decline (Table 3).

Table 4

Generalized linear regression models relating avian abundance on Breeding Bird Survey routes to proportions of land area in forest (Forest), in public ownership (Public), in hardwood forest (Hardwood), in softwood forest (Pine), and the proportion of hardwood forest with bottomland species (BLH), as well as the proportions of forest land in large-diameter (i.e., sawtimber) tree size-class (Mature) and in early-successional, small-diameter (i.e., seedling-sapling and nonstocked) tree size-class (Young) within 25 ecoregions of the southeastern United States. Model parameters with strong support are identified in **boldface**; they were identified as having a confidence interval for the estimated coefficient that did not include 0 and a confidence interval on the odds ratio that did not include 1 (i.e., equal odds).

Species	Intercept	Forest	Public	Hardwood	Pine	BLH	Mature	Young
Acadian flycatcher ^a	-0.81 ± 1.12	1.85 ± 0.45	-0.35 ± 0.57	0.55 ± 0.54	-0.53 ± 0.63	-	1.01 ± 1.21	-1.50 ± 1.40
Blue-winged warbler ^a	-3.22 ± 2.60	3.53 ± 0.84	-6.63 ± 1.44	1.50 ± 1.82	-2.51 ± 2.11	-	-	-
Brown-headed nuthatch ^a	-3.11 ± 0.52	2.30 ± 0.56	-1.11 ± 0.76	-	3.04 ± 0.52	-0.18 ± 0.26	-	-
Carolina wren	2.88 ± 0.19	0.37 ± 0.16	-	-	1.50 ± 0.15	-	-	-2.00 ± 0.28
Cerulean warbler ^a	-6.73 ± 1.47	5.60 ± 0.92	-	-	-	-	-	2.54 ± 2.57
Chuck-will's-widow ^a	4.24 ± 0.68	0.40 ± 0.53	0.24 ± 0.42	-0.21 ± 0.32	0.11 ± 0.19	-	-5.95 ± 0.70	-
Eastern towhee	4.87 ± 0.49	0.63 ± 0.41	0.93 ± 0.74	0.11 ± 0.21	-	-	-4.16 ± 0.65	-
Hooded warbler	-3.41 ± 0.68	3.20 ± 0.50	-	-2.14 ± 0.49	-	-	4.35 ± 0.86	-
Indigo bunting	3.39 ± 0.29	1.32 ± 0.39	0.07 ± 0.40	-	-1.86 ± 0.34	-0.86 ± 0.21	-	-
Kentucky warbler ^a	-2.70 ± 0.84	3.78 ± 0.47	-	-	-2.14 ± 0.41	-	1.06 ± 0.87	-
Louisiana waterthrush ^a	0.37 ± 0.97	0.58 ± 0.65	-0.51 ± 0.74	-0.86 ± 0.50	-	-2.78 ± 0.36	-	-
Pine warbler	1.00 ± 0.68	3.08 ± 0.46	-	-3.31 ± 0.36	-	1.04 ± 0.26	-	-
Prothonotary warbler ^a	-3.60 ± 1.10	0.01 ± 0.71	-	1.78 ± 0.59	-	3.06 ± 0.38	0.37 ± 0.64	-
Red-shouldered hawk	-0.41 ± 0.41	-0.05 ± 0.27	1.39 ± 0.36	-0.92 ± 0.22	-	1.38 ± 0.18	-	-
White-eyed vireo	0.23 ± 0.34	2.15 ± 0.37	-0.70 ± 0.43	-	-1.02 ± 0.37	1.73 ± 0.26	-	-
Wood thrush ^a	0.83 ± 0.90	4.6 ± 0.52	-4.68 ± 0.73	0.25 ± 0.38	-	-	-	-3.18 ± 0.82
Yellow-throated vireo	-3.22 ± 0.39	2.73 ± 0.28	-1.50 ± 0.39	-	-	-	2.05 ± 0.38	-
Yellow-throated warbler ^a	-3.76 ± 1.10	3.48 ± 0.50	1.02 ± 0.99	0.18 ± 0.30	-	-	0.68 ± 0.83	-0.51 ± 0.76

^a Model-averaged estimate based on two or more competing models.

Predicted increased abundances of pine warbler (*Dendroica pinus*) and brown-headed nuthatch (*Sitta pusilla*) were likely spurred by the projected increase in pine habitat (Fig. 3). Abundances of Acadian flycatcher, prothonotary warbler (*Protonotaria citrea*), and chuck-wills-widow were predicted to increase in ≥ 12 ecoregions while decreasing in ≤ 5 ecoregions (Fig. 3). Conversely, we predicted abundance of blue-winged warbler will decrease in six ecoregions but increase in only three ecoregions (Fig. 3).

4. Discussion

The forest variables most strongly associated with each species were generally representative of documented habitat associations. For example, area of pine forest was positively associated with abundance of brown-headed nuthatch whereas the area of hardwood forest was negatively associated with abundance of pine warbler, consistent with the habitat associations of these species (Withgott and Smith, 1998; Rodewald et al., 1999). Similarly, abundance of prothonotary warbler was positively associated with area of hardwood and bottomland hardwood forest, as indicated by Pettit (1999), although total forest area had little influence on abundance of this species.

Notably, forest area was not strongly associated with any of the six species for which the most-supported models poorly ($R^2 < 0.32$) modeled their relationship with forest variables. The lack of association of these species with forest variables was not unexpected as five of these species tend to frequent overgrown fields, thickets, open woodland, or residential areas (Hamel, 1992); the exception, Swainson's warbler, may be poorly sampled by roadside bird surveys (Brown and Dickson, 1994).

Although FIA data were collected using a systematic grid sampling scheme, use of county-based estimates that were subsequently aggregated within ecoregions was effective for our analyses, as we were able to identify forest–bird relationships for 18 of 24 species evaluated. Similarly, Fearer et al. (2007) believed county level projection of FIA data mimicked the spatial characteristics of Thiessen polygons and thus afforded relatively precise interpolation of FIA data.

Even though the Breeding Bird Survey is well established as a large-scale survey method for birds, it has well-documented flaws (O'Connor et al., 2000; Bart et al., 2005). For example, BBS routes are

surveyed only one morning per year, survey locations are restricted to roadways, detections are influenced by time of year, weather conditions, and observer differences, and the probability of not detecting a bird when it is present is not addressed. We attempted to account for differences among observers and among years using MCMC simulations within hierarchical models but we were unable to mitigate other deficiencies in survey methodology.

Despite assignment of BBS routes to secondary roads so as to be representative of surrounding landscape conditions, recent studies revealed bias in the landscapes being surveyed by BBS routes that may be problematic for estimation of trends of some species (Betts et al., 2007). Even so, Harris and Haskell (2007) concluded bird species associated with late-successional habitats were less influenced by landscape bias than were species associated with early-successional habitats. Notably, we found little association between avian abundance on BBS routes and forest condition for two species (eastern towhee and prairie warbler) that were markedly influenced by roadside bias (Harris and Haskell, 2007).

Landscape context (e.g., patch size, shape, and connectivity) has been shown to be an important determinate of avian distribution (Donovan and Flather, 2002; Thogmartin et al., 2004), abundance (Twedt et al., 2007), and productivity (Boulinier et al., 2001). Indeed, current remote sensing and geographic information system technologies make incorporation of landscape characteristics requisite within most regional wildlife habitat assessments – yet we did not include landscape variables in our analyses. Although FIA data include some measures of spatial features (e.g., patch size) these data were rarely and inconsistently reported within the hardcopy archives of FIA data and were only available for recent periodic surveys. Furthermore, readily assessable digital data for landscape conditions within our study area do not span the 40-year breath of our historical archive of FIA and BBS data.

Recent nationwide depictions of forested land cover, such as the 1992 and 2001 National Land Cover data (Vogelmann et al., 2001) combined with earlier national land cover depictions (e.g., circa 1980 Land Use Land Cover data; U.S. Geological Survey, 1986) suggest that including landscape variables is possible when evaluating data from recent decades. We believe incorporation of landscape data to complement FIA-derived forest condition data would refine our ability to forecast avian population change. Toward that end, forest modelers have undertaken to define conservation priorities using fragmentation forecasts (Wear et al.,

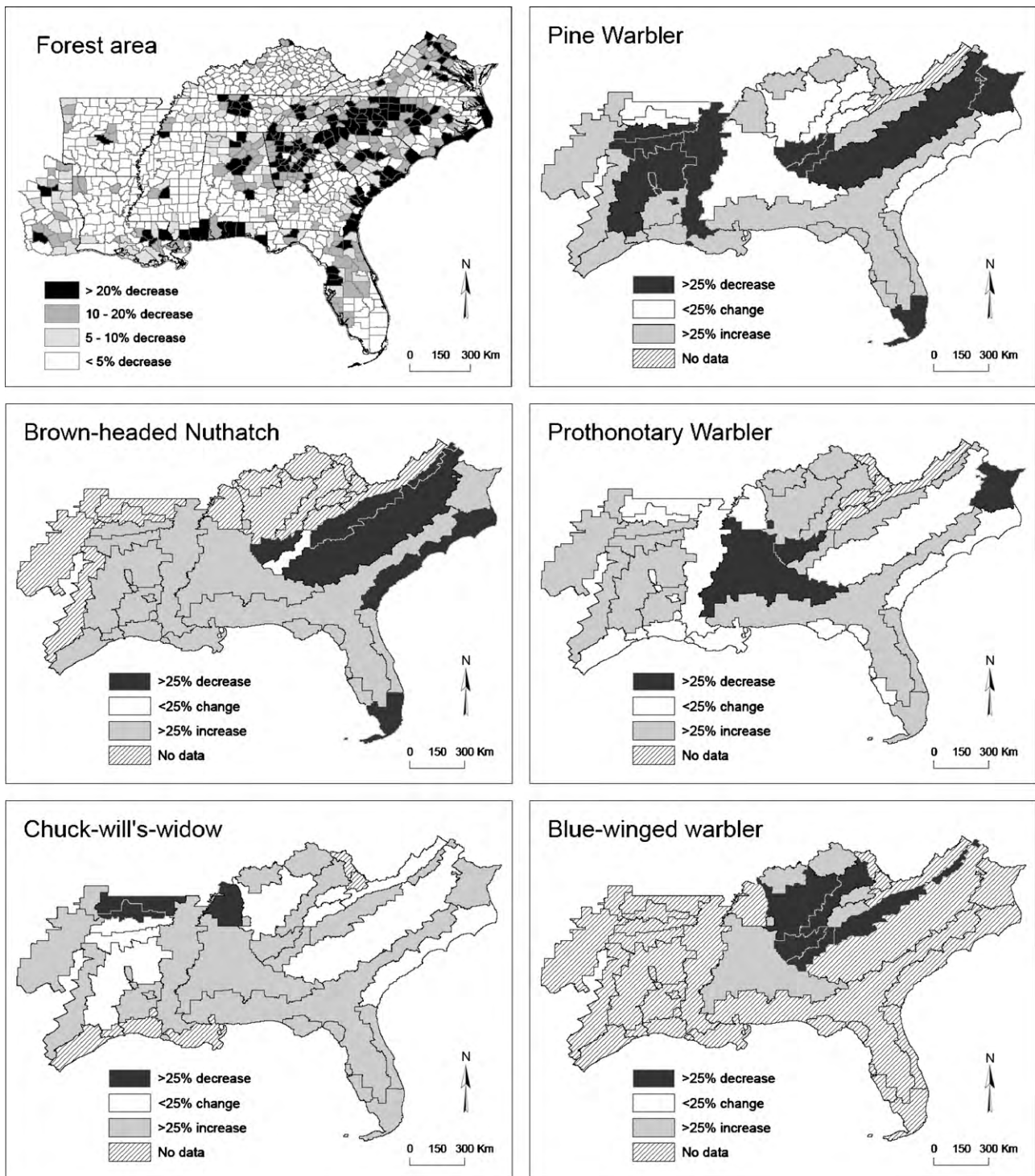


Fig. 3. Predicted change in the southeastern United States by 2040 for forest area within counties and avian abundance (mean number of detections per Breeding Bird Survey route) within ecoregions for: pine warbler (*Dendroica pinus*), brown-headed nuthatch (*Sitta pusilla*), prothonotary warbler (*Protonotaria citrea*), chuck-will's-widow (*Caprimulgus carolinensis*), and blue-winged warbler (*Vermivora pinus*).

2004). For example, the Southern Forest Futures Project (URL: <http://www.srs.fs.usda.gov/futures/>) is using quantitative models to forecast the effects of the different forces of change on land area and forest inventories. Similarly, efforts such as the Southern Wildland–Urban Interface Assessment (Macie and Hermansen, 2003) assess human influences on forest ecosystems. Clearly, landscape changes resulting from increased human encroachment on forested ecosystems will be an important predictor of the ability of these systems to continue to provide quality avian habitat.

The most notable predicted change in forest condition within the southeastern United States is the increase in planted pine (plantations) and concurrent loss of other forest management types, especially natural pine and hardwood stands (Prestemon and Abt, 2002). This change in forest management will likely influence their associated bird communities (LeGrand et al., 2007). Unfortunately, historical FIA documents did not consistently report area of planted pine and we were unable to incorporate this fundamental change in forest management in our models of bird–forest

Table A1

Predicted relative change in abundance (number of detections per Breeding Bird Survey route increase by >25% [+], decrease by >25% [–], <25% change [0], or not predicted [*]) for 24 species in 25 ecoregions of the southeastern United States.

Species	Ecoregion number ^a																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Acadian flycatcher	0	–	+	–	0	+	*	+	+	+	0	+	0	–	–	*	+	+	–	+	+	+	+	+	0	
Brown-headed nuthatch	*	–	–	*	+	+	–	+	+	+	*	*	+	+	+	*	+	*	–	*	–	0	*	*	+	
Brown thrasher	0	–	+	+	–	–	+	+	0	+	0	0	+	0	–	0	+	+	0	0	0	0	+	–	+	
Blue-winged warbler	–	*	–	+	+	*	*	*	*	*	*	–	+	*	*	*	*	*	*	*	–	–	*	*	*	
Carolina wren	–	–	+	0	0	0	+	0	0	0	–	0	0	0	–	–	+	–	0	–	0	+	+	0	–	
Cerulean warbler	+	*	+	–	*	*	*	*	*	*	+	–	*	*	*	*	*	*	*	*	+	*	*	*	+	*
Chuck-will's-widow	*	0	+	0	+	+	+	+	+	+	0	+	0	+	+	0	0	–	0	+	+	+	+	–	+	
Eastern towhee	+	0	–	0	+	+	+	+	+	+	–	0	+	0	+	–	*	*	0	+	–	0	*	0	+	
Hooded warbler	–	–	–	–	0	+	*	0	+	–	+	+	0	–	–	*	+	*	+	+	+	+	*	+	0	
Indigo bunting	+	–	+	0	0	–	*	0	+	+	0	0	–	–	–	+	–	–	–	+	0	–	+	–	–	
Kentucky warbler	–	+	0	–	+	–	*	+	+	–	–	0	–	0	–	–	–	–	0	+	–	–	+	0	–	
Louisiana waterthrush	+	–	+	–	0	+	*	*	+	*	0	+	0	–	+	*	0	–	+	+	+	+	+	0	0	
Pine warbler	+	0	+	0	0	+	–	+	+	+	0	+	–	–	–	*	–	0	–	0	–	–	+	+	+	
Prairie warbler	–	–	+	+	+	+	–	+	+	+	0	–	+	–	0	+	–	+	–	0	+	0	+	0	+	
Prothonotary warbler	*	0	+	–	+	+	+	0	0	+	+	+	–	0	*	+	0	0	+	–	+	+	0	+	+	
Red-bellied woodpecker	+	0	+	+	–	0	0	0	0	+	–	+	0	0	–	–	+	–	0	0	–	0	0	0	0	
Red-headed woodpecker	*	+	+	+	0	0	–	+	+	–	–	0	0	–	0	–	+	–	0	+	0	+	0	0	0	
Red-shouldered hawk	–	+	+	+	0	0	–	0	+	0	+	+	0	–	+	*	0	–	0	–	0	0	0	0	0	
Swainson's warbler	*	0	+	+	+	+	*	–	+	+	*	*	+	–	+	*	*	*	+	*	+	+	*	+	+	
White-eyed vireo	–	0	+	+	0	+	–	+	0	+	–	+	–	–	+	+	–	–	0	0	–	–	+	0	–	
Worm-eating warbler	0	–	–	–	+	+	*	*	*	+	+	+	–	–	+	*	0	+	+	0	0	–	*	+	+	
Wood thrush	+	–	–	–	+	+	–	+	–	–	0	0	+	–	–	+	+	+	–	0	–	–	+	0	+	
Yellow-throated vireo	0	–	+	0	0	0	*	0	0	+	–	0	0	–	–	0	–	+	–	0	0	–	+	+	0	
Yellow-throated warbler	–	–	+	–	+	+	*	0	–	–	–	0	+	–	+	*	+	+	0	–	+	+	+	+	+	

^a 1 = Northern Cumberland Mountains, Southern Unglaciated Allegheny Plateau; 2 = Atlantic Coastal Flatlands; 3 = Blue Ridge Mountains; 4 = Central Ridge and Valley; 5 = Coastal Plains, Middle; 6 = Coastal Plains and Flatwoods, Lower; 7 = Everglades; 8 = Florida Coastal Lowlands (Eastern); 9 = Florida Coastal Lowlands (Western); 10 = Prairies and Marshes, Central Gulf, Eastern Gulf, and Louisiana Coast; 11 = Interior Low Plateau, Highland Rim; 12 = Interior Low Plateau, Bluegrass and Shawnee Hills; 13 = Mid Coastal Plains, Western; 14 = Middle Atlantic Coastal Plain; 15 = Mississippi Alluvial Basin; 16 = Northern Ridge and Valley; 17 = Arkansas Valley and Ouachita Mountains; 18 = Boston Mountains and Ozark Highlands; 19 = Southern Appalachian Piedmont; 20 = Southern Cumberland Mountains; 21 = Southern Cumberland Plateau; 22 = Southern Ridge and Valley; 23 = Cross Timbers and Prairie, Osage Plains, and Oak Woods and Prairies; 24 = Upper Gulf Coastal Plain; 25 = Coastal Plains and Flatwoods, West Gulf.

relationships. However, because this change in management is so pervasive within the southeastern United States, we believe that incorporating forest management type into future modeling efforts will be critical for effective forecasting of change in avian populations.

Despite predicted increases in planted pine, we recognize that economic forces, such as those associated with recent precipitous declines in the housing market, fluctuation in prices for pulpwood, shifting agricultural prices, and changing ownership patterns, may radically alter predicted change in future forest condition. For example, Sheffield (2009) found: ‘The rate at which forest plantation acreage has increased over the past several decades is not likely to continue. Although some increases will probably occur, the rate of increase will moderate for two reasons. First, the number of acres planted in the past decade has dropped compared with planting rates for the 1980s and early 1990s. Rates of planting in the South region during this earlier period were elevated due to incentive programs that encouraged the planting of certain agricultural lands with trees. Changes in ownership of forests are another possible factor in reduced planting rates. The second reason for moderation in the rate of increase in forest plantations is that an increasing number of planted stands are being harvested as they mature. A high percentage of these stands may be reestablished as a plantation with no impact on net area in plantations.’

5. Conclusions

For several avian species of conservation concern in the southeastern United States, we successfully established relationships between their abundance on Breeding Bird Survey routes and historical forest conditions as reported from Forest Inventory and Analysis data. We were able to exploit these empirically derived relationships to forecast population change for these species in response to anticipated change in forest area through 2040.

Although abundances of some species are expected to remain relatively stable in some ecoregions, an anticipated increase in area of pine plantations presages increased populations of species, such as pine warbler and brown-headed nuthatch, which are associated with pine habitats. Even so, the direction and magnitude of predicted population change varied among species and ecoregions. We believe our predictive models could be improved through incorporation of variables that assess landscape context and variables that quantify the type and intensity of forest management.

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Appendix A.

See Table A1.

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