Projected long-term response of Southeastern birds to forest management

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ARTICLE INFO

ABSTRACT

Numerous studies have explored the influence of forest management on avian communities empirically, but uncertainty about causal relationships between landscape patterns and temporal dynamics of bird communities calls into question how observed historical patterns can be projected into the future, particularly to assess consequences of differing management alternatives. We used the Habplan harvest scheduler to project forest conditions under several management scenarios mapped at 5-year time steps over a 40-year time span. We used empirical models of overall avian richness, richness of selected guilds, and probability of presence for selected species to predict avian community characteristics for each of the mapped landscapes generated for each 5-year time step for each management scenario. We then used time series analyses to quantify relationships between changes in avian community characteristics and management-induced changes to forest landscapes over time. Our models of avian community and species characteristics indicated habitat associations at multiple spatial scales, although landscape-level measures of habitat were generally more important than stand-level measures. Our projections showed overall richness, richness of Neotropical migrants, and the presence of Blue-gray Gnatcatchers and Eastern Wood-pewees varied little among management scenarios, corresponding closely to broad, overall landscape changes over time. By contrast, richness of canopy nesters, richness of cavity nesters, richness of scrub-successional associates, and the presence of Common Yellowthroats showed high temporal variability among management scenarios, likely corresponding to short-term, fine-scale changes in the landscape. Predicted temporal variability of both interior-forest and early successional birds was low in the unharvested landscape relative to that in the harvested landscape. Our results also suggested that early successional species can be sensitive to both availability and connectivity of habitat on the landscape. To increase or maintain the avian diversity, our projections indicate that forest managers need to consider landscape-scale configuration of stands, maintaining a spatially hetero-geneous distribution of age classes. Our findings suggest which measures of richness or species presence may be appropriate indicators for monitoring effects of forest management on avian communities, depending on management objectives.

Published by Elsevier B.V.

1. Introduction

Understanding the relationship between landscape structure and wildlife diversity requires consideration of both spatial and temporal variation because landscapes vary over space and time.

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Most empirical research thus far has focused on the spatial component of landscape variation (Dunning et al., 1992; Gustafson, 1998; Hargis et al., 1997; Tischendorf, 2001). For example, many studies cite spatial heterogeneity (e.g., habitat configuration) as an important factor influencing wildlife communities (Hanowski et al., 1997; Manolis et al., 2000; Mitchell et al., 2001; Villard et al., 1999). Spatial heterogeneity in landscape structure, however, can change over time, which may have consequences for the long-term stability and viability of wildlife populations (Dunn et al., 1990). Although the importance of temporal dynamics in wildlife populations has been recognized historically (e.g., population stability; Holling, 1973; MacArthur, 1955) and studied extensively at the forest stand scale, explicit examinations of population and community dynamics associated with changes in landscape structure over time are rare (Boulinier et al., 1998). Thus, the causal relationships that result in variation in animal communities over broad spatial and long temporal scales are poorly understood; little is known about landscape changes that result directly in changes in animal communities, or the time periods where these changes take place. This lack of understanding, combined with the complexity of addressing environmental variation in both space and time, makes predicting future patterns of animal diversity on landscapes highly tenuous.

For all this uncertainty, forest managers must regularly decide how to manage forest landscapes over extended planning periods, where implications of their decisions for wildlife could extend well into the future. Projecting observed empirical relationships into the future across alternative management scenarios has the potential to inform such decisions, illustrating how different management practices are likely to influence wildlife over extended time horizons. Insights into these associations could prove useful for land managers seeking to meet ecological objectives, such as maintaining biodiversity as required by sustainable forestry certification programs (e.g., the Sustainable Forestry Initiative; Sustainable Forestry Board, 2005). For landscapes managed under scenarios that create high variability in landscape characteristics over time (e.g., short rotation of timber harvests), species that show highly correlated temporal variability might represent ideal candidates for monitoring efforts (i.e., "indicator species;" Landres et al., 1988). Further, because such species often carry a relatively high risk of extinction (Gilpen and Soule, 1986; Shaffer, 1987), management for retention of these species on the landscape could focus on scenarios that minimize temporal variation.

Understanding wildlife-habitat relationships requires an explicit consideration of spatial and temporal scales because ecological processes are scale dependent (Reynolds-Hogland and Mitchell, 2007; Allen, 1998; Allen and Hoekstra, 1992; Levin, 1992; Turner, 1989). For example, previous studies on predator–prey dynamics (O'Neill and Smith, 2002), ecosystem resiliency (Peterson et al., 1998), and biodiversity (Lawton, 1999; Loehle et al., 2006; Mitchell et al., 2006) yielded different results when studied at different spatial scales. Moreover, processes observed at small scales may be caused by larger scale phenomena (Reynolds-Hogland and Mitchell, 2007; Lawton, 1999). Similarly, short-term studies may not encompass the dynamics of a biological system, and could yield misleading results (e.g., Brongo et al., 2005; Reynolds-Hogland and Mitchell, 2007; Sallabanks et al., 2000; Turner et al., 2001). Long-term, broad-scale empirical studies, however, are relatively uncommon and thus insights into how future dynamics are likely to unfold is limited. Simulation modeling is one way to overcome this limitation and is commonly used to evaluate the predicted effect of management alternatives on habitat quality for wildlife (Marzluff et al., 2002).

To understand how avian communities respond to changes brought about by different forest management practices over an extended period of time, we developed empirically derived, multi-scale models of avian richness and presence using avian and forest inventory data from 4 managed forest landscapes in the south-eastern United States (Loehle et al., 2006; Mitchell et al., 2006). We then used the Habplan forest harvest scheduler (Van Deusen, 2006) to simulate realistic implementation of alternative forest management scenarios on a simulated landscape 40 years into the future; the management scenarios and landscapes were the same as those presented by Loehle et al. (2006). We evaluated how these landscapes changed over time under each management scenario using time series analysis (TSA). We then used our avian models to predict overall avian richness, richness of select guilds, and the presence of select species on landscapes at each 5-year step in the time series for each management scenario. For each management scenario, we assessed changes in the avian community over time using TSA and evaluated how these related to corresponding changes in the landscape. Correlations in change between avian communities and landscape configuration over time suggest hypothesized causal relationships between spatio-temporal variation in landscape patterns and the distribution and abundance of bird species.

2. Study areas

We used data collected from 4 study sites located in the southeastern US. These sites were selected by Mitchell et al. (2006) because they represented large, managed forests with detailed forest inventory data as well as standardized avian point count data. Descriptions of the study sites reflect conditions for the years data were collected (1995–2002).

2.1. Arkansas

The Arkansas study site (AR) was located near Hot Springs, AR in the Ouachita Mixed Forest-Meadow Province. The land comprised eroded sedimentary rock formations with mountain folds and ridges, ranging from 460 to 790 m in elevation. Vegetation was dominated by pine-oak (*Pinus* spp; *Quercus* spp.) –hickory (*Carya* spp.) forests and managed pine forests including plantations managed on rotations of approximately 30–35 years. Even in mixed stands, pine species constituted as much as 40% of the overstory cover (short-leaf pine [*P. echinata*] in the uplands and loblolly pine [*P. taeda*] on alluvial soils). Average annual temperature was 17 °C, and rainfall was approximately 1050 mm per year.

2.2. South Carolina

We had data for two sites in South Carolina: the Woodbury/Giles (SC1) and the Ashley/Edisto (SC2) landscapes, both located in the Bailey Province 232. This Province comprises the flat and irregular Atlantic and Gulf Coastal Plains down to the sea. Local relief is <90 m. Average annual temperature is 16–21 °C and average annual precipitation ranges from 1020 to 1530 mm. The Woodbury/Giles landscape, located in Marion County near Conway, South Carolina, was largely composed of sandhill ridges with interspersed bottomland hardwoods and isolated wetlands. Both hardwood stands and planted pine stands dominated this area, which varied in age from recently harvested to mature (i.e., >50 years). Management strategies, such as harvest schedules, varied by stand type.
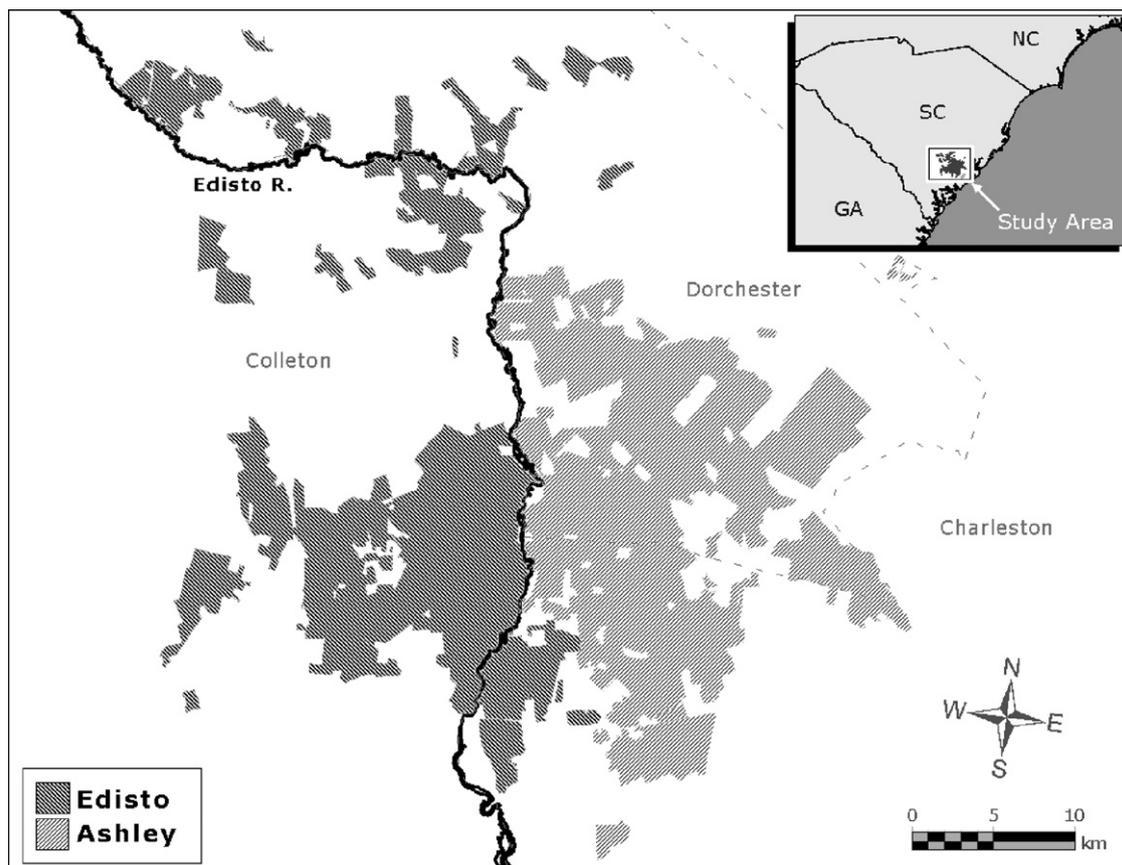
Fig. 1. The South Carolina Ashley/Edisto site was used as the initial landscape for simulation of the harvest scheduler Habplan for a 40-year planning horizon (map taken from Loehle et al., 2006).

The Ashley/Edisto site (Fig. 1) was located in the Outer Coastal Plain Mixed Province in the Atlantic and Gulf Coastal Plains. The region was characterized by upland loblolly pine forests, upland hardwood forests, and both riverine and non-riverine hardwood forests. It also included a well-developed understory with variable vegetation such as shrubs, ferns, and herbaceous plants. The study area contained streamside management zones and "habitat diversity zones" that created a network of corridors extending across the landscape.

2.3. West Virginia

The West Virginia (WV) site was located in the Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow Province. Low mountains, valleys, and mountainous plateaus ranging in elevation between 90 and 1800 m characterized this area. The WV site is in the temperate zone, with average temperatures ranging from 10 to 18 °C. Precipitation was distributed throughout the year, with a range of 890–2040 mm. Vegetation varied with elevation, ranging from mixed mesophytic plant communities (e.g., Northern red oak [*Q. rubra*], white ash [*Fraxinus americana*], black birch [*Betula lenta*]) and xeric oak-hickory communities at low elevations, northern hardwood forests (e.g., red maple [*Acer rubrum*], sugar maple [*A. saccharum*], American beech [*Fagus grandifolia*], and yellow birch [*B. alleghaeniensis*]) at intermediate elevations, and mixed stands of northern hardwoods, red spruce (*Picea rubens*), and eastern hemlock (*Tsuga canadensis*) forests at higher elevations. The pattern of vertical zonation also varied with topography and substrate.

3. Methods

3.1. Avian data

Standardized 5 min, fixed-radius (50 m) point counts (Ralph et al., 1993) were used to survey birds in each of the 4 landscapes (see Loehle et al., 2006; Mitchell et al., 2006). Surveys were conducted during May through June from 1995 to 1998 in Arkansas, 1995 to 1999 in South Carolina Woodbury/Giles Bay, and 1996 to 1998, 2001 and 2002 in West Virginia. Surveys were conducted during late April through May in South Carolina Ashley/Edisto from 1995 to 1999. Sampling points were located at least 200 m apart on either a grid system or a stratified random scheme. Each sampling point was surveyed at least once per year. In instances where sampling points were surveyed multiple times per year, we randomly selected one for analysis (Mitchell et al., 2006).

Because the four landscapes were under active forest management, landscape conditions changed among years so we considered visits to plots on successive years to be independent observations. The number of plots was 1865 in AR, 1762 in SC1, 715 in SC2, and 703 in WV. Due to low numbers of species observed per point (3.66 ± 2.01 S.D.), sampling points were aggregated to the stand-level. Using three points from each stand increased the number of species observed (6.83 ± 3.43 S.D.), providing an adequate sample size ($n = 700$; Mitchell et al., 2006). We used these data to develop logistic regression models to establish a predicted relationship between forest management and avian response.

We used definitions of Peterjohn and Sauer (1993) to identify the following guilds: canopy nesters, cavity nesters, Neotropical

migrants, and scrub-successional associates. Additionally, we focused on selected species of management interest in the southeastern US that are of conservation interest (i.e., Acadian Flycatcher {*Empidonax virescens*} and Blue-gray Gnatcatcher {*Polioptila caerulea*}; Partners In Flight, 2007) as well as species that represent late successional habitats (e.g., Eastern Wood-pewee {*Contopus virens*}) and early successional habitats (i.e., Common Yellowthroat {*Geothlypis trichas*}).

3.2. Land cover data

All GIS layers were projected to an Albers Equal Area projection with Albers coordinates. Coarse-scale (1:100,000) road and water feature data were available through USGS databases. Timber landowner companies provided fine-scale (1:24,000) water and road data, as well as detailed forest inventory layers. Land cover types were classified as hardwood (<25% pine), pine (>75% pine), mixed hardwood-pine (25–75% pine), and non-forest. These data were used to calculate forest and environmental metrics at "fine" (100 m), "fine/moderate" (250 m), "moderate" (500 m) and "broad" (1000 m) spatial scales around each of three sampling points. Potential explanatory variables included stand character-istics (e.g., stand age, stand area, or stand cover type) and neighborhood variables (e.g., mean forest age calculated at multiple spatial scales). For a complete list and justification of variables used see Mitchell et al. (2006). Mitchell et al. (2006) and Loehle et al. (2006) used topographic metrics as predictors for avian richness; we excluded these variables because the regional variability in topography among the four study sites rendered non-topographical variables relatively unimportant in model selection. Thus, our models retained the ecological generality that stemmed from using data from all four study sites, but removed regional effects of topographical variation.

3.3. Models of avian richness and presence

Using avian and land cover data from all four study sites, we used stepwise logistic regression (SAS Institute, 1990) to develop predictive models of overall avian richness, richness for selected guilds (canopy nesters, cavity nesters, Neotropical migrants, and scrub-successional associates), and the presence of selected species (Acadian Flycatcher, Blue-gray Gnatcatcher, Eastern Wood-pewee, Common Yellowthroat). Similar to Mitchell et al. (2006), we classified overall richness and richness within guilds for

each stand as high or not high by dividing observations across all sampling points into quartiles and assigning observations in each stand to the fourth quartile (high richness) or the first three quartiles (not high richness). Explanatory variables were selected for model inclusion and retention at the $\alpha = 0.05$ level. Prior to the development of each model, we eliminated redundant variables. When two habitat variables or the same habitat variable at two spatial scales were highly correlated (Spearman's $p \geq 0.70$), we retained the variable with the largest test statistic in Kruskal–Wallis tests comparing habitat variables among classes of overall richness and richness within guilds. Though Mitchell et al. (2006) and Loehle et al. (2006) used these same data sets to generate their models similarly, our models differed from theirs because we excluded topographic variables important to explaining differ-ences among the 4 sites that contributed data. Thus, our models did not have the capability to distinguish patterns between sites, but retained the ecological generality of habitat use by birds common to all sites. Further, topography of the SC2 landscape we used in our simulations varied little, characteristic of the coastal plain of South Carolina; the exclusion of topographic variables from our models had little effect on the predictive capacity of the models we used.

We assessed model fit using the receiver operator characteristic (ROC) statistic, which evaluates how well each model fits the data (Hosmer and Lemeshow, 2000). An ROC value of 0.5 indicates that the model failed to discriminate between our richness classes. ROC values between 0.7 and 0.8 indicate acceptable model discrimina-tion, values between 0.8 and 0.9 indicate excellent model discrimination, and ROC values >0.9 indicate outstanding dis-crimination. We used global odds ratios to evaluate the relative contribution of each variable to the given model, and calculated 95% Wald's confidence intervals for each odds ratio. Confidence intervals that include the value one indicate that the variable does not make a strong contribution to model fit, although it does lend information to the model.

3.4. Harvest scheduling

The Habplan harvest scheduler generated proposed manage-ment actions over time based on user specifications, such as cut size restrictions. Habplan output consisted of forest inventory data (e.g., stand age, overstory type, etc.) indicating the projected changes over time in the forest inventory layer resulting from the proposed management actions. These output were used to construct projected forest inventory layers for six alternative

Table 1

Logistic regression model relating the probability of high overall avian richness to forest structure variables at multiple spatial scales based on data from four managed landscapes located in AR, SC, and WV, USA

Parameter	Scale (m)	Slope	Odds ratio	95% Confidence intervals		ROC[a]
				Lower	Upper	
Overall avian richness						
Intercept		−2.4922				0.76
Standard deviation of forest age	250	0.0474	1.049	1.031	1.067	
Road length (coarse[b])	100	0.00605	1.006	1.002	1.010	
Road length (fine[c])	100	−0.00284	0.997	0.996	1.000	
Road length (coarse)	1000	0.000107	1.000	1.000	1.000	
Stream length (coarse)	1000	0.000186	1.000	1.000	1.000	
Area of mixed forest	1000	−1.3E−6	1.000	1.000	1.000	
Stand area		3.119E−7	1.000	1.000	1.000	

The odds ratio indicates the relative contribution of each variable to the overall model, an odds ratio ≈ 1 indicates little contribution. The receiver operator characteristic (ROC) statistic represents model fit (ROC = 0.50 indicates no fit, ROC = 0.70 indicates acceptable fit, ROC = 1.0 indicates perfect fit).

[a] The receiver operator characteristic (ROC) statistic evaluates how well each model fits the data. An ROC value of 0.5 indicates the model failed to discriminate between the data. ROC values between 0.7 and 0.8 indicate acceptable model discrimination, values between 0.8 and 0.9 indicate excellent model discrimination, and ROC values >0.9 indicate outstanding discrimination.

[b] Coarse = 1:100,000 scale.

[c] Fine = 1:24,000 scale.

management scenarios for the South Carolina Ashley/Edisto landscape (Fig. 1) across a 40-year planning horizon at 5-year time increments. The management scenarios reflected guidelines sometimes proposed for commercial forest landscapes in the southeastern United States or required by sustainable forestry certification programs such as the Sustainable Forestry Initiative (Sustainable Forestry Board, 2005; Loehle et al., 2006). The six scenarios included:

1–4. *Cut size limits*: This guideline restricted silvicultural treatments to a maximum cut size. We explored 4 different size restrictions: 60 acre cut limit, 120 acre cut limit, 180 acre cut limit, and no-limit cut sizes.
5. *Set-asides*: This scenario allowed all stands >40 years old at the initial time step to age during the 40-year horizon. Most stands >40 years old at the initial time step were hardwoods, therefore, most stands designated as set-asides were hard-

woods. Approximately 24.5% of forested stands were designated as set-asides, but management actions were applied to the remainder of the landscape.
6. *Unmanaged*: All stands were allowed to age for the 40-year planning period. By the end of the scenario, most pine stands were between 40 and 60 years old and most hardwood stands were between 80 and 160 years old.

The initial forest layer (i.e., time = 0), which was the same for each scenario, comprised 71% pine stands and 29% hardwood stands. Habplan manipulated only stand age through harvesting in each scenario and did not change overstory composition of stands. At time = 0, 2.9% of the landscape was harvested for all management scenarios. An "even-flow" constraint (Ducheyne et al., 2004) was applied to area and wood volume harvests to represent operational limitations and to prevent unusually high volume harvests at the end of the planning period. Amount of area

Table 2
Logistic regression models relating the probability of guild species richness to forest structure variables at multiple spatial scales based on data from four managed landscapes located AR, SC, and WV, USA

Parameter	Scale (m)	Slope	Odds ratio	95% Confidence intervals		ROC
				Lower	Upper	
Richness of canopy nesters						
Intercept		−3.4590				0.72
Fragmentation of forest type	1000	1.6742	5.335	1.477	19.262	
Standard deviation of forest age	100	0.0219	1.022	1.004	1.041	
Stream length (fine)	100	0.00273	1.003	1.000	1.005	
Road length (coarse)	500	0.000267	1.000	1.000	1.001	
Area in age class (0–4 years)	100	−0.00014	1.000	1.000	1.000	
Area of hardwoods	100	0.000033	1.000	1.000	1.000	
Area in age class (5–30 years)	250	−5.54E−6	1.000	1.000	1.000	
Area in age class (0–4 years)	1000	1.809E−6	1.000	1.000	1.000	
Stand area		1.842E−7	1.000	1.000	1.000	
Richness of cavity nesters						
Intercept		−4.1368				0.68
Fragmentation of age class	100	2.0019	7.403	2.106	26.027	
Fragmentation of forest type	1000	1.8118	6.122	1.714	21.860	
Area in age class (0–4 years)	100	−0.00007	1.000	1.000	1.000	
Area of hardwoods	100	0.000015	1.000	1.000	1.000	
Area in age class (0–4 years)	1000	1.431E−6	1.000	1.000	1.000	
Stand area		2.179E−7	1.000	1.000	1.000	
Richness of Neotropical migrants						
Intercept		−3.5214				0.77
Fragmentation of forest type	1000	3.9214	50.469	5.172	492.482	
Evenness of overstory type	1000	−3.4786	0.031	0.007	0.135	
Standard deviation of forest age	250	0.0559	1.058	1.039	1.076	
Road length (coarse)	100	0.00957	1.010	1.006	1.013	
Road length (fine)	100	−0.00552	0.994	0.992	0.997	
Stream length (coarse)	1000	0.000296	1.000	1.000	1.000	
Road length (fine)	1000	0.000112	1.000	1.000	1.000	
Area of pine	100	−0.00002	1.000	1.000	1.000	
Area of mixed forest	250	−0.00001	1.000	1.000	1.000	
Stand area		2.417E−7	1.000	1.000	1.000	
Richness of scrub-successional associates						
Intercept		−0.900				0.84
Fragmentation of age class	1000	−2.9867	0.050	0.009	0.292	
Standard deviation of forest age	1000	0.0545	1.056	1.033	1.080	
Mean forest age	100	−0.0526	0.949	0.926	0.972	
Stand age		0.0214	1.022	1.001	1.043	
Distance to roads (fine)		−0.00597	0.994	0.992	0.996	
Road length (fine)	500	−0.00045	1.000	0.999	1.000	
Distance to water (coarse)		0.000690	1.001	1.000	1.001	
Stream length (coarse)	1000	0.000265	1.000	1.000	1.000	
Road length (coarse)	1000	0.000197	1.000	1.000	1.000	
Area of mixed forest	100	−0.00003	1.000	1.000	1.000	
Area of pine	250	6.636E−6	1.000	1.000	1.000	
Non-forested area	1000	1.607E−6	1.000	1.000	1.000	

The odds ratio indicates the relative contribution of each variable to the overall model, an odds ratio ≈ 1 indicates little contribution. The receiver operator characteristic (ROC) statistic represents model fit (ROC = 0.50 indicates no fit, ROC = 0.70 indicates acceptable fit, ROC = 1.0 indicates perfect fit).

harvested was not constrained to be equal among scenarios, so we calculated the proportion of landscape harvested for each year for each scenario.

3.5. Model application

We used a Spatial Analysis Tool (Rutzmoser and Mitchell, 2006) to map predictions of our logistic regression models for each forest inventory layer representing a 5-year increment for each management scenario produced using Habplan. Model predictions for each landscape were projected as probability surfaces (e.g., probability of high species richness across the landscape) in ArcGIS® 9.0. We imported these probability surfaces and the forest inventory layers for each 5-year increment of each management scenario into IDRISI (Version 14.02; Eastman, 1997) for time series analyses.

3.6. Time series analyses: landscapes

We used a spatially explicit time series analysis (TSA) to evaluate changes in the landscape resulting from each of the management scenarios over a 40-year planning period. TSA can be used to evaluate spatial changes over a series of maps arranged sequentially by analyzing the map sequence as standardized principal components, generating uncorrelated component images (Eastman, 1997). The series of maps we used were the nine forest inventory layers, representing the landscape at time steps 0 through 40 at 5-year increments, for each management scenario. For each series of maps, TSA produced 2 principal component maps illustrating trends across the maps in the time series, with each successive component explaining less variability in the data. Component 1 ($C1_A$) mapped values held in common over the series of maps, or stability. Component 2 ($C2_A$) mapped the greatest change in values over the series of maps (Eastman, 1997). Because only stand age varied within each time series, $C1_A$ mapped the relative stability of age of stands that were uncut, $C2_A$ represented changes in stand age due to harvesting. For each time series, we correlated each map of stand age for each time step with $C1_A$ ($rC1_{Ai}$) and $C2_L$ ($rC2_{Ai}$) for that series. A high value of $rC1_{Ai}$ indicated little changed in that time step, relative to overall change. A high value of $rC2_{Ai}$ indicated strong change in that time step, relative to overall change. For each time series, values of $C2_A$ were relative to $C1_A$ (Eastman, 1997); to make $rC2_{Ai}$ comparable

Table 3
Logistic regression models relating the probability of species presence to forest structure variables at multiple spatial scales based on data from four managed landscapes located AR, SC, and WV, USA

Parameter	Scale (m)	Slope	Odds ratio	95% Confidence intervals		ROC
				Lower	Upper	
Acadian Flycatcher						
Intercept		−1.2311				0.85
Fragmentation of age class	250	5.0277	152.578	19.185	>999.999	
Standard deviation of forest age	1000	−0.0655	0.937	0.903	0.971	
Mean forest age	1000	−0.0615	0.940	0.922	0.959	
Stand age		0.0464	1.047	1.034	1.061	
Stream length (coarse)	100	0.00747	1.007	1.003	1.012	
Non-forested area	1000	−2.27E−6	1.000	1.000	1.000	
Stand area		1.092E−6	1.000	1.000	1.000	
Area of mixed forest	1000	−9.53E−7	1.000	1.000	1.000	
Blue-gray Gnatcatcher						
Intercept		0.2337				0.86
Fragmentation of forest type	1000	3.5053	33.292	3.093	358.361	
Mean forest age	1000	−0.1151	0.891	0.872	0.911	
Standard deviation of forest age	250	0.0464	1.047	1.019	1.076	
Stand age		0.0208	1.021	1.010	1.032	
Stream length (fine)	100	−0.00579	0.994	0.989	0.999	
Stream length (fine)	250	0.00290	1.003	1.002	1.004	
Area in age class (5–30 years)	1000	−4.82E−7	1.000	1.000	1.000	
Road length (fine)	1000	−0.00009	1.000	1.000	1.000	
Area in age class (0–4 years)	100	−0.00007	1.000	1.000	1.000	
Area of hardwoods	100	0.000031	1.000	1.000	1.000	
Non-forested area	1000	−3.0E−6	1.000	1.000	1.000	
Stand area		1.195E−6	1.000	1.000	1.000	
Common Yellowthroat						
Intercept		−5.6726				0.86
Standard deviation of forest age	250	0.0467	1.048	1.012	1.085	
Standard deviation of forest age	1000	0.0398	1.041	1.004	1.078	
Mean forest age	250	−0.0241	0.976	0.969	0.994	
Area in age class (0–4 years)	100	0.000036	1.000	1.000	1.000	
Road length (coarse)	1000	0.000336	1.000	1.000	1.000	
Area of pine	250	0.000013	1.000	1.000	1.000	
Eastern Wood-pewees						
Intercept		−4.0178				0.85
Stand area		0.0495	1.051	1.032	1.070	
Road length (coarse)	250	0.00191	1.002	1.000	1.004	
Area of hardwoods	100	−0.00012	1.000	1.000	1.000	
Non-forested area	500	0.000012	1.000	1.000	1.000	
Area in age class (5–30 years)	1000	−6.36E−7	1.000	1.000	1.000	
Area of mixed forest	1000	−2.52E−6	1.000	1.000	1.000	

The odds ratio indicates the relative contribution of each variable to the overall model, an odds ratio ≈ 1 indicates little contribution. The receiver operator characteristic (ROC) statistic represents model fit (ROC = 0.50 indicates no fit, ROC = 0.70 indicates acceptable fit, ROC = 1.0 indicates perfect fit).
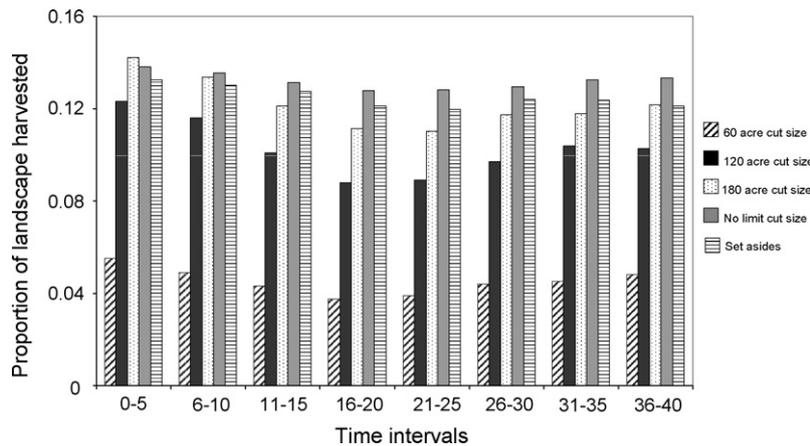
Fig. 2. Proportion of the South Carolina Ashley/Edisto landscape that was harvested under each management scenario during the 40-year planning horizon.

across scenarios, we standardized $rC2_{Ai}$ for $rC1_{Ai}$ for each map in each scenario. We compared change over time among the management scenarios by plotting $rC2_{Ai}/rC1_{Ai}$ for each management scenario over the time series.

3.7. Time series analyses: birds

We used TSA to examine predicted variation in avian response (i.e., probability of high species richness, high guild richness, or species presence) to changes in the landscape for each of the management scenarios, over a 40-year horizon. The series of maps we used for bird analyses were the nine probability surfaces that were calculated for each of the nine time steps, for each avian group and each management scenario. Here, Component 2 ($C2_B$) represented the greatest change in the probability of presence or richness, Component 1 ($C1_B$) represented stability. As with the time series analyses for the landscapes, we evaluated change over time for overall richness, richness within guilds, and the presence of selected species by standardizing the correlation with $C2_B$ ($rC1_{Bi}$) by the correlation for $C1_B$ ($rC1_{Bi}$) and plotting this ratio over the time series.

4. Results

4.1. Models of avian presence and richness

Model fit for predicted overall richness, guild richness, and species presence varied from acceptable to excellent (ROC values;

Tables 1–3). Variables that represented heterogeneity of stand age (e.g., fragmentation of age class, standard deviation of forest age) were strong predictors for all models (i.e., odds ratio values $\neq 1$), except for the Eastern Wood-pewee for which no landscape variables were important. Slope values for heterogeneity of stand age were positive for most models, except for the richness of scrub-successional associates where fragmentation of age classes had a strong negative effect and the Acadian Flycatcher where effects were mixed, depending on scale. Most models included variables representing area of habitat (e.g., area in a particular range of age classes) and landscape features other than those pertaining to forest age (e.g., distance to nearest road, distance to nearest water), but these variables made weak contributions (i.e., odds ratio values = 1).

Scales at which important landscape variables had influence varied among models. Variation of forest age had a positive influence on overall richness on a relatively fine-scale (Table 1). Fragmentation of forest type and variation in forest age were positively related to richness of canopy nesters on broad and fine-scales, respectively (Table 2). Richness of cavity nesters was influenced positively by fragmentation of age classes and forest type on fine- and broad-scales, respectively (Table 2). Richness of Neotropical migrants was related positively to fragmentation of forest type at a broad-scale, negatively to evenness of overstory type at a broad-scale, and positively to variability of forest age on a fine-scale (Table 2). Richness of scrub-successional associates was related positively to fragmentation of age classes and variability of
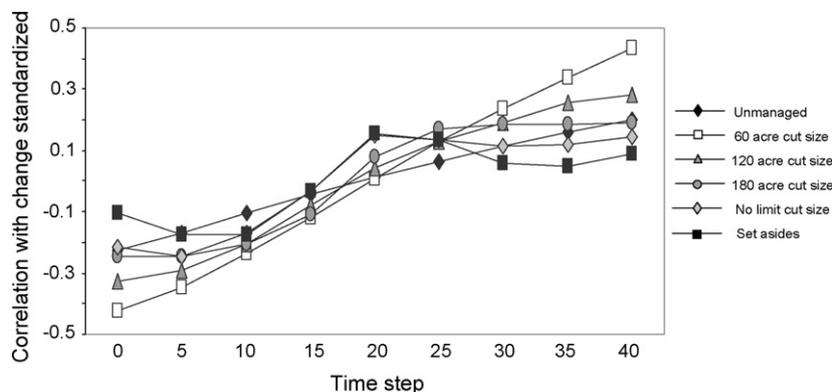

Fig. 3. Correlation of landscapes at time step *i* with change over all landscapes in the time series, standardized by stability ($rC2_{Ai}/rC1_{Ai}$: see text), for 6 forest management scenarios projected over 40 years. A positive correlation indicates a positive association of a landscape at time step *i* with overall landscape change across the time series (e.g., change occurred on the landscape during that time step that contributed to long-term change within the time series). A negative correlation indicates an association of a landscape at time step *i* with stability across the time series (i.e., little change occurred during that time step that contributed to long-term change within the time series).

forest age on a broad-scale, and negatively to mean forest age on a fine-scale (Table 2). Presence of the Acadian Flycatcher was related positively to fragmentation of age class on a fine-scale and negatively related variation in forest age and mean forest age on a broad-scale (Table 3). Presence of the Blue-gray Gnatcatcher was related positively to fragmentation of forest type and related negatively to mean forest age on a broad-scale and positively related to variation in forest age on a fine-scale. Presence of the Common Yellowthroat was related positively to variation in forest age at both fine- and broad-scales, and negatively to mean forest age on a fine-scale (Table 3).

Among variables describing stand characteristics, stand age was positively, though modestly, related to richness of scrub-successional associates (Table 2) and to presence of Acadian Flycatchers and Blue-gray Gnatcatchers (Table 3). Stand area was the most important variable explaining presence of Eastern Wood-pewees, though its contribution was not strong (Table 3).

4.2. Time series analysis: landscapes

The amount of area harvested each year varied among management scenarios (Fig. 2). During any given 5-year time interval, the proportion of the landscape harvested under the "60-acre cut size limit" scenario was less than half that harvested under all other scenarios. The scenario under which the most area was harvested during the 40-year horizon was the "no-limit cut size" scenario. Several stands were harvested more than once during the 40-year horizon because 20-year, 35-year, and 40-year rotation periods were used.

Landscape change due to these harvests varied strongly over the entire time series for the management scenarios ($rC2_{Ai}$ ranged from -3.9 to 3.9), though year-to-year changes were relatively small (mean $rC1_{Ai}$ across scenarios was 0.96 [S.D. = 0.02]). Patterns of change for each scenario showed a progression from negative to positive correlation with change ($C2_A$) over the time series, reflecting increasing effects of forest management on each landscape over time (Fig. 3). Rates of change differed somewhat among scenarios. The "60 acre cut size" showed a constant but relatively high rate of change over time, the "no management" scenario showed a constant but relatively low rate of change (reflecting only the gradual aging of stands), and all other scenarios showed a sigmoidal pattern of accelerating then decelerating change, suggesting cycles between stability and change whose period and magnitude depended on amount of acreage cut in each scenario. All cycling among scenarios appeared to center on a line of positive slope, indicating that even through periods of relative stability effects of change were cumulative on each landscape. Of the scenarios showing a cyclic pattern of change, only the "set-aside" and "no-limit cut size" scenarios appeared to complete >1 cycle within the 40-year period we evaluated.

4.3. Time series analysis: birds

Most measures of avian and guild richness, as well as presence of select species, showed significant, sigmoidal response to change over the entire time series under all management scenarios ($rC2_{Bi}$ ranged from -3.0 to 2.0), though year-to-year changes were relatively small (mean $rC1_{Bi}$ across scenarios was 0.98
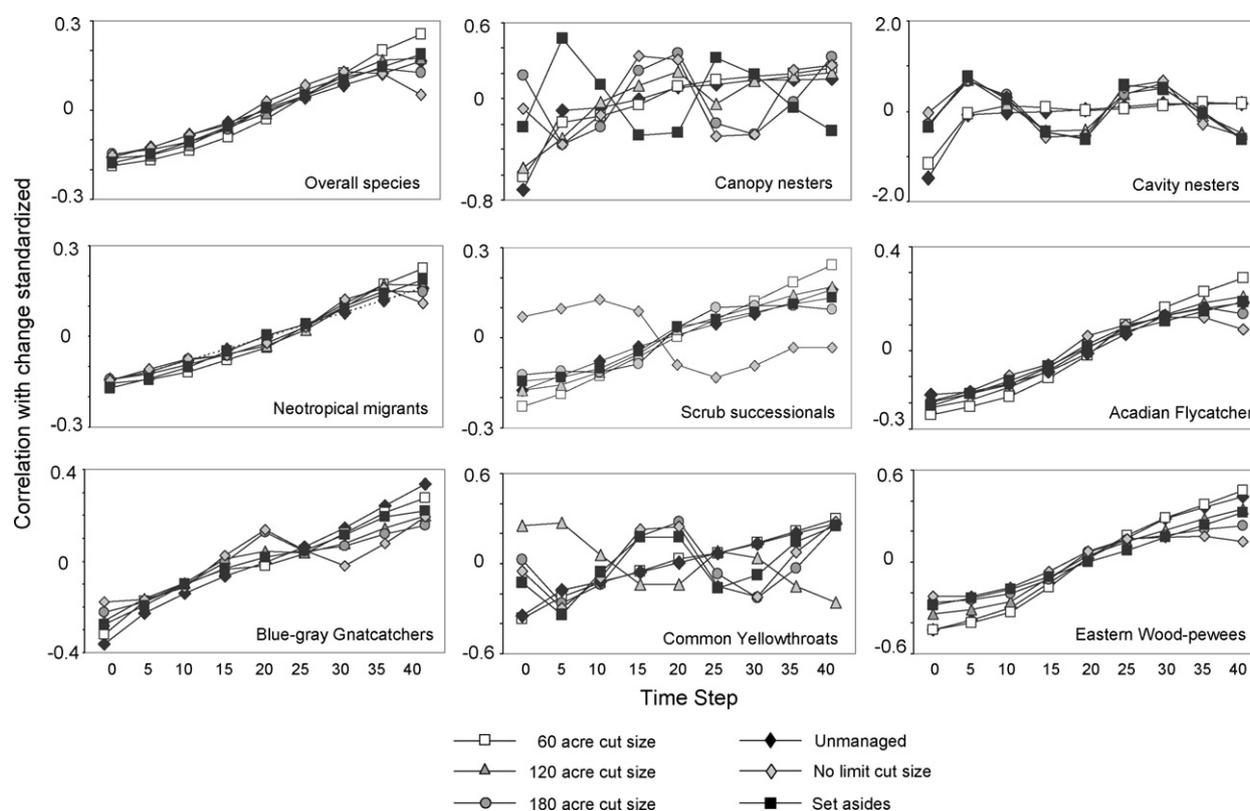
Fig. 4. Correlation of mapped probabilities of overall avian richness, richness of canopy nesters, richness of cavity nesters, richness of Neotropical migrants, richness of scrub-successional associates, presence of Acadian Flycatchers, presence of Blue-gray Gnatcatchers, presence of Common Yellowthroats, and presence of Eastern Wood-pewees at time step i with change over all maps in the time series, standardized by stability ($rC2_{Bi}/rC1_{Bi}$; see text), for, projected over 40 years. Positive correlations indicate a positive association of mapped probabilities at time step i with overall change in probabilities across the time series (e.g., change occurred on the landscape during that time step that contributed to long-term change within the time series). A negative correlation indicates an association between mapped probabilities at time step i and stability in probabilities across the time series (i.e., little change occurred during that time step that contributed to long-term change within the time series).

[S.D. = 0.01]), similar to patterns of landscape change. Canopy nesters and Common Yellowthroats, however, demonstrated relatively high-predicted temporal variability in response to most management scenarios (except the "unmanaged" and "60-acre cut size limit" scenarios; Fig. 4), with indications of cycling whose period and magnitude varied strongly (at times inversely) among scenarios. Cavity nesters also showed indications of cycling that was similar among all scenarios except for "unmanaged" and "60-acre cut size limit," which showed little change over time. Predicted temporal variability for Blue-gray Gnatcatchers was modest for the "no-limit cut size" scenario, but minimal for other management scenarios. Temporal variability for scrub-successional associates was low for all scenarios except for the "no-limit cut size" scenario, where correlation with patterns of change over time were inverse to the other scenarios, suggesting stronger responses to changes in the beginning of the time series than later. Acadian Flycatchers, Eastern Wood-pewees, Neotropical migrants, and overall richness of species showed comparatively modest temporal variability for most management scenarios, mirroring broad landscape changes over time (Fig. 4). Predicted responses for all measures of richness and presence of species showed relatively little temporal variation under both the "unmanaged" and "60-acre cut size limit" scenarios, where rates of change (i.e., changes in $rC2_{Bi}/rC1_{Bi}$ over the time series) were least and greatest, respectively, but constant over time (Fig. 4).

5. Discussion

Little theoretical foundation exists for predicting how landscape patterns influence the distribution of animals, or the scales at which these influences take place. Thus, most empirical studies that seek to identify these relationships are correlative and exploratory (Levin, 1992; Wiens, 1992; Wiens et al., 1993; Mitchell et al., 2001). Further, most such studies are of short duration, offering limited insights into how animal communities might vary on dynamic landscapes such as managed forests over long periods of time (Sallabanks et al., 2000). Finally, explicit theoretical and empirical links between spatial and temporal expressions of ecological processes are rare, with uncertainty about these processes increasing directly with spatial and temporal extents and degrees of temporal discontinuities (Bissonette, 2007). Conceptually, a landscape influenced by a continuously applied management practice will vary over time, with landscape patterns (e.g., connectivity, fragmentation, etc.) emerging and receding depending on the intensity and frequency of landscape manipulations. Whether these changes in landscape patterns will result in concomitant changes in wildlife communities is generally unknown; thus, forecasting the long-term responses of wildlife communities to land management practices is tenuous, at best.

To address these issues, we used multi-scale data on avian presence and landscape configuration from 4 different landscapes to generate models for predicting richness of bird species, select bird guilds, and presence of select species on managed forests in the southeastern United States. Though correlative, these models were robust because of the replicated study design used to generate them. We used a harvest scheduler to project landscape configuration of a managed forest 40 years into the future, then used our avian models to predict the distribution of avian community characteristics and species presence at 5-year time steps. Using time series analysis, we developed hypothesized cause–effect relationships between changes in landscapes under the different management scenarios and changes in the avian community over time. Based on these relationships, we assessed the strength of relationship between avian communities and forest management over long periods, suggesting community characteristics and species that could be monitored depending on management goals for forest productivity and conservation of biodiversity.

5.1. Models of avian presence and richness

We developed models for explaining avian richness, richness for selected avian guilds, and presence for selected species, using bird count data and forest inventory data obtained from 4 managed forests located in the southeastern United States. Results of our models indicate the importance of landscape configuration to avian communities, which agreed with findings of Bolger et al. (1997), Hanowski et al. (1997), Saab (1999), Loehle et al. (2006), Manolis et al. (2000), Mitchell et al. (2006), and Villard et al. (1999). Our results conflict with those from Robbins et al. (1989), Drolet et al. (1999), Lichstein et al. (2002), and Cushman and McGarigal (2004). None of the latter studies evaluated landscape configuration in terms of fragmentation of forest type, fragmentation of stand or forest age, or heterogeneity of stand age, which were the strongest predictors for all but 1 of the species and guilds in our study; this suggests that findings on effects of landscape configuration among studies may vary according to the landscape features that are measured. Some of this may also be a regional phenomenon, where different species of birds under different ecological settings respond differently to landscape configuration. Variation in observed responses to landscape configuration among studies calls into question which of the myriad findings across studies possess generality and which are artifacts of the unique conditions or analytical choices inherent in each study. Our study represents, in essence, a replicated study incorporating identically collected data on birds and forest inventory on 4 managed forest landscapes. The results of our models can thus be generalized with some confidence across managed forests in the southeastern United States. The applicability of our findings to other ecological and management contexts would be the subject for further research.

Our findings on scale are consistent with other studies that showed the importance of scale in identifying ecological patterns (Peterson et al., 1998; Lawton, 1999; O'Neill and Smith, 2002; Loehle et al., 2006; Mitchell et al., 2006) and that the scale(s) at which habitat characteristics are important vary between and within species (Saab, 1999; Mitchell et al., 2001; MacFaden and Capen, 2002; Rahbek and Graves, 2001; Cushman and McGarigal, 2004). Differences between our findings and those of other studies, therefore, could also be attributed to differences in scales evaluated (explicitly or implicitly) in each study. Our results suggest that heterogeneity of forest ages at both fine- and broad-scales is important to many southeastern birds, though distribution and abundance of some (e.g., the Eastern Wood-pewee) may be more dependent on stand characteristics. Our analyses of scale evaluated only a portion (i.e., buffers from 100 to 1000-m in radius) of the available spectrum. Conceivably, measurements taken at finer or broader scales would potentially show different relationships, begging the question about scales of measurement that are ecologically justified. Though the importance of scale to ecological research is well recognized (Levin, 1992), no consensus has developed among ecologists for identifying when and where different scales are important to understanding observed phenomena (Bissonette, 1997). Until such a consensus forms and scales for analyzing ecological patterns can be defined a priori, it seems insights can only be derived a posteriori across multiple studies evaluating a variety of scales. Our study suggests (A) scale is important, (B) scales of habitat relationships vary among and within species, and (C) although relationships might exist at scales finer or broader than we evaluated, the patterns we observed suggest landscape variation on the scale of managed forests can have a strong influence on avian communities.

5.2. Time series analysis: landscapes

We evaluated landscape changes under different management scenarios implemented realistically (i.e., cost-effectively, given forest conditions, with the exception of the "no management scenario") using the Habplan harvest scheduler. Change characterized each landscape under each management scenario over the 40-year projections, either due to timber harvesting or to aging of the forest (Fig. 3). Except for management scenarios where change was most gradual ("no management" and "60 acre cut size" scenarios), landscape changes appeared to be cumulative and cyclic, suggesting oscillations around gradually increasing levels of cumulative change (i.e., the change due only to overall forest aging seen for the "unmanaged" scenario; Fig. 3). It is unclear if extending the time series beyond 40 years would show cycles of change oscillating around constantly increasing cumulative change, or if cumulative change and thus the cycles would settle on an asymptote. The cycles we observed are likely an emergent property of the harvest scenarios themselves, driven by the scheduling priorities of the management scenarios and the availability of age classes on the landscape. Interestingly, only 2 of the scenarios ("set-asides" and "no-limit cut size") showed suggestions of having completed a cycle and begun a new one within the 40-year time series. Unlike other scenarios, both of these operated under potentially limiting constraints (lack of new land to set-aside or lack of new areas of suitably aged timber to cut), requiring relatively early re-use of previously harvested stands, thus forcing cycles of change to occur on shorter intervals than for other scenarios. In the case of the "no-limit cut scenario," such intensive re-use of stands could result in homogenization of forest age classes over time. By contrast, the harvesting scenario that influenced age structure on the landscapes the least, "60 acre cut size," had a near-constant rate of change, suggesting no limitations or re-use of harvested stands; cycling under this scenario, should it occur, would likely have much longer period and lower magnitude than other scenarios.

Cyclic landscape changes are evocative of the fluid mosaic concept of forest management where turnover in stand age over time creates local instability (i.e., changing relatively mature forest to an early successional sere), but forest age distributions, and their respective animal communities, remain relatively stable across the landscape due to regeneration and growth of previously harvested and unharvested stands. Our simulations suggest this could be a reasonable model of landscape changes brought about by forest management over time, where rates of change increase or decrease but oscillate around a point of stability. Evidence would be more compelling if the accumulated change around which our landscapes appeared to oscillate over time under some management scenarios indeed asymptoted. Our analytical time span of 40 years, however, was too short to capture asymptotic behavior in accumulated change clearly. Our results suggest some validity for the concept, but further work is needed to evaluate (A) the potential for stability of forest age structure under forest management scenarios across a variety of timelines, and (B) management scenarios that result in instability and their respective time lines. Such work is needed to assess how and when the fluid mosaic concept can be used to understand the contribution of forest management to conservation of biodiversity.

5.3. Time series analysis: birds

For each of our management scenarios, we used our models to predict how avian richness, richness within select guilds, and presence of select species would change over time in response to landscape changes brought about by management. Change over time in overall avian richness increased gradually and similarly for all management scenarios, with suggestions of asymptotic or cycling behavior and some divergence toward the end of the time series with change decreasing for the scenarios with heaviest timber harvests ("180 acre cut size" and "no-limit cut size"; Fig. 4). This pattern was repeated for richness of Neotropical migrants and presence of Acadian Flycatchers and Eastern Wood-pewees. These results indicate that overall richness, richness of Neotropical migrants, and presence of Acadian Flycatchers and Eastern Wood-pewees respond to forest management generally but are insensitive to variation among the management practices. Presence of Blue-gray Gnatcatchers showed only slightly more pronounced cycling and variation among the management scenarios. Richness of scrub-successional associates showed a similar pattern, except for the "no-limit cut size" scenario which showed changes opposite to those seen in the other scenarios. This unique response of the scrub-successional guild to the "no-limit cut size" scenario suggests only very large harvests can create a landscape where the habitat relationships portrayed in the model we generated for them (negative relationship to fragmentation of age classes on a broad-scale, negative relationship to forest age on a fine-scale; Table 2) come into strong effect.

Changes in richness of canopy nesters, richness of cavity nesters, and presence of Common Yellowthroats showed considerable variation among the management scenarios, demonstrating relative stability for the scenarios that minimized timber harvests ("no management" and "60 acre cut size") and strong 15-year cycles between change and stability among the other scenarios. These cycles were synchronous among management scenarios for cavity nesters, but varied strongly among scenarios for richness of canopy nesters and presence of Common Yellowthroats. It is not clear why these cyclic patterns occurred, they do not appear to be correlated directly to overall patterns of landscape change among the scenarios (see below). Nonetheless, our models were deterministic, driven only by landscape characteristics, therefore, these patterns indicate strong influences on some portions of the avian community driven by landscape changes other than those captured in our time series analyses. Models for richness of cavity nesters, richness of canopy nesters, and presence of Common Yellowthroats had in common predominant sensitivity to heterogeneity of forest age (in 1 form or another) at fine spatial scales, distinguishing them from other groups and species sensitive primarily to heterogeneity on broad spatial scales; their responses to landscape changes thus suggest strong short-term, fine-scale dynamics that are not reflected in an assessment of overall change across landscapes.

Interestingly, the unmanaged and "60-acre limit cut size" scenarios failed to elicit a highly variable response over time for all species and guilds (Fig. 4). Hence, the "unmanaged" and "60-acre limit cut size" scenarios may not strongly influence avian species richness or presence. Even more interesting is the implication that the "60-acre limit cut size" scenario is functionally similar to an unmanaged landscape over the time span we evaluated. This finding suggests that effects of disturbances due to small (i.e., 60 acres or less) harvests, representing <6% of the landscape, may have imperceptible effects on avian species and guilds we evaluated in our study. The amount of area harvested under the "60-acre cut size" scenario, however, was less than half that harvested under all other harvest scenarios (Fig. 2). Therefore, the low predicted temporal variability in avian response to the "60-acre limit cut size" scenario may have occurred simply because relatively little landscape area was harvested over the time span we assessed.

5.4. Relating avian changes to landscape changes

All species (except the Eastern Wood-pewee) and the guilds we considered were strongly sensitive to landscape heterogeneity (Tables 1–3), which may help explain the similar responses among the groups. Our results for richness of scrub-successional associates (Table 2; Fig. 4) raise interesting questions about habitat sensitivity among early successional species, for which recent population declines have caused considerable concern (James et al., 1992; Askins et al., 1990; Askins, 2001; Thompson and DeGraaf, 2001). Researchers and managers often focus on understanding landscape effects of management on interior-forest species (see review by Faaborg et al., 1995) because of concerns about area sensitivity and habitat connectivity (Austen et al., 2001; Robbins et al., 1989). Yet our results corroborate earlier findings that early successional species may also be sensitive to connectivity of habitat available on landscapes (Mitchell et al., 2001) and suggest that harvesting stands on a landscape, without considering interactions between harvest extent and spatial arrangement, may not be sufficient to maintain diversity of early successional species. Indeed, scrub-successional associates showed strong negative associations with fragmentation of age classes and mean forest age (Table 2). These results indicate connectivity of early successional stands, may drive an important portion of the response of scrub-successional species to forest management. The response of scrub-successional associates to the "no-limit cut" scenario, however, suggests that a limit to the benefits of the "no-limit cut size" scenario for these species may exist. Because landscape heterogeneity was important to richness of this guild (Table 2), we hypothesize that the "no-limit cut size" scenario resulted in a positive response of early successional species early in the time series that declined over time as extensive timber harvests and rapid re-use of harvested stands gradually homogenized the landscape.

Our results provided further support that short-term studies may be inadequate for the examination of patterns or processes that operate at broader temporal scales (e.g., Brongo et al., 2005; Fahrig, 1992; Reynolds-Hogland and Mitchell, 2007; Turner et al., 2001). Specifically, the cyclic patterns in predicted response for some guilds (cavity nesters, canopy nesters, scrub-successionals) and species (Common Yellowthroats, Blue-gray Gnatcatchers) would be unobservable with a relatively short-term data set (i.e., 1–5 years). Thus, short-term glimpses into ecological processes could be misleading, depending on whether observations were made as response variables were increasing or decreasing. Sallabanks et al. (2000) similarly concluded that studies lasting <3 years may show trends that have little to do with forestry practices being studied. Despite recognition of the importance of long-term datasets and efforts to collect them (Callahan, 1984; Hobbie et al., 2003), long-term data remain relatively rare. Management decisions based on biased or incomplete results are likely to be ineffective or even deleterious, yet managers tasked with increasing or maintaining a "rare" or "sensitive" species often lack the necessary long-term data they need to make informed decisions. While simulated data are not a true surrogate for empirical data, they represent a useful tool to overcome the limitation of short-term data (Marzluff et al., 2002; Thompson et al., 2000).

For our study, we made several assumptions. First, we assumed that ecological processes regarding avian species and forest management were captured at the four spatial scales we used. For the logistic models, we assumed that our threshold level for estimating high richness (i.e., observations within the fourth quartile; Mitchell et al., 2006) was biologically illustrative. Relationships in nature are often nonlinear or lagged in time, but our analyses assumed a linear, non-lagged relationship between change in avian communities and change in landscape structure. Further research should evaluate the potential for these more complex relationships. Finally, we assumed that avian habitat relationships depicted by our logistic regression models would remain constant across 40 years of landscape change. Because such relationships could conceivably change under conditions different from which existed when data used to generate the models were collected, our results should be tested using independent data to verify their predictive capacity.

6. Management implications

Planning for avian diversity on landscapes that are managed for timber production is relatively simple if habitat area alone drives wildlife response to management (Fahrig, 1997). Planning is more complicated when habitat configuration is important (Lichstein et al., 2002). We found landscape configuration was more important to avian community characteristics than amount of habitat area (i.e., amount of area harvested) except where harvesting large areas homogenized landscapes over time. Our results suggest managers should consider both where and when harvests are scheduled across the landscape to optimize the effects of management actions on avian diversity, particularly where cut sizes will be large (e.g., our "no-limit cut size" scenario) or large volumes of timber will be harvested (e.g., all our scenarios except "60 acre cut size;" Fig. 3). Small cut sizes (e.g., our "60 acre cut size" scenario) appeared to have little effect on landscape configuration, at least for the rotation lengths (20–40 years) of our harvests, spatial extent of our landscape (Fig. 1), and temporal extent (40 years) of our analyses.

Our results have implications for evaluating effects of forest management on avian diversity through monitoring (i.e., indicator species; Landres et al., 1988). The relative insensitivity of overall avian richness, richness of Neotropical migrants, and presence of Acadian Flycatchers, Eastern Wood-pewees, and Blue-gray Gnatcatchers to variation in the forest management practices we evaluated suggest they would not be good indicators. The strong response of richness of scrub-successional associates to the "no-limit cut size" scenario that differed from all other scenarios suggests this guild could be useful for monitoring important transitions in landscape configuration and avian diversity that could result from extensive timber harvests. Our results suggest that richness of canopy nesters, richness of cavity nesters, and presence of Common Yellowthroats could be useful indicators for evaluating fine-scale variation in effects of forest management on the avian community, where other guilds or species we assessed are likely to reflect only broad, general effects measured across entire landscapes. Indicators such as these with strong, short-term responses to fine-scale variation on a landscape would also be good for distinguishing effects of relatively subtle differences among management scenarios where harvest intensity varies. Richness of cavity nesters would distinguish reliably between low-intensity and high-intensity harvest scenarios, and the strongly variable, asynchronous responses of richness of canopy nesters and presence of Common Yellowthroats could provide for excellent discrimination among a wide variety of scenarios.

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