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Avian community composition associated with interactions between local and landscape habitat attributes

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ABSTRACT

As human demand for ecosystem products increases, managers of landscapes used for commodity production require information about effects of management regimes on biological diversity. Landscape attributes, however, may moderate ecological responses to local-scale conservation and management actions. As a result, uniform application of local management prescriptions may yield variable biodiversity responses. We examined how interactions between local habitat structure and landscape forest cover were associated with avian community composition in the Ouachita Mountains, Arkansas, USA, 1995–1998. We used Bayesian hierarchical models to estimate occupancy for 63 breeding bird species, while accounting for variable detection with data collected from 1941 temporally replicated point count stations. Specifically, we estimated how interactions of four local habitat covariates (canopy cover of mature coniferous and hardwood trees, number of snags, and shrub cover) with percentage of mature hardwood forest at the landscape scale were associated with species occupancy and richness. Average predictive comparisons indicated that snag count and shrub cover had the strongest associations with species richness. Estimated associations for each of the four local forest cover variables was similar across all levels of landscape forest cover, suggesting weak or negligible interactions between these local measures and the landscape covariate. We found little support for our main prediction that local/landscape habitat interactions would be strongest at low levels of landscape forest cover (1–20%). Consequently, we suggest that forest managers consider prescriptions that result in a broad spatial distribution of heterogeneous habitat structural conditions (e.g., variation in understory cover and composition), irrespective of landscape context, to maintain a diverse avian breeding assemblage on landscapes in this region.

1. Introduction

Information on responses of floral and faunal communities to landscape attributes can inform decisions about management of terrestrial ecosystems. Forest landscapes are often managed for multiple objectives such as retaining populations and communities of native organisms, maintaining ecosystem services, and commodity production (Beschta et al., 2004; Perrings et al., 2010). However, management at smaller scales (e.g., patches or stands) over time produces variation in habitat configuration and composition across moderately or heavily modified landscapes (Tittler et al., 2012; Linden and Roloff, 2013). Quantifying cumulative effects of specific management practices on ecological responses is of critical importance, as even modest changes to current practices can provide substantial ecological benefits (Bunnell et al., 1999; Kroll et al., 2012a; Linden et al., 2012; Giovanini et al., 2013).

Landscape structure may moderate ecological responses to local-scale conservation and management actions (e.g., conservation field margins, set-asides, structural retention), and a recent review identified this mechanism (the "intermediate landscape-complexity hypothesis") as one of eight alternative hypotheses to explain how landscape effects influence biological diversity (Tscharntke et al., 2012). Specifically, in landscapes retaining moderate amounts of native vegetation cover (e.g., the dominant historical cover type), local management should yield the largest positive ecological response at the local scale. Conversely, response to local management will be minimal at the local scale in

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landscapes retaining either negligible (management intensity is highest) or high (management intensity is lowest) proportions of native cover types (Fig. 1A). Thus, a local-scale management action (solid line in Fig. 1A) is predicted to yield a larger ecological response than no management (dashed line in Fig. 1A), but local responses should be largest when 1–20% of the landscape (Tscharntke et al., 2005) is composed of a native cover type.

General linear models can be used to evaluate these predictions (Fig. 1B). Ecological response is predicted to be lowest in cleared (retaining <1% of native cover types) landscapes (bottom line) and will change only slightly (the slope will not differ significantly from 0) regardless of local management enhancements (i.e., increasing the covariate value along the *x*-axis). The same is true for complex (retaining >20% cover of native cover types) landscapes (dashed line, Fig. 1B), although the ecological response is always higher (i.e., the terms have different y-intercepts in the model, but the interaction with local management is not significant). However, in simple (1–20% cover of native cover types) landscapes, local management enhancements have a substantial effect on the local response (the interaction between landscape composition and local management terms will be significant).

To evaluate predictions from the intermediate landscape complexity hypothesis, we examined relationships between avian species and community responses and indicators of forest management intensity in Arkansas, USA. Intensive forestry practices typically include clearcutting of existing stands, chemical and/or mechanical site preparation, rapid regeneration of single-species stands, fertilization, and chemical or mechanical control of competing vegetation (Hayes et al., 2005; Brockerhoff et al., 2008). At the local scale, intensive management can modify structural conditions of forests, resulting in single-species plantations, reductions in snag abundance or understory vegetation cover, altered canopy cover, and shortened successional stages (Thompson et al., 1995; Bunnell et al., 1999; Carnus et al., 2006; Linden and Roloff, 2013). As a result, species that rely on structurally complex habitat types and/or longer disturbance intervals may be reduced in distribution and abundance because of reductions in habitat quality and availability (Chambers et al., 1999; Lindh and Muir, 2004; Ellis and Betts, 2011).

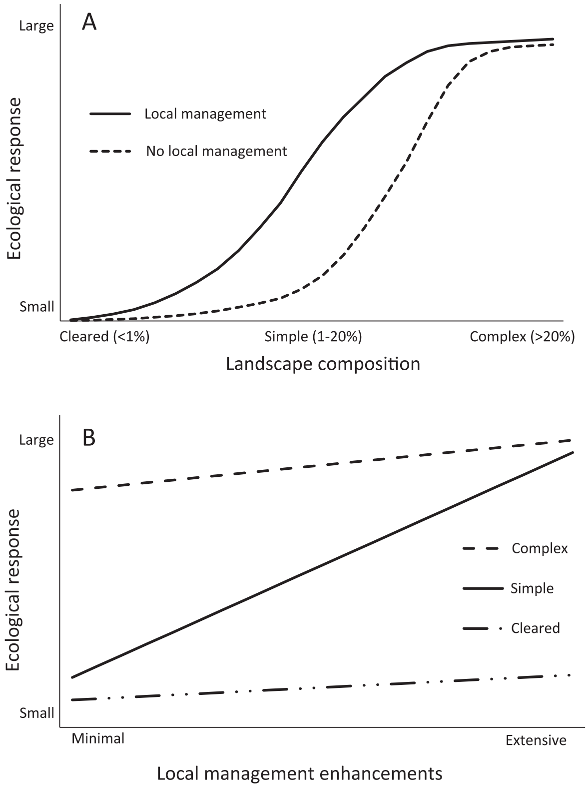

Fig. 1. Hypothetical relationship between an ecological response and local habitat management for three categories (based on percent cover) of landscape composition (A; based on Fig. 6 in Tscharntke et al. (2012)). Predicted relationships from a general linear model for the association of an ecological response with the interaction of local habitat management and landscape composition (B).

Avian species respond strongly to habitat structure and are reasonable candidate taxa to evaluate the intermediate landscape-complexity hypothesis (Hansen et al., 1995; Kroll and Haufler, 2010). We examined how differences in avian species-level occupancy and community richness at sample points (i.e., the “local” scale) varied based on interactions between four local habitat covariates (canopy cover of mature coniferous and hardwood trees, number of snags, and shrub cover, all of which are modified by forest management) and amount of mature hardwood-dominant forest in the landscape (Hunter et al., 1993; Fitzgerald and Pashley, 2000). Oak (*Quercus* spp.) and pine (*Pinus* spp.) dominated pre-settlement forest composition in our study area (Fitzgerald and Pashley, 2000). As a result, we expected amount of mature hardwood-dominant forest in the landscape to decline as pine management intensity increased. We summarized responses of cavity-nesting (CN) species and species of conservation concern (PIF; as defined by Partners-in-Flight in Fitzgerald and Pashley (2000)) separately, given sensitivity of some of these species to increases in forest management intensity (Martin, 1992; Fitzgerald and Pashley, 2000).

2. Methods

2.1. Study area and management prescriptions

We sampled forested plots in four watersheds in the Ouachita Mountains in Garland and Saline Counties, Arkansas, USA. The Ouachita Mountains consisted of east–west oriented ridges and mountains with elevations ranging from 100 to 900 m. Climate was characterized by hot, humid summers and mild winters (Skiles, 1981). The primary forest type throughout the area was mixed pine-hardwood forest with stands of pure hardwood also present. Most pine-dominated forest included some component of hardwoods. This hardwood component was diverse (>32 species) and included oaks (*Quercus* spp.), hickories (*Carya* spp.), maple (*Acer rubra*), and sweetgum (*Liquidambar styraciflua*). Watersheds ranged in size from 1500 to 4000 ha, and were owned and managed by the United States Department of Agriculture Forest Service (USFS) and Weyerhaeuser Company. Forest management prescriptions on Weyerhaeuser lands included clearcutting and planting of loblolly pine (*Pinus taeda*) plantations, whereas various even- and uneven-aged prescriptions were applied to USFS lands. Mature (>50 years old) forest stands with no active management other than fire suppression were a dominant component in three of the watersheds. The four watersheds contained a range of forest cover types and structural conditions (Tappe et al., 2004). Little Glazypeau (LG; 2275 ha) was owned by Weyerhaeuser Company and was managed largely for saw-log production using intensive, short-rotation (~35 years) pine management; Bread Creek watershed (BC; 1535 ha) was managed primarily by USFS using a mix of regeneration treatments, including group selection and single-tree selection; North Alum Creek watershed (NAC; 3960 ha) was of mixed ownership, with about half of the area under Weyerhaeuser Company management and half under USFS management; and South Alum Creek watershed (SAC; 1500 ha) was owned almost entirely by USFS and received minimal management for several decades prior to this study, resulting in primarily mature, mixed pine-hardwood forest.

2.2. Bird sampling

Each year (1995–1998), we sampled ~500 plots distributed among the four watersheds. Our goal was to maximize the total number of plots sampled over the 4 years while ensuring all sampled plots were ⩾100 m apart. In 1995, we established 26 parallel transects approximately 700 m apart (~113 km total length in the 4 watersheds), with plots located 200 m apart along these transects. In 1996, we used the same transects, but placed new plots between the 1995 plots (new plots were100 m from the previous year's plots). In 1997, we established 24 additional transects (~113 km total length) between the original transects (minimum of 200 m from previous transects) and placed a new set of plots (200 m apart). In 1998, we placed new plots between the 1997 plots along transects established in 1997. Thus, each plot was separated by a minimum of 200 m each year and 100 m across years.

We used a standardized point count protocol (Ralph et al., 1993) to sample birds 3 times per year between May 6 and June 9. At each point count station, we recorded all birds seen or heard within 50 m of the station during a 5 min sampling period (Ralph et al., 1993). Surveys began at sunrise and ended 3.5 h later on days with little or no rain and with wind speeds <11 kph. Groups of points (generally along a single transect) were sampled during the same day, with number of points sampled by an individual limited by the time constraints. We sampled these groups of point count stations in random order during each day. Number of point count stations and number of detections by species and watershed are summarized in Table S1.

Table 1
Codes and definitions for covariates used to examine associations between local and landscape habitat attributes and avian communities, Ouachita Mountains, Arkansas, USA, 1995–1998.

Term	Definition
CCC	% Coniferous canopy cover
DCC	% Deciduous canopy cover
SNAGS	Number of snags
SHRUBS	Percent shrub cover (<1.25 m)
MHDF_Low	<1% Landscape cover of mature hardwood-dominant forest (1 km radius)
MHDF_Medium	1–20% Landscape cover of mature hardwood-dominant forest (1 km radius)
MHDF_High	>20% Landscape cover of mature hardwood-dominant forest (1 km radius)
MHDF_L_SHRUBS	Interaction of MHDF_Low and SHRUBS
MHDF_H_SHRUBS	Interaction of MHDF_High and SHRUBS
MHDF_L_DCC	Interaction of MHDF_Low and DCC
MHDF_H_DCC	Interaction of MHDF_High and DCC
MHDF_L_CCC	Interaction of MHDF_Low and CCC
MHDF_H_CCC	Interaction of MHDF_High and CCC
MHDF_L_SNAGS	Interaction of MHDF_Low and SNAGS
MHDF_H_SNAGS	Interaction of MHDF_High and SNAGS
WS_BC	Watershed categorical term, Bread Creek
WS_SA	Watershed categorical term, South Alum
WS_LG	Watershed categorical term, Little Glazypeau
WS_NA	Watershed categorical term, North Alum
Spatial	Spatial autocorrelation term

2.3. Vegetation sampling

To characterize local habitat conditions, we sampled habitat covariates (Table 1) at 4, 3-m radius subplots at each point count station, with one subplot located at plot center and three subplots (120° apart) located 25 m from the center. At each subplot, we measured coniferous and deciduous canopy cover (%) with a spherical densiometer. Using a 0.5-m^2-density board (Nudds, 1977), we estimated vertical percent understory vegetation coverage (shrub cover; %); we visually estimated percent of the board obscured by vegetation at a distance of 15 m and a height of 1.25 m. We counted snags (⩾10 cm dbh and ⩾2 m in height) within each subplot. To calculate one value per point count station, we averaged measurements across sub-plots.

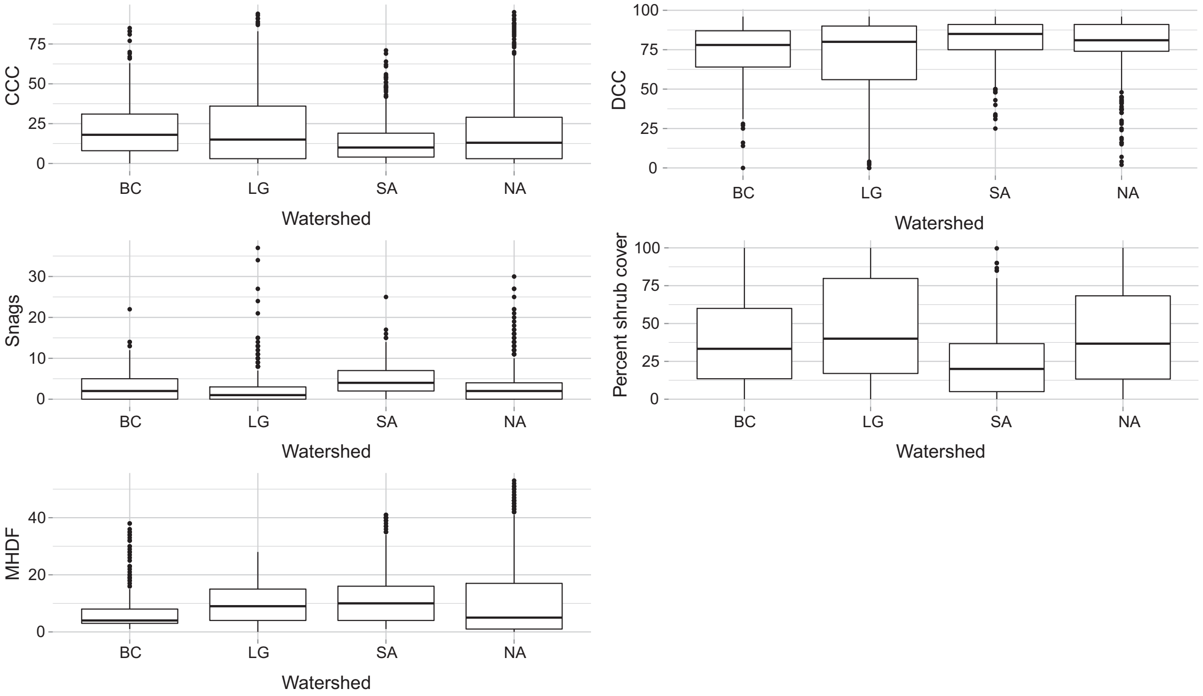

Fig. 2. Boxplot summaries of covariate values for one landscape (MHDF) and four local habitat covariates by watershed in the Ouachita Mountains, Arkansas, USA, 1995–1998. Covariate definitions are in Table 1.

We derived 12 landscape cover classes from supervised classification using spectral images identified using Landsat Thematic Mapper (TM) data, Digital Orthophoto Quarter-Quadrangles (DOQQs), and color infrared aerial photographs (Tappe et al., 2004). We based landscape cover classes on a classification scheme in Hagan et al. (1997). Additional details on classification of remotely sensed data are found in Tappe et al. (2004). We calculated percentage cover of mature hardwood-dominant forest (MHDF) in a 1 km radius circle (a landscape) surrounding each point count station. We summarized vegetation covariates by watershed (Fig. 2).

2.4. Analytical approach for estimating species occupancy and community composition

We used the Dorazio–Royle community occupancy model (Dorazio and Royle, 2005) to evaluate the intermediate landscape-complexity hypothesis. This model estimates occupancy for multiple species simultaneously, treating species as random effects, and provides community level summaries such as species richness. We used the model to estimate species-level covariate effects and population-level measures of occupancy, including species richness and similarity (Dorazio and Royle, 2005; Zipkin et al., 2009). Following previous examples (Russell et al., 2009; Jones et al., 2012; Giovanini et al., 2013), we did not account for contribution of unobserved species in our population estimates, instead conditioning on the set of observed breeding species in our study. This model assumes community closure between the survey dates of May 6 and June 9 in each year.

We let $z_{i,j}$ denote true occupancy status, in which $z_{i,j} = 1$ if species i occupies site j for the study interval, or $z_{i,j} = 0$ otherwise. The occupancy state is considered to be a Bernoulli random variable, $z_{i,j} \sim Bern(\psi_{i,j})$, where $\psi_{i,j}$ is the probability that species i occupies site j. We considered species detection to follow again a Bernoulli distribution: $y_{i,j,t} \sim Bern(p_{i,j,t} \cdot z_{i,j})$, where $y_{i,j,t}$ is 1 if the species i is detected at site j during visit t, or 0 otherwise. Note that in this parameterization, probability of detecting the species i at site j was 0 if the species does not occupy site j, as $z_{i,j} = 0$.

We modeled species-specific occupancy probabilities as a function of the five habitat covariates using a logit link function. We categorized mature hardwood-dominant forests into three levels in order to model the intermediate landscape complexity hypothesis: low, medium and high (<1%, 1–20%, and >20%, respectively). We parameterized the model to allow for interactions among the local and landscape covariates depicted in Fig. 1. Terms were also included in the model to account for any variation in species-level occupancy related to watershed (WS) and year:

$$\begin{aligned}
&\text{logit}(\psi_{i,j}) = a_{0i} + a_{1i} \cdot \text{Coniferous canopy cover}_j + a_{2i} \cdot \text{Deciduous canopy cover}_j + a_{3i} \cdot \text{Snags}_j + \\
&a_{4i} \cdot \text{Shrubs}_j + a_{5i} \cdot I_j(\text{MHDF} = \text{Low}) + a_{6i} \cdot I_j(\text{MHDF} = \text{High}) + \\
&a_{7i} \cdot I_j(\text{MHDF} = \text{Low}) \cdot \text{Shrubs}_j + a_{8i} \cdot I_j(\text{MHDF} = \text{High}) \cdot \text{Shrubs}_j + \\
&a_{9i} \cdot I_j(\text{MHDF} = \text{Low}) \cdot \text{Deciduous canopy cover}_j + a_{10i} \cdot I_j(\text{MHDF} = \text{High}) \cdot \text{Deciduous canopy cover}_j + \\
&a_{11i} \cdot I_j(\text{MHDF} = \text{Low}) \cdot \text{Coniferous canopy cover}_j + a_{12i} \cdot I_j(\text{MHDF} = \text{High}) \cdot \text{Coniferous canopy cover}_j + \\
&a_{13i} \cdot I_j(\text{MHDF} = \text{Low}) \cdot \text{Snags}_j + a_{14i} \cdot I_j(\text{MHDF} = \text{High}) \cdot \text{Snags}_j + \\
&a_{15i} \cdot I_j(\text{Year} = 1996) + a_{16i} \cdot I_j(\text{Year} = 1997) + a_{17i} \cdot I_j(\text{Year} = 1998) + \\
&a_{18i} \cdot I_j(\text{WS} = \text{Bread Creek}) + a_{19i} \cdot I_j(\text{WS} = \text{South Alum}) + a_{20i} \cdot I_j(\text{WS} = \text{Little Glazypeau}) + a_{21i} \cdot A_{ij},
\end{aligned} \tag{1}$$

where I is an indicator function taking the value of 1 if the argument is true and 0 if otherwise.

We summarized responses for both CN and PIF species separately and as part of the overall avian community. In addition, we summarized responses by migratory status (Neotropical migrant, resident, and short-distance; Robinson et al., 1995; Flather and Sauer, 1996; Mitchell et al., 2001).

We included an autologistic term to account for spatial autocorrelation in species occupancy (Linden, 2012; Mattsson et al., 2013). The term was calculated as follows:

$$A_{ij} = \frac{1}{n_j} \sum_{l:\sim j} \hat{z}_{il}, \tag{2}$$

where point count stations l were the neighbors of the point count station j, n_j was number of neighbors of point count station j, and $\hat{z}_{il}$ was the imputed (latent) occupancy of species i at point count station l. A value of 1 (on the log scale) for the coefficient a_{21i} indicates that a species has an estimated 2.7 times greater odds of occupying a site if the same species occupies all neighboring point count stations, or a factor of 1.6 times if the same species occupies half of the neighboring point count stations. Neighboring point count stations j and l must have been within 600 m radius of one another and be visited in the same year.

We modeled species-specific detection probabilities as a function of the four local vegetation covariates while allowing for seasonal variation (detection was allowed to vary within an individual year). In addition, our model included random observer effects to allow for differences in detection probability across the 14 observers used in this study:

$$\begin{aligned}
\text{logit}(p_{i,j,t}) = {} & \beta_{0i} + \beta_{1i} \cdot \text{Coniferous canopy cover}_j \\
& + \beta_{2i} \cdot \text{Deciduous canopy cover}_j + \beta_{3i} \cdot \text{Snags}_j \\
& + \beta_{4i} \cdot \text{Shrubs}_j + \beta_{5i} \cdot \text{Julian Date}_{jt} + \beta_{6i} \cdot \text{JulianDate}_{jt}^2 \\
& + \eta_1 I_{jt}(O=1) + \eta_2 I_{jt}(O=2) + \eta_3 I_{jt}(O=3) + \eta_4 I_{jt}(O=4) \\
& + \eta_5 I_{jt}(O=5) + \eta_6 I_{jt}(O=6) + \eta_7 I_{jt}(O=7) + \eta_8 I_{jt}(O=8) \\
& + \eta_9 I_{jt}(O=9) + \eta_{10} I_{jt}(O=10) + \eta_{11} I_{jt}(O=11) + \eta_{12} I_{jt} \\
& \times (O=12) + \eta_{13} I_{jt}(O=13) + \eta_{14} I_{jt}(O=14),
\end{aligned} \tag{3}$$

where O identifies individual observers and η is the coefficient for the indicator function I.

We centered and scaled each covariate prior to analyses. We included each of our primary variables of interest in both the occupancy and detection models. We used this approach to limit potential bias in our estimates by separating occupancy effects, which were of primary interest, from potential detection effects.

Under the hierarchical community model, we assumed that species-specific effects for a given covariate were drawn from a common normal distribution, e.g., that $\alpha_{l,i} \sim N(\mu_l, \sigma_l^2)$ for parameter α_l of species i, where the mean and variance of the normal distribution were population-level hyper-parameters, with prior distributions $\pi(\mu_1) = N(0,1)$ and $\pi(\sigma_l^2) \sim Inv - \chi^2(1,1)$. The same prior distributions were used for the detection and occupancy parameters. This population-level distribution provided a summary of community response, both in terms of mean behavior and variability in behavior. The extent to which information was shared across species depended on both degree of uniformity across the population, as estimated by population-level parameters, and amount of information available for each species. For species for which we were less certain of parameter estimates (those with low detection probabilities), estimates tended to shrink toward the population mean value. The observer random effects in the probability model were drawn from a normal distribution $\eta_d \sim N(0, \sigma_n^2)$, for $d = 1, \ldots, 14$, with $\pi(\sigma_n^2) \sim Inv - \chi^2(1, 1)$.

We estimated species richness (N) for each of the 1941 point count stations separately as:

$$N_j = \sum_{i=1}^{nspc} \hat{z}_{i,j}, \tag{4}$$

where *nspc* was number of species and $\hat{z}_{i,j}$ was the imputed (latent) occupancy of species i at point count station j. In addition to estimating species richness, we estimated species similarity between pairs of watersheds by calculating proportion of species that occupied both watersheds (Dorazio and Royle, 2005). Species similarity (S) in year g for watersheds h_1 and h_2, was defined as:

$$S_{g,h_1,h_2} = \frac{2\sum_i \left(\hat{z}_{i,g,h_1} \times \hat{z}_{i,g,h_2}\right)}{\sum_i \hat{z}_{i,g,h_1} + \sum_i \hat{z}_{i,g,h_2}}. \tag{5}$$

We calculated similarity for all pairwise combinations of watersheds.

All computations were performed in R (R Development Core Team, 2010) using Markov-chain Monte Carlo (MCMC) by Gibbs sampling. We describe the joint likelihood (Text S2). We ran 3 chains of length 150,000 each, after a burn-in of 50,000 and 1/50 thinning. We assessed convergence using the Gelman–Rubin statistic (Gelman et al., 2004) and visual inspection of chains, with both measures indicating a reasonable assumption of convergence. Posterior predictive checks (aka Bayesian *p*-value) did not indicate problems with the fitted model (Text S3). We provide R code and data for this model and our own MCMC implementation in Text S4.

Our primary interests for this analysis were associations between species richness and model covariates (e.g., estimating how much species richness differs between sites with a one unit difference in shrub cover, holding other variables constant). However, species richness is not modeled directly in the Dorazio–Royle community occupancy model, so such estimates are not immediately available from the model. Visual displays provide a useful, but non-quantitative approach towards exploring the association between estimated species richness and model covariates (Zipkin et al., 2009). Jones et al. (2012) suggested using average predictive comparisons (Gelman and Pardoe, 2007) to quantify the association (and uncertainty) between *predicted* species richness and each model covariate.

In a linear model, coefficients estimate the expected difference in response for a unit difference in each covariate. However, in non-linear models, such as the logistic models used for species occupancy, model coefficients do not map directly to an expected difference in response. Instead, the expected difference in response depends on both the level of the covariate of interest and levels of other covariates being 'held constant'. A common approach for dealing with this issue is to set all other covariates to their mean values. For example, from Eq. (1), the expected difference in species i occupancy for a one standard deviation difference in shrub cover at an intermediate level of MHDF, holding all other covariates at their mean values is given by $\text{logit}^{-1}(\alpha_{0i} + \alpha_{4i}) - \text{logit}^{-1}(\alpha_{0i})$ (all covariates were centered at their mean values prior to analysis). The expected difference for a 0.5 standard deviation difference is given by $\left(\text{logit}^{-1}(\alpha_{0i} + 0.5 \cdot \alpha_{4i}) - \text{logit}^{-1}(\alpha_{0i})\right)/0.5$. These quantities would be the same in a linear model without the logit link, but are not the same for the logit model. Additionally, not all differences in covariate values, e.g., a one standard deviation difference, are equally likely. In contrast to this approach, average predictive comparisons evaluate the difference in expected response for a unit difference in an input covariate, using the fitted model, and averaging over the distribution of all other covariates. These estimates are predictive in the sense that they are based on predictions from the fitted model, and are not estimated as part of the model fitting process.

Jones et al. (2012) extend the average predictive comparison approach to species richness by summing over species-specific predictions to obtain averaged expected differences in species count. That is, we make use of the fact that the expected species richness under our model is the sum of expected occupancies over all species. A description of how average predictive comparisons are calculated for a community occupancy model follows. For our dataset $(x, z)_j$, $j = 1, \ldots, n$, we denoted our variable of interest u, and all other variables v, such that $x = (u,v)$, where n was number of sites. We let $i = 1, \ldots, N$, be the index of species, where N was total number of observed species. We estimated average predictive comparisons for species richness using Eq. (6).

$$\hat{\Delta}_u = \frac{\sum_{j=1}^{n}\sum_{k=1}^{n}\sum_{s=1}^{S} w_{jk} \sum_{i=1}^{N} \left(E(z_i|u_k, v_j, \theta_i^S) - E(z_i|u_j, v_j, \theta_i^S)\right) sign(u_k - u_j)}{\sum_{j=1}^{n}\sum_{k=1}^{n}\sum_{s=1}^{S} w_{jk}(u_k - u_j) sign(u_k - u_j)} \tag{6}$$

A set of $s = 1, \ldots, S$ simulations were sampled from the posterior distribution, where θ_i^S is the Sth sample from the posterior distribution of parameter vector θ for species i. The weighting factor w_{ij} is calculated from an estimate of the Mahalanobis distance, as suggested by Gelman and Pardoe (2007). E is the expectation operator. We calculated predictive comparisons for all model inputs, treating each in turn as the input of interest. Based on these estimates, we are able to make claims regarding the predicted difference in species richness associated with unit differences in each covariate, using our fitted model and distribution of observed covariates.

We estimated standard errors for $\hat{\Delta}_u$ as described in Gelman and Pardoe (2007), and accounted for uncertainty in model parameter estimates, while treating all covariates as fixed. Unlike the richness estimator described in Dorazio and Royle (2005), the approach described here is based on the model prediction and does not directly consider observed occupancy status of each site. We provided all code used to estimate average predictive comparisons in Text S4.

3. Results

Our main prediction, that response of species richness to local management at sample points would be greatest in landscapes where mature hardwood dominant forest ranged from 1–20% cover (i.e., the slope of the predicted relationship would be steepest of the three interaction terms), was not supported (center column in Fig. 3). Median species richness at the point count scale was associated negatively with deciduous canopy cover for all three levels of mature hardwood-dominant forest at the landscape scale (Fig. 3). However, we did find substantial differences in species richness across landscapes and years (Table 2 and Figs. 4 and 5). Species richness was ~200% greater in the Little Glazypeau (LG) watershed compared to the South Alum (SA) watershed. Similarly, species richness at the watershed scale was at least 130% greater in 1997 than any of the other 3 years (Fig. 4). Median species similarity across the four watersheds ranged from 0.94–0.98, indicating near complete overlap in the avian communities among the four watersheds.

Population-level mean occupancy at the point count scale was positively associated with shrub cover up to 1.25 m in height and negatively associated with snag count and landscape cover of

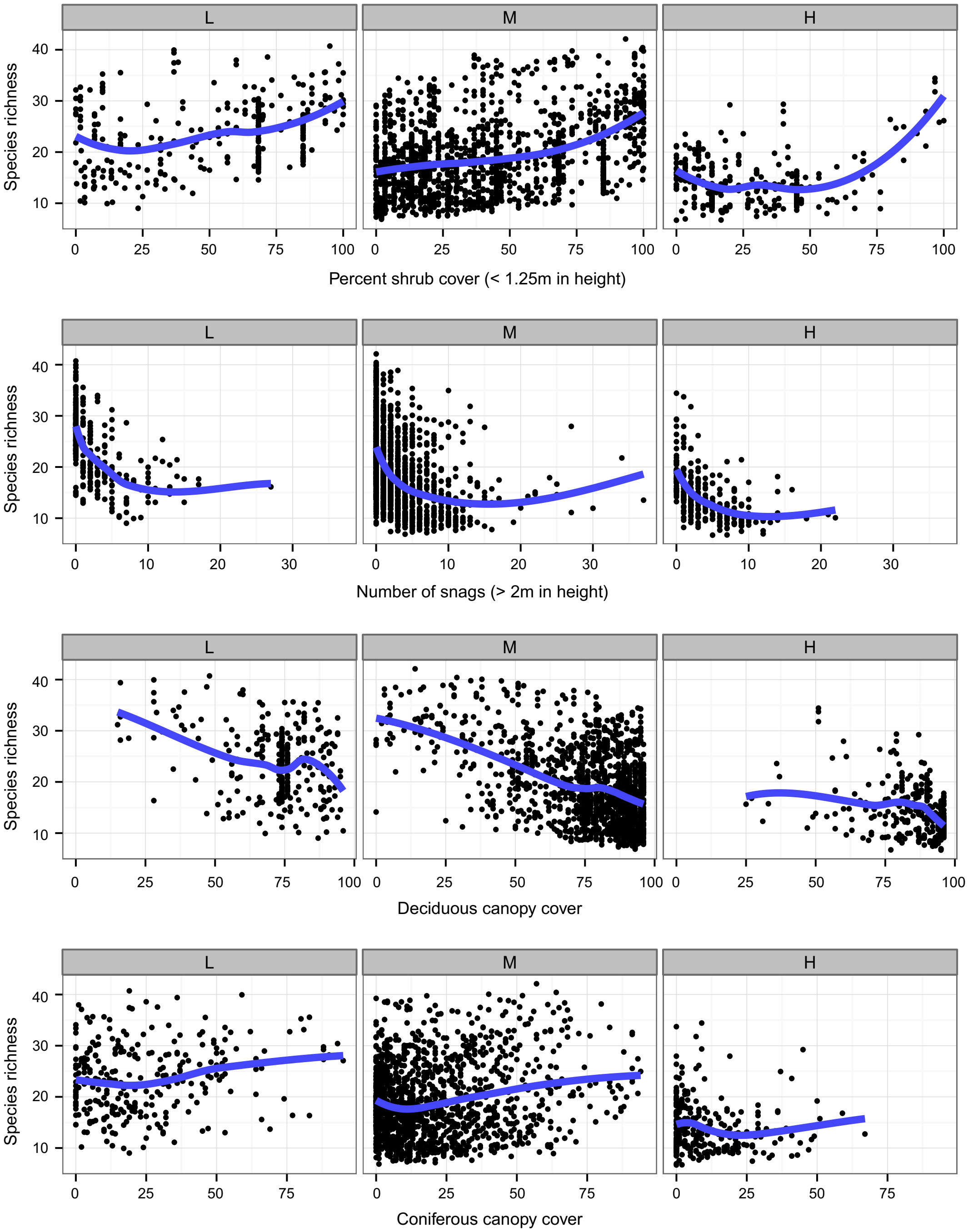

Fig. 3. Estimated avian species richness at each point count station as a function of the interaction between amount of mature hardwood-dominant forest at the landscape scale (*L* = <1%; *M* = 1–20%; and *H* ⩾ 20%) and four local habitat covariates, Ouachita Mountains, Arkansas, USA 1995–1998. The blue line in each panel is a loess smoother used to illustrate the overall trend. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mature hardwood-dominant forest >20% (Table 2). These results indicate that, on average, occupancy probabilities across all species tended to be higher at point count stations with greater amounts of shrub cover, lower in stands with higher snag counts, and lower in landscapes with >20% cover of mature hardwood-dominant forest. In contrast, posterior estimates of community hyper-parameters for other covariates were smaller and credible intervals (the Bayesian equivalent of a confidence interval) included 0, indicating little overall population-level effect of these covariates.

We did not find evidence of strong interactions between local and landscape covariates. We found evidence of a negative association between species richness and number of snags (Fig. 6). The estimated decline in species richness was largest at the lowest level of landscape cover of mature hardwood-dominant two snags/0.01 ha (the area of the four vegetation sampling subplots). In contrast, species richness was positively associated with shrub cover, with the increase in species richness being greatest at the lowest level of mature hardwood-dominant forest (0.6 additional bird species for a 10% increase in shrub cover). However, for both snags and shrub cover, we do not have clear evidence of effect differences (i.e., interactions) across the three levels of mature hardwood-dominant forest. We did not find strong evidence for an

Table 2
Community-level summaries of the hyper-parameters for occupancy covariates used to examine associations between local and landscape habitat attributes and avian communities, Ouachita Mountains, Arkansas, USA 1995–1998. Effects for 1995 (year), North Alum, MHDF_Medium, and associated interactions are included in the intercept term.

Model term	Community-level hyper-parameter	Posterior mean	95% Credibility interval
Intercept	$\mu_{\alpha 0}$	−1.84	−2.27, −1.41
CCC	$\mu_{\alpha 1}$	0.06	−0.12, 0.22
DCC	$\mu_{\alpha 2}$	−0.11	−0.29, 0.07
SNAGS	$\mu_{\alpha 3}$	−0.24	−0.41, −0.08
SHRUBS	$\mu_{\alpha 4}$	0.25	0.09, 0.42
MHDF_Low	$\mu_{\alpha 5}$	0.22	−0.02, 0.46
MHDF_High	$\mu_{\alpha 6}$	−0.59	−0.95, −0.23
MHDF_L_SHRUBS	$\mu_{\alpha 7}$	−0.01	−0.22, 0.19
MHDF_H_SHRUBS	$\mu_{\alpha 8}$	0.07	−0.19, 0.31
MHDF_L_DCC	$\mu_{\alpha 9}$	0.02	−0.22, 0.28
MHDF_H_DCC	$\mu_{\alpha 10}$	0.04	−0.23, 0.35
MHDF_L_CCC	$\mu_{\alpha 11}$	0.06	−0.15, 0.29
MHDF_H_CCC	$\mu_{\alpha 12}$	0.00	−0.29, 0.31
MHDF_L_SNAGS	$\mu_{\alpha 13}$	−0.07	−0.31, 0.17
MHDF_H_SNAGS	$\mu_{\alpha 14}$	−0.05	−0.31, 0.20
1996	$\mu_{\alpha 15}$	−0.17	−0.48, 0.14
1997	$\mu_{\alpha 16}$	0.87	0.58, 1.19
1998	$\mu_{\alpha 17}$	0.12	−0.15, 0.42
WS_BC	$\mu_{\alpha 18}$	−0.58	−0.82, −0.35
WS_SA	$\mu_{\alpha 19}$	−0.79	−1.09, −0.50
WS_LG	$\mu_{\alpha 20}$	0.39	0.05, 0.72
Spatial effect	$\mu_{\alpha 21}$	0.80	0.48, 1.13

association between species richness and either deciduous or coniferous canopy cover (i.e., 95% credibility intervals included 0 for all interactions; Fig. 6).

Associations of CN and PIF species with local habitat covariates were mixed (Fig. 7). Four (Carolina wren *Thryothorus ludovicianus*, great-crested flycatcher *Myiarchus crinitus*, hairy woodpecker *Picoides villosus*, and white-breasted nuthatch *Sitta carolinensis*) of the 12 (33%) CN species were associated positively with snag count at the local scale (Table S1). Nine of 18 (50%) PIF species were associated negatively with conifer canopy coverage at the local scale, although change in occupancy as a function of conifer canopy coverage for these species was small (Fig. 7). Thirteen of 18 (72%) PIF species were associated negatively with deciduous canopy coverage, with occupancy for both great-crested flycatcher and field sparrow (*Spizella pusilla*) declining ~40% across the range of the covariate (Table S1). For 36/63 (57%) species, occupancy was lowest in landscapes with the largest amount of mature hardwood-dominant forest (Table 2, Fig. 8). Probability of occupancy as a function of amount of mature hardwood-dominant forest ranged from 0.01–0.85 among bird species. We included posterior summaries of occupancy and detection, and parameter estimates and 95% credible intervals for occupancy and detection covariates, in Table S1.

We found strong evidence (i.e., 95% credibility intervals did not include 0) of a positive spatial effect on occupancy for 16/63 (25%) species (Fig. 9). We did not find any associations with taxonomic group (e.g., cavity-nesting birds) or conservation status (PIF species). In general, species that demonstrated strong spatial auto-correlation were common in the sample (>100 detections; Table S1) and had relatively small average territory sizes (<1.5 ha; Poole and Gill, 1992).

For many species, detection probabilities were low, ranging from 0.01–0.49 (at the average value of local habitat covariates and survey date; Table S1). We found relatively large differences in estimated detection probability among observers (Table 3). Average probability of detecting a species at a sample unit, when present, ranged from 2.5–7.5% across the 14 observers in our study. That is, the observer with the highest estimated detection probability was ~3 times more likely to detect a species than the obser-

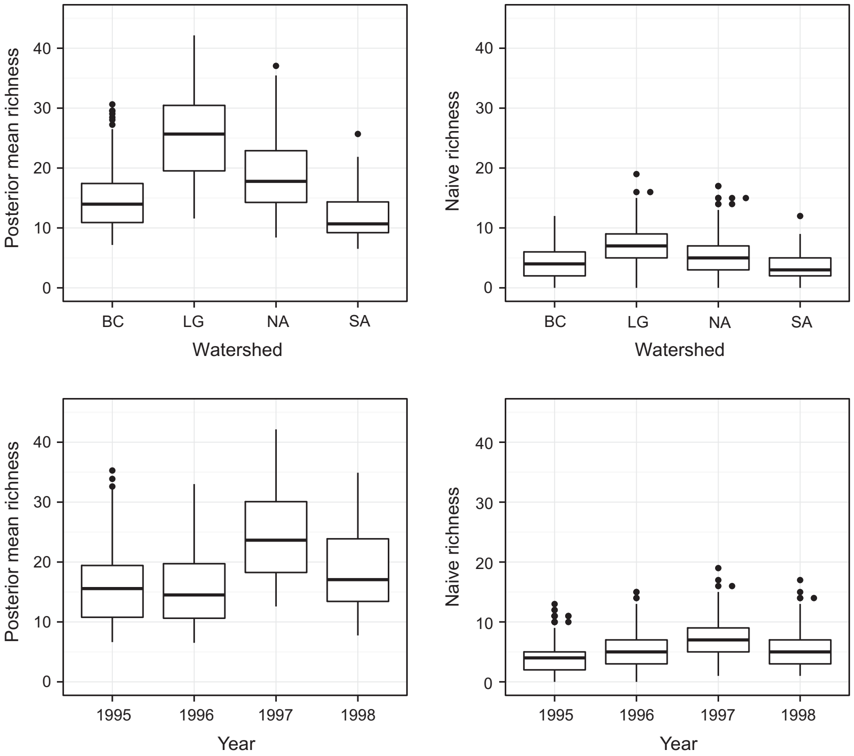

Fig. 4. Boxplot summaries of estimated avian species richness at a point count location by watershed and year, Ouachita Mountains, Arkansas, USA, 1995–1998. Naïve richness estimates species richness while ignoring variation in detection (right-hand column).

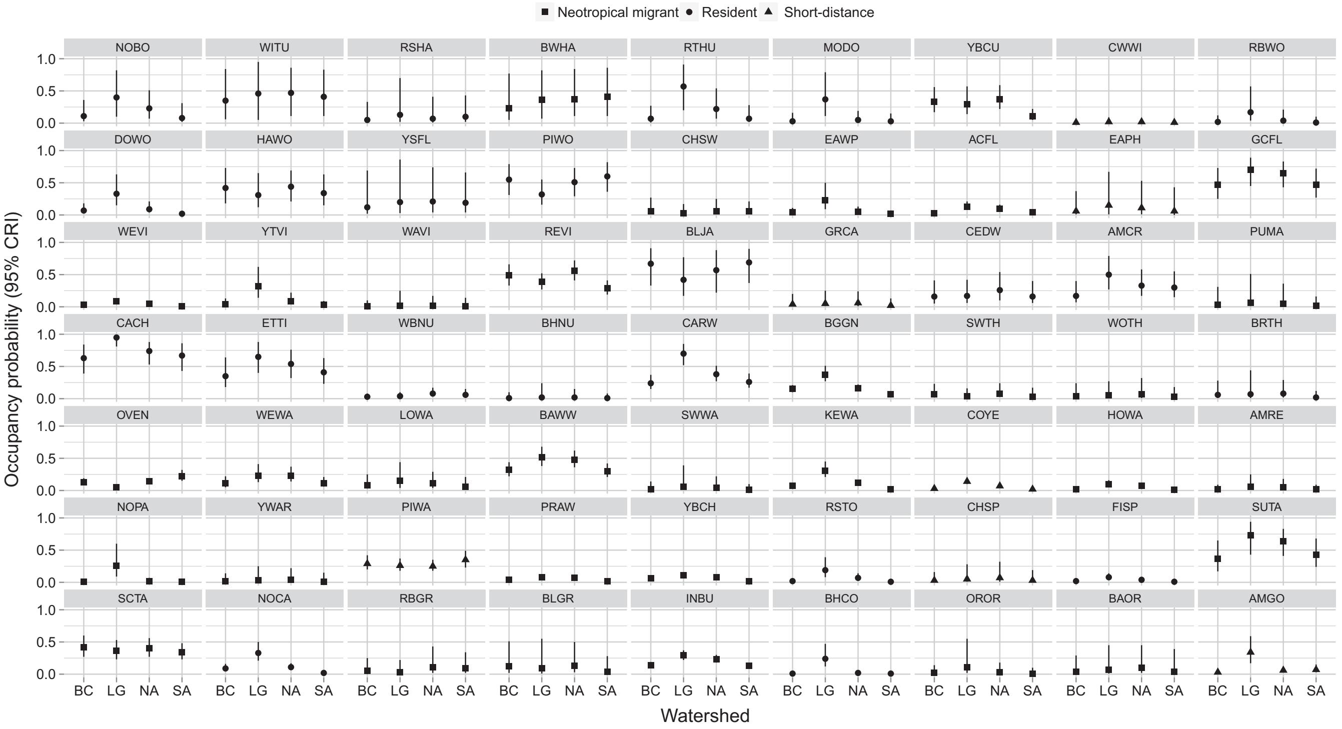

Fig. 5. Median occupancy (95% CRI) of 63 avian species in four forested watersheds (BG, LG, NA, and SA) and by migratory status, Ouachita Mountains, Arkansas, USA, 1995–1998. Definitions for species codes are located in Table S1.

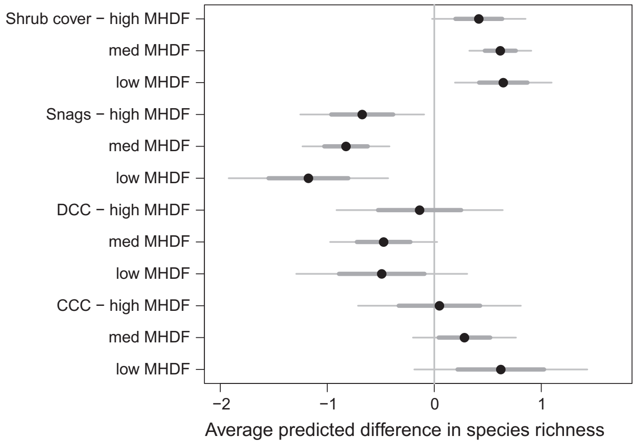

Fig. 6. Average predictive comparisons (±1 and 2 standard errors) for difference in species richness as a function of interactions between three levels of MHDF (low = <1%; medium = 1–20%; and high ⩾ 20%) and shrub cover, number of snags, deciduous canopy cover (DCC), and conifer canopy cover (CCC) in the Ouachita Mountains, Arkansas, USA, 1995–1998. Difference in species richness is estimated for a 10% increase in shrub cover, DCC, and CCC, and for an additional two snags within each 50 m radius point count station. Comparisons were calculated based on a modification of methodology described in Gelman and Pardoe (2007).

ver with the lowest estimated detection probability. Median detection probability for all observers was 5%.

4. Discussion

We did not find strong evidence for our main prediction regarding interactions between local and landscape covariates and species richness in a temperate forest avian community. In our study, species occupancy and community richness were associated with local covariates, and the association did not change significantly at different levels of the landscape covariate. We note two substantial differences between our study and previous research on ecological responses to local and landscape habitat attributes. First, invertebrates have been the focal species in many tests of local/landscape habitat interactions (reviewed in Tscharntke et al. (2012)). Second, researchers conducted most tests in agricultural landscapes where native habitat types had been converted to non-habitat (i.e., crops). In our landscapes, forest cover types were not converted to non-habitat, but rather altered in terms of forest age, structure, and/or species composition. In short, forest management in these landscapes may not be comparable to activities that convert habitat to non-habitat cover types in agricultural landscapes.

Evidence for relative effects of local vs. landscape habitat conditions on avian communities is mixed. Lichstein et al. (2002a) concluded that landscape effects were less important than local effects, although Mitchell et al. (2001) reported the opposite result (despite ~40% overlap in species across the two studies). However, integrating results across studies is difficult due to differences in ecological responses (e.g., occurrence, abundance, reproductive success), community composition, variation in forest cover types, disturbance regimes, and statistical methods used to assess associations or treatment effects (Villard et al., 1999; Mitchell et al., 2006; Betts et al., 2010). For example, Lichstein et al. (2002a) examined landscapes composed primarily of mature forest and not managed actively, whereas McGarigal and McComb (1995), Trzcinski et al. (1999), and Mitchell et al. (2006) studied landscapes that were managed actively. Also, many landscape studies considered only species that had sufficient detections for estimation of quantities of interest. Contemporary methods (Dorazio et al., 2006; Zipkin et al., 2009; Jones et al., 2012) allow investigators to evaluate a larger proportion of the avian community and not restrict analyses to the most prevalent species. Including rare species in analyses increases estimates of species richness and may

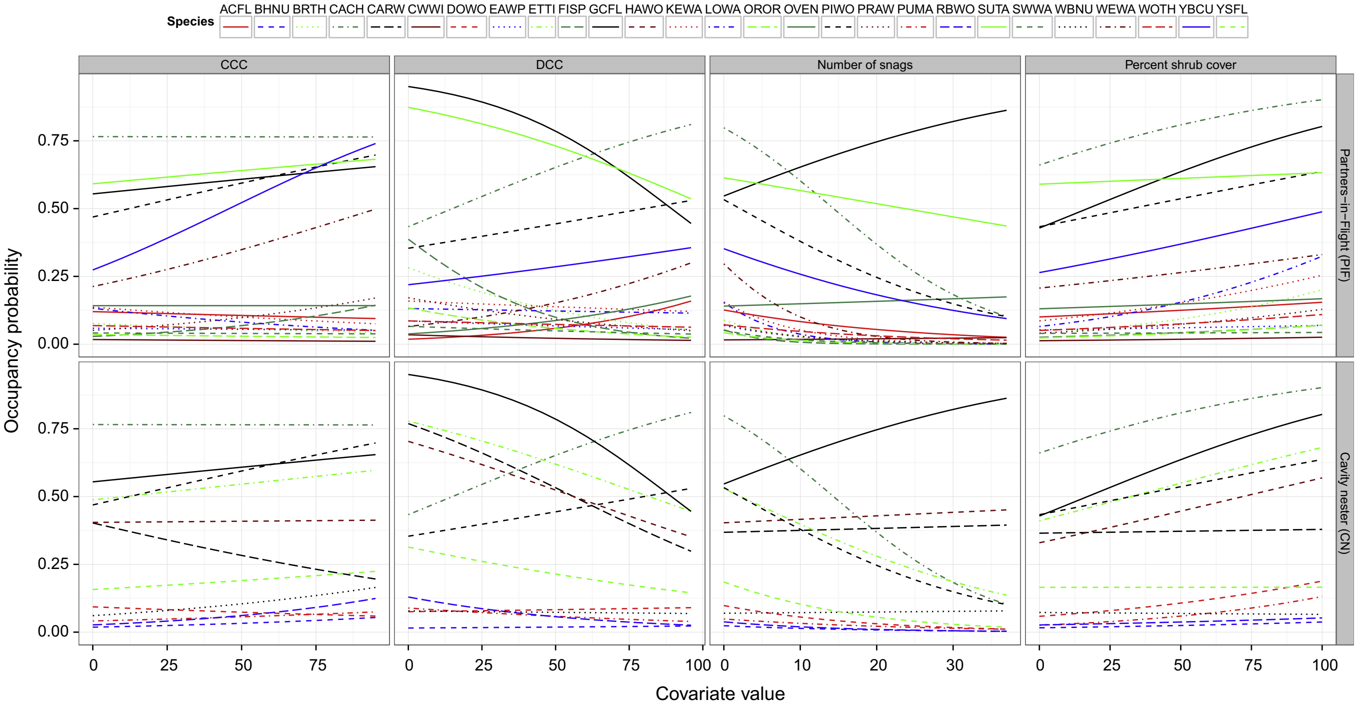

Fig. 7. Estimated mean occupancy probabilities for 18 Partners-in-Flight (PIF) and 12 cavity-nesting (CN) species as a function of conifer canopy coverage (CCC), deciduous canopy coverage (DCC), number of snags, and percent shrub cover (<1.25 m in height), Ouachita Mountains, Arkansas, USA, 1995–1998. Definitions for bird species codes are located in Table S2.

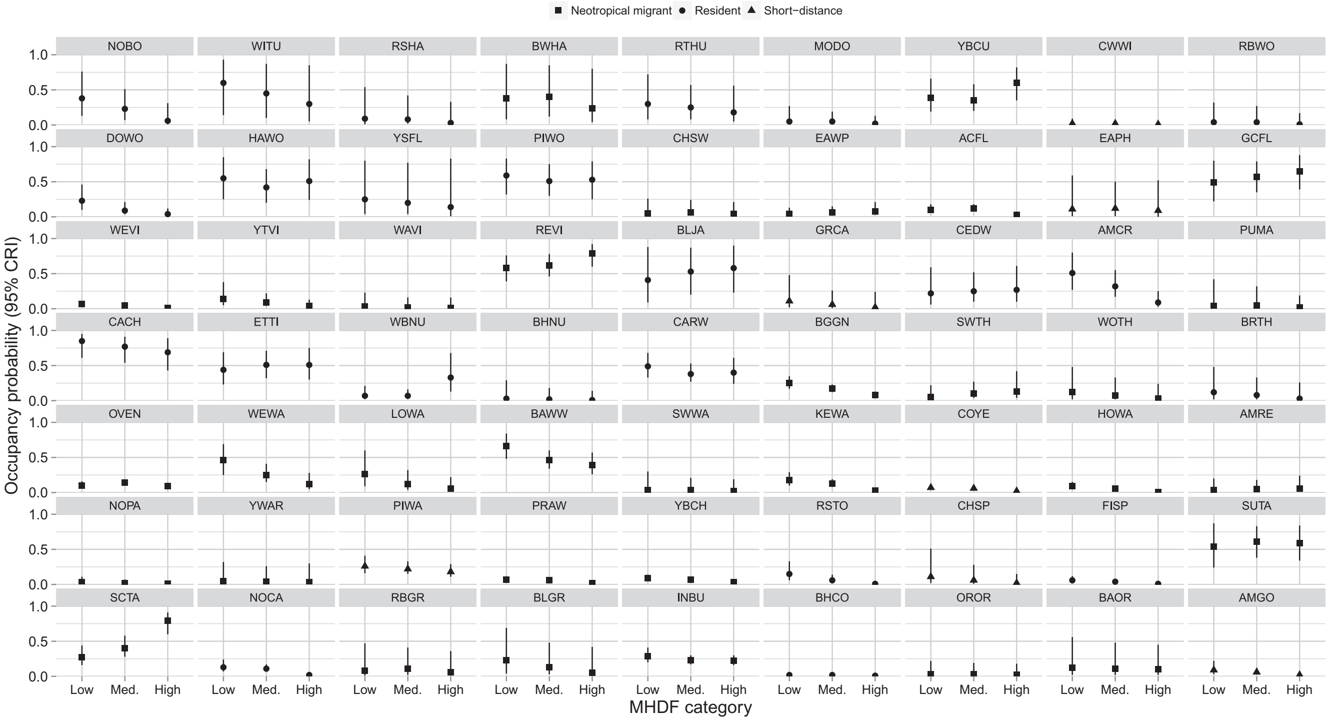

Fig. 8. Median occupancy (95% CRI) of 63 avian species at three levels of mature hardwood-dominant forest (MHDF; low, <1%; medium, 1–20%; and high, >20%) sampled at the landscape scale (1 km radius around each sample unit) and by migratory status, Ouachita Mountains, Arkansas, USA, 1995–1998. Definitions for species codes are located in Table S1.

alter magnitude of relationships between community responses and habitat covariates (this study; (Jones et al., 2012)). Finally, previous investigations have addressed variation due to spatial autocorrelation (Lichstein et al., 2002b; Betts et al., 2007). However, Bayesian frameworks provide opportunities for including spatial effects in a coherent and robust manner (Mattsson et al., 2013) and may change inferences about population responses to habitat conditions summarized at multiple scales of analysis.

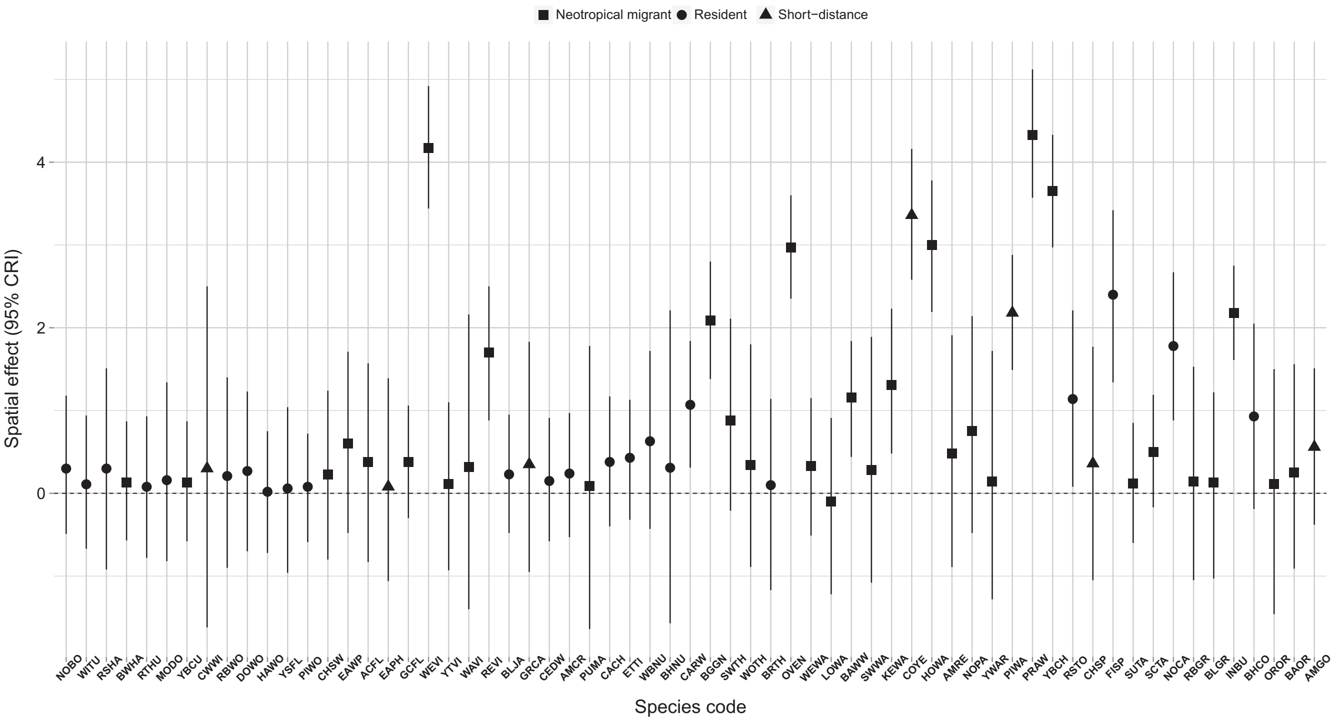

Fig. 9. Estimate (95% CRI) of spatial correlation for 63 avian species by migratory status, Ouachita Mountains, Arkansas, USA, 1995–1998. A value of 1 (on the log scale) indicates that a species has an estimated 2.7 times greater odds of occupying a site if the same species occupied all neighboring point count stations, or a factor of 1.6 times if the same species occupied half of the neighboring point count stations. Definitions for species codes are located in Table S1.

Table 3
Estimates (95% CRI) of observer effects on avian detection via point count surveys, Ouachita Mountains, Arkansas, USA, 1995–1998. Estimates represent average probability of detecting any species, when present, at a point-count station across all watersheds and years.

Observer	Median detection probability	95% Credibility interval
1	0.074	0.068, 0.08
2	0.044	0.040, 0.048
3	0.055	0.051, 0.06
4	0.066	0.062, 0.071
5	0.069	0.064, 0.075
6	0.052	0.049, 0.056
7	0.048	0.043, 0.053
8	0.066	0.061, 0.072
9	0.031	0.028, 0.034
10	0.048	0.044, 0.052
11	0.025	0.023, 0.028
12	0.051	0.047, 0.055
13	0.053	0.047, 0.059
14	0.041	0.037, 0.046

Concern exists about influences of plantation forestry on avian populations and communities (Hartley, 2002; Nájera and Simonetti, 2010; Paquette and Messier, 2010), although evidence supports the ability of these landscapes to contribute to retention of avian populations (Kroll et al., 2007; Iglay et al., 2012; Jones et al., 2012). Interestingly, we found little evidence for either strong negative or positive overall effects of conifer canopy coverage (conifers dominated plantations on our study area) on species richness. Responses of PIF species were mixed and the two species (field sparrow and prairie warbler *Dendroica discolor*) for which we had strong evidence of a positive association with conifer canopy coverage are both common in early successional habitat conditions (Perry and Thill, 2013). Also, intensive forest management practices often include management of vegetation (under- and midstory shrubs) that competes with regenerating conifers (Jones et al., 2012; Betts et al., 2013). Although a modest positive association existed between all PIF species and shrub cover, we found strong evidence (i.e., 95% CRI that did not include 0) of positive associations for only 3/18 (17%) species (Kentucky warbler *Geothlypis formosa*, prairie warbler, and yellow-breasted chat *Icteria virens*). Similarly, snags are often felled within plantations because of interference with management operations (Ohmann and Waddell, 2002; Kroll et al., 2012b). We found a modest negative association between all PIF species and number of snags, although only 4/18 (22%) species-specific estimates had 95% CRI that did not include 0.

Finally, we did not find any evidence that migratory status was associated with species responses. Neotropical migrant species composed most of the sample (33/63; 52%) and within this group we found both strong positive (red-eyed vireo *Vireo olivaceous* and scarlet tanager *Piranga olivacea*) and negative (black and white warbler *Mniotilta varia*, blue-gray gnatcatcher *Polioptila caerulea*, Louisiana waterthrush *Seiurus motacilla*, and worm-eating warbler *Helmitheros vermivorus*) associations with amount of mature hardwood-dominant forest (we expect this cover type would decline as management intensity increased) in the landscape.

We found strong evidence for differences in species richness at the point-count level across watersheds (we note that species richness at the watershed scale was nearly the same for all four watersheds). These results may be associated with heterogeneity in local habitat conditions, as richness was highest at point count stations in the Little Glazypeau watershed, which was intensively managed for saw-log production. Richness was lowest in South Alum, which was managed as an experimental forest and consisted primarily of unmanaged, mature forest. Mitchell et al. (2006) determined that avian species richness was associated positively with habitat heterogeneity across multiple intensively managed landscapes (including the landscapes evaluated in the present study). Active management, paired with topographic and hydrological features, may create a variety of conditions at the local scale that facilitates use by a broad group of species (Mitchell et al., 2006, 2008).

However, because we only sampled four watersheds, we caution against an interpretation that, at the watershed scale, active management does not preclude occurrence of species that are sensitive to forest management. Species that are acutely sensitive to forest disturbance (either anthropogenic or natural) may not have been present in any of the watersheds, or may have been absent because suitable habitat conditions did not exist in any of the watersheds.

We found that detection probabilities were low for most species and varied by both habitat covariates and observer, results that support arguments for including variable detection in ecological investigations (MacKenzie et al., 2006; Etterson et al., 2009; Reidy et al., 2011). In particular, we found evidence for large observer effects. Other avian investigations, which frequently train relatively inexperienced observers on an annual basis, may experience a similar magnitude of variation in detection probability for study species. We suggest that future investigations, if reliant on seasonal technicians, consider design-based approaches to control for variability induced by the detection process (Etterson et al., 2009).

Species richness is frequently measured in research studies and management programs to assess community responses to forest disturbances (Cam et al., 2000; Zipkin et al., 2010), but reasons exist for considering species richness as only a preliminary, and potentially uninformative, assessment. First, species occupancy (e.g., at the point-count level) may remain unchanged even if demographic measures such as survival and reproduction have changed, a critical result for management of individual populations (Van Horne, 1983). Second, species richness can remain constant despite substantial changes in community membership. For example, Harvey and Villalobos (2007) reported bird assemblages that were abundant, speciose, and diverse in both agro-forestry systems and unmanaged forests. However, species composition between these two assemblages was highly modified, with fewer forest-dependent species, more open area species, and different dominant species in the agro-forestry system. At the very least, we advocate use of contemporary statistical methods to estimate species similarity across treatments or other units used for inference (Dorazio et al., 2006; Giovanini et al., 2013).

5. Management Implications

Intensive land use plays a critical role in provisioning a rapidly growing human population, but alters the spatial distribution of habitat structures and vegetation cover types. However, information is limited about vertebrate responses to interactions between habitat attributes at local and landscape levels. Our results indicate weak or negligible associations between species richness and habitat covariates measured at the local and landscape scales, and highly variable responses of individual avian species to local/landscape interactions. For example, a specific management action (e.g., increasing amount of shrub cover within a stand) at the local scale yielded a similar ecological response regardless of the landscape context (amount of mature hardwood-dominant forest surrounding the stand). We did find support for associations between species richness and both number of snags (negative association) and shrub cover (positive association). Consequently, we suggest that forest managers consider prescriptions that result in a broad spatial distribution of heterogeneous habitat structural conditions (e.g., variation in understory cover and composition, number of snags), irrespective of amount of mature hardwood dominant forest in the landscape, to maintain diverse avian breeding assemblages within watersheds in this region.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.04.011.

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