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Forest Ecology and Management 232 (2006) 56–67

Forest Ecology and Management

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A method for landscape analysis of forestry guidelines using bird habitat models and the Habplan harvest scheduler

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Received 17 October 2005; received in revised form 12 May 2006; accepted 14 May 2006

Abstract

Wildlife-habitat relationship models have sometimes been linked with forest simulators to aid in evaluating outcomes of forest management alternatives. However, linking wildlife-habitat models with harvest scheduling software would provide a more direct method for assessing economic and ecological implications of alternative harvest schedules in commercial forest operations. We demonstrate an approach for frontier analyses of wildlife benefits using the Habplan harvest scheduler and spatially explicit wildlife response models in the context of operational forest planning. We used the Habplan harvest scheduler to plan commercial forest management over a 40-year horizon at a landscape scale under five scenarios: unmanaged, an unlimited block-size option both with and without riparian buffers, three cases with different block-size restrictions, and a set-asides scenario in which older stands were withheld from cutting. The potential benefit to wildlife was projected based on spatial models of bird guild richness and species probability of detection. Harvested wood volume provided a measure of scenario costs, which provides an indication of management feasibility. Of nine species and guilds, none appeared to benefit from 50 m riparian buffers, response to an unmanaged scenario was mixed and expensive, and block-size restrictions (maximum harvest unit size) provided no apparent benefit and in some cases were possibly detrimental to bird richness. A set-aside regime, however, appeared to provide significant benefits to all species and groups, probably through increased landscape heterogeneity and increased availability of older forest. Our approach shows promise for evaluating costs and benefits of forest management guidelines in commercial forest enterprises and improves upon the state of the art by utilizing an optimizing harvest scheduler as in commercial forest management, multiple measures of biodiversity (models for multiple species and guilds), and spatially explicit wildlife response models.

Keywords: Avian richness; Biodiversity; Extended rotations; Habitat model; Habplan; Harvest scheduler; Forest management; Riparian zone; Sustainable forestry initiative®

1. Introduction

The practice of forestry is increasingly guided by sustainable forestry concepts designed to protect environmental and aesthetic values (Loehle et al., 2002). Myriad guidelines and regulations developed to implement these concepts potentially affect management activities and the spatial structure of managed forest landscapes (e.g., rotation length, riparian buffer width, harvest method, regeneration method, retention patches, corridors, set-asides, cut-block size, green-up requirements), but they can sometimes have considerable economic cost (e.g., Barrett et al., 1998; Carter et al., 1997; Gustafson and Rasmussen, 2002; Hummel and Calkin, 2005; Kant, 2002; Nieuwenhuis and Tiernan, 2005; Ohman, 2000; Onal et al., 1998). The benefits of habitat features such as corridors are rarely known quantitatively (see Hannon and Schmiegelow,

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doi:10.1016/j.foreco.2006.05.040

2002; Loehle et al., 2002). Thus, guidelines are sometimes based on surrogates of assumed ecological benefits (e.g., measures of fragmentation or edge) rather than on direct measures of wildlife or biodiversity response.

Forest managers commonly use computer software to schedule future silvicultural activities and identify harvest schedules that optimize (or nearly optimize) economic return. However, with the development of sustainable forestry certification programs, managers increasingly need to also consider environmental constraints as part of harvest scheduling exercises (Van Deusen, 1996). For example, the Sustainable Forestry Initiative® (SFI®; Sustainable Forestry Board, 2005) requires participants to ‘‘manage the quality and distribution of wildlife habitats and contribute to the conservation of biological diversity by developing and implementing stand- and landscape-level measures that promote habitat diversity.’’ In this guidance, ‘‘quality’’ of habitats is not defined. A number of studies have incorporated spatial restrictions (e.g., limiting fragmentation) into planning problems as goals (Baskent and Jordan, 2002; Bertomeu and Romero, 2001; Liu et al., 2000; Nieuwenhuis and Tiernan, 2005; Rempel and Kaufmann, 2003) using tools such as simulated annealing or Tabu search, but usually without basing the objective on measures that directly correlate with wildlife benefits. Others (e.g., Larson et al., 2004) have spatially and temporally simulated the implications of forest management for selected components of biological diversity. However, using wildlife-habitat relationship models in concert with harvest scheduling software (Wigley et al., 2001) would allow managers to assess implications of alternative harvest schedules for biological diversity and the associated economic costs in commercial forest operations.

A wide range of techniques has been employed to estimate the future ecological benefits of managing forests in the context of protecting other resource values. The most tractable approach is stand-based and considers area in different categories to produce various ancillary (non-timber) benefits (e.g., Maness and Farrell, 2004; Wikstrom and Eriksson, 2000). However, most field studies relating wildlife response to forest structure have been performed at fine scales, generally at the level of the plot or forest stand. Relationships established at this scale rarely extrapolate well to broader landscape scales because processes driving the distribution of individual species (e.g., habitat selection, foraging and mating behaviors, population dynamics) may be taking place on much broader scales than those at which they are commonly studied (Maurer and Villard, 1994; Villard et al., 1995; Wiens, 1995). That is, wildlife benefits may not simply sum up as a function of acres in various age class/forest type categories.

A recent trend is the use of spatially explicit, landscape-scale wildlife suitability or response models (Arthaud and Rose, 1996; Calkin et al., 2002; Li et al., 2000; Larson et al., 2003; Mitchell et al., 2001) rather than models that rely exclusively on stand-level or patch-based information to predict wildlife responses to management. This is important because forest management activities play out over time to create landscapes with complex spatial patterns. Use of such models in concert with output from a harvest scheduler (e.g., Azevedo et al., 2005; Bettinger et al., 2003) would allow managers to evaluate tradeoffs (e.g., Zhou and Gong, 2005), particularly using production possibility frontier analysis (e.g., Arthaud and Rose, 1996; Calkin et al., 2002). This approach would help managers understand conflicts and tradeoffs between forest resources and values and make difficult decisions about alternative management strategies.

In this study, our objective was to evaluate and demonstrate an approach for frontier analyses of wildlife benefits using spatially explicit wildlife response models in the context of operational forest planning. We used the Habplan harvest scheduler (Van Deusen, 1996, 1999, 2001) to estimate the flow of wood under several types of forestry guidelines over a 40-year planning horizon for an industrial forest in South Carolina. To evaluate the potential biodiversity implications of the alternative forestry guidelines, we used the Habplan output with habitat-relationship models developed to predict overall bird richness, richness of several bird guilds, and presence of selected bird species on a regional scale, based on measures of habitat structure at multiple spatial scales (Mitchell et al., 2006).

2. Methods

2.1. Study site

Our study landscape comprised MeadWestvaco Corporation's Ashley-Edisto Districts located south of Summerville, South Carolina (Charleston, Colleton, and Dorchester counties, Fig. 1) in Bailey Province 232, the Outer Coastal Plain Mixed Province. The province is comprised of the flat and irregular Atlantic and Gulf Coastal Plains. Local relief is <90 m, and soils are mainly ultisols, spodosols, and entisols. Mean annual temperature ranges from 16 to 21 °C and average annual precipitation ranges from 102 to 153 cm. Regional vegetation is characterized by loblolly pine (*Pinus taeda*) forests on upland sites and interior swamps dominated by gum (*Nyssa* spp.) and bald cypress (*Taxodium* spp.). Many upland forests contain isolated depressional wetlands with hardwood and/or pine overstories.

Stand boundaries (polygons) and forest type/age were derived from operational inventory data provided by MeadWestvaco, including some GIS layers such as roads, streams, and elevation. There were 2788 polygons (stands) on the map. Classification errors were considered minor as only pine and hardwood types were used. Of the forested land on the landscape, 71% was pine and 29% was hardwood. These data do not reflect current conditions on the Ashley-Edisto Districts due to ongoing harvests, land transactions, and other changes. More detail on data collection and analysis can be found in Loehle et al. (2005) and Mitchell et al. (2006). The study area was virtually all farmed historically and then abandoned or planted to pine. Much of the area has been harvested several to many times. Thus, there is little old forest and no ‘‘old-growth,’’ and logging operations on fairly short rotations keep the average age relatively young (Figs. 2 and 3).

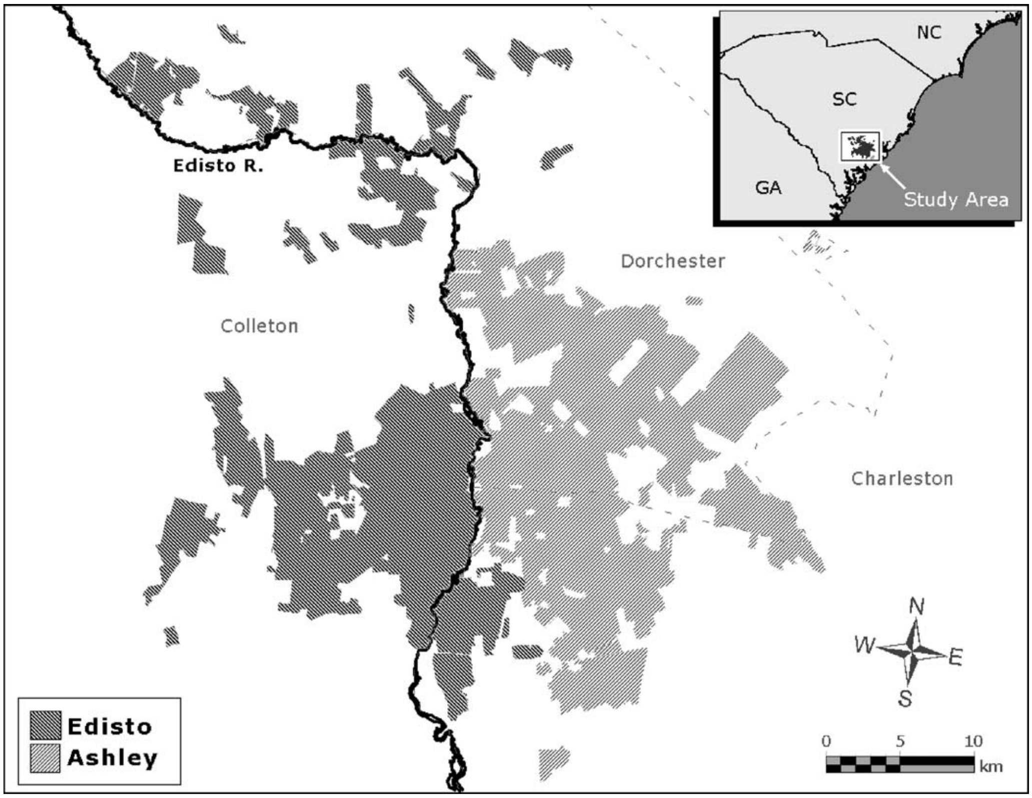

Fig. 1. Study location.

2.2. Harvest scheduling approach

We used the Habplan harvest scheduler (Van Deusen, 1996, 1999, 2001) to schedule harvests over a 40-year planning period. Habplan differs from landscape simulators such as LANDIS or HARVEST, which use fixed regimes and make no attempt to derive an optimal management regime (Klaus et al., 2005; Larson et al., 2004; Wintle et al., 2005). Habplan uses a variation of the Metropolis et al. (1953) algorithm to iteratively consider new regimes as substitutes for the current regime of each polygon. This tool allows spatial management goals to be included along with financial and operational goals. It is thus superior to Linear Programming approaches for spatial problems, such as in our study. It is not the only tool we could have used (e.g., simulated annealing (Crowe and Nelson, 2005)), but was adequate and readily available. Comparison of Habplan with other existing approaches, as well as its pros and cons, has been documented (Van Deusen, 1996, 1999, 2001).

Harvest scheduling, as defined for Habplan, requires a land area divided into polygons with a list of potential management regimes for each polygon. A management regime defines a set of activities that are expected to occur over the planning horizon. Specifically, a regime denotes the timing of outputs (wood in this case) and of stand ages/types that will occur if this regime is followed. A schedule is produced by assigning one regime to each polygon. Spatial and even-flow constraints are entered in Habplan as components of the goal function.

Habplan is a stochastic tool and will produce an infinite set of outcomes if allowed to run. It is necessary to manually stop the program when goal functions are met and it is producing only minor variations in results. Thus, the result produced for each scenario is a representative case of many similar possible outcomes that would have approximately the same output values, but different spatial configurations. Different Habplan results could slightly alter the wildlife results we obtained. Different initial conditions or landscapes (e.g., different topography,

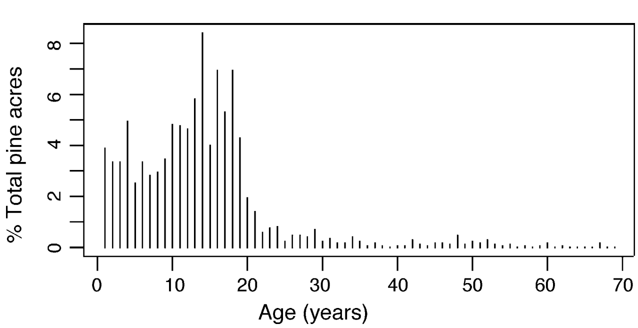

Fig. 2. Pine age class distribution at start of planting period.

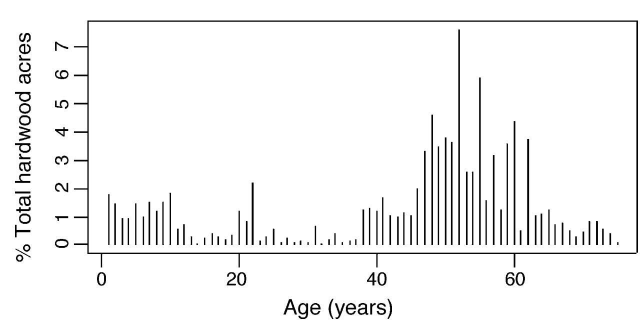

Fig. 3. Hardwood age class distribution at start of planting period.

degree of company land blocking) could alter our results more significantly. Using the same initial landscape configuration for all scenarios minimized the likelihood that such effects might bias our analyses.

2.3. Growth and yield

The Habplan harvest scheduler requires information on the wood yield that results from each harvesting regime. For pine stands, the commercial yield from clearcutting at different ages was calculated using the University of Georgia PMRC lower coastal plain model (Harrison and Borders, 1996). We allowed a stand to be cut again after a minimum of 20 years. Initial inventory was based on typical values for an industrial forest. Stands were replanted at 1235 stems per ha with a 4% improvement in site index, reflecting improved planting stock. For the road closure scenario, roads were ‘‘planted’’ to pine at 1235 stems per acre and assigned a site index of 23 m (a typical value).

For hardwood stands, we used the natural loblolly pine model of Brender and Clutter (1970) as a reasonable approximation of growth and yield in mixed hardwood forest based on expert judgment. Stands were given a site index of 15.2 m (base age of 50 years) to prevent overestimation of hardwood growth by the loblolly model. Hardwood stands could be thinned to 16 m^2 per ha basal area on harvest, with the ‘‘thinned’’ volume being the harvest. At least 10 years were required between thinnings. Hardwood basal area is not a variable in any wildlife model we used, and thus contributes only to wood yield calculations.

2.4. Scenario descriptions

Using Habplan, we scheduled harvests under 5 scenarios which reflect management guidelines sometimes proposed for commercial forest landscapes or required by sustainable forestry certification programs such as the SFI®:

1. An unmanaged scenario allowed all stands to age over the 40-year planning horizon.
2. A set-asides scenario assigned an ‘‘unmanaged’’ regime to all pine and hardwood stands older than age 40 at time 0 (about 24.5% of the area) and allowed them to age over the 40-year planning horizon. Most of these stands were hardwood. To estimate the full commercial benefits of extended rotations, we would need to include the economics of sawtimber and veneer products, but our data did not allow us to differentiate wood by size/value.
3. The SFI® Standard (Sustainable Forestry Board, 2005) recommends an average blocksize (set of adjacent stands cut in a time period) of 48.6 ha. Because Habplan can only model maximum blocksize (handled using adjacency restrictions), we set 48.6 and 72.9 ha maxima to approximate this guideline, and also an unlimited (unrestricted) scenario.
4. Fragmentation caused by roads could be an issue, so we designed a scenario to eliminate all roads. In the road closure scenario, all roads were planted to pine at year 0 and allowed to age, which obviously would prevent any stands from being managed. This scenario was not designed to be operational.
5. Finally, we created a riparian buffer scenario. The stand definitions we acquired from MeadWestvaco did not identify riparian buffers. A width of 50 m is used by some forest products companies, so we established buffers 50 m wide on each side of streams described on the 1:100,000-scale USGS map layer (see Mitchell et al., 2006) (i.e., on larger streams only), designated the forested buffers as unmanaged hardwoods, and allowed them to age over the 40 years. These buffers occupied 5.6% of the landscape.

None of these scenarios exactly represents what a company would do, but rather they allowed us to test our approach under a variety of landscape management alternatives. In all scenarios except the unmanaged case, an even-flow harvest constraint was imposed on area and wood volume to represent operational limitations and to prevent an unusually large harvest at the end of the planning period.

2.5. Bird habitat models

To characterize implications of the scenarios for biodiversity, we used multiple indices of biodiversity based on different components of the bird community. Multiple indices are often necessary because no single index can universally represent all aspects of biological diversity. In a prior study (Mitchell et al., 2006), we developed stepwise ordinal logistic regression (SAS Institute, 1990) models for probability of belonging to richness classes (low [lowest quartile of richness], medium [2 intermediate quartiles of richness], and high [highest quartile of richness]) of total bird richness and of multiple bird guilds, and probability of detection of selected species based on stand characteristics (e.g., stand area, forest type, forest age) and measures of landscape pattern in circular buffers of arbitrary size (radii of 100, 250, 500 m, and 1 km) around bird sample plot centers. The models were developed using four landscapes located throughout the southeastern US and were thus regional in scope. Logistic regression models took the form:

$$P = \frac{e^{\beta_0+\beta_1 x_1+\cdots+\beta_n x_n}}{1 + e^{\beta_0+\beta_1 x_1+\cdots+\beta_n x_n}} \quad (1)$$

where P is the probability of belonging to a richness class or probability of detection for a species, β_0 is the model intercept, and $\beta_1 x_1, \ldots, \beta_n x_n$ are landscape and stand variables and their respective coefficients. Through step-wise selection, variables were included in logistic models when their contribution significantly increased model fit ($p < 0.05$). Landscape metrics included variables such as road and stream density, topographic position, area by forest age and type, and measures of age class and forest type heterogeneity. Details of computation are presented in the Glossary and in Loehle et al. (2005) and Mitchell et al. (2006). The underlying bird and habitat data used to develop the models were gathered from landscapes in Arkansas, West Virginia, and two regions of South Carolina, including the Ashley-Edisto districts used in this study. The models for richness (for all birds and several guilds) predict the probability of a location supporting high richness (in the top quartile of richness observed across the four study landscapes). For species, the models predict the probability of detection of a species. Detailed methods are described in Mitchell et al. (2006).

We used models from Mitchell et al. (2006) for probability of high richness (top quartile of richness) for all bird species, and for the following bird guilds: canopy nesters, cavity nesters, neotropical migrants, and scrub-successional associates. In addition, we used models predicting probability of detection for Acadian flycatcher (*Empidonax virescens*), blue-gray gnatcatcher (*Polioptila caerulea*), common yellowthroat (*Geothlypis trichas*), and eastern wood-pewee (*Contopus virens*) developed using the same methodology as Mitchell et al. (2006) (Table 1). These guilds and species were chosen to be diverse in habitat requirements and conservation priority.

Table 1
Intercepts and stand and landscape parameters included in stepwise ordinal logistic regression models developed for predicting probability of belonging to highest quartile of richness for overall avian richness (OV), richness within guilds (canopy nesters, CN; cavity nesters, CV; neotropical migrants, NM; scrub-successional species, SS), and probability of detection for Acadian flycatchers (AF), blue-gray gnatcatchers (BG), common yellowthroats (CY) and eastern wood peewees (EW)

Parameter[a]	Model								
	OV	CN	CV	NM	SS	AF	BG	CY	EW
AC5_1		−0.00011	−0.00005			−0.00004	0.000052	0.000059	
AC5_K		9.693E−07	6.269E−07				−1.55E−06		
AC30_1							0.000038		
AC30_2		−5.47E−06							
AC30_K								3.992E−07	−8.06E−07
AGE_STD_1		0.0359							
AGE_STD_2	0.0456		0.026	0.0551			0.0199	0.0336	
AGE_STD_K					0.0545			0.0399	
ASPECT		−0.3564							
CURV	0.962	1.3349		1.4997					
DST2_RDS_A					−0.00597				
DST2_WTR_A								0.000615	
DST2_WTR_C					0.00069				
EVNS_K				−3.4312					
FRGAC_2						1.3024			
FRGAC_K					−2.9867				
HARD_1		0.000027	0.000024						−0.00006
HARD_K							−7.31E−07		
INTERCEPT	−2.4282	−2.6882	−3.4479	−3.3153	−0.9000	−1.9679	−4.0640	−6.0841	−9.3322
IS_AGE			0.008		0.0214	0.0228			0.0493
IS_AREA	3.116E−07			2.519E−07					−1.63E−06
LANDPO_5									0.6663
LANDPO_K	−0.4618			−0.5926		−0.6626			
M_AGE_1		0.0112			−0.0526				
M_AGE_2								−0.0399	
M_AGE_K						−0.0318			
MIX_1					−0.00003				
MIX_2				−0.00001					
MIX_K	−1.25E−06					−3.55E−07			
NON_1						−0.00023			
NON_5								5.998E−06	
NON_K					1.607E−06				
PFRGM_K				3.6023					4.926
PINE_1				−0.00002					
PINE_2					6.636E−06			0.000012	
PINE_K									1.715E−06
RL_BA_1	−0.00266			−0.00527					
RL_BA_5					−0.00045				
RL_BA_K				0.000102			0.000066		
RL_CEN_1	0.00651			0.00978		0.0027			
RL_CEN_K	0.000091				0.000197	−0.00012		0.000109	
SL_BA_2		0.000704							
SL_BA_5						−0.00042			
SL_CEN_1						0.00482			
SL_CEN_K	0.000146	0.000111		0.000257	0.000265	0.000159			−0.00025
SLOPE							0.0208		

Values shown are coefficients for variables included in models indicating relative strength of relationship (i.e., magnitude of value) and whether the contribution of the variable was positive or negative (i.e., sign of coefficient).

[a] See Glossary for parameter definitions.

We interpreted increasing probability of high richness (PHR) and probability of detection (PD) over time or between scenarios to indicate a ‘‘benefit’’ for guilds and species, respectively.

Based on area under the receiver operating curve (ROC) (Hosmer and Lemeshow, 2000), the models provided acceptable discrimination among levels of richness for all birds, canopy nesters, cavity nesters, and neotropical migrants (ROC = 0.766, 0.752, 0.705, and 0.788, respectively) and excellent discrimination among levels of richness for scrub-successional species (ROC = 0.842). The models for Acadian flycatcher, blue-gray gnatcatcher, common yellow throat, and eastern wood-pewee provided excellent discrimination (ROC = 0.833, 0.853, 0.853, and 0.851, respectively) between plots where these species were and were not detected. These four species had Partners in Flight regional combined breeding season scores for the Southeastern Coastal Plain of 15, 11, 13, and 14, respectively (Panjabi et al., 2005). The Acadian flycatcher is designated by Partners in Flight as a species for which long-term planning actions are needed in the Southeastern Coastal Plain to ensure that sustainable populations are maintained. The eastern wood-pewee is designated in that region as a species requiring management or other on-the-ground conservation actions to reverse or stabilize population declines or reverse high threats. In general the coefficients in the logistic regression models were interpretable in terms of common perceptions of the habitats for the species we sampled.

2.6. ArcGIS extension for applying the wildlife models

Because the wildlife models utilize a suite of spatial variables computed at various scales, many of which change at each iteration of Habplan across all times covered by a regime for a stand, linking these models into Habplan as constraints or goals was computationally infeasible. Therefore, the wildlife models were computed externally to Habplan using the ArcGIS tool (see below) for each scenario over time using the Habplan output. Prior work that has computed spatial relations with an economic analysis (e.g., Bettinger et al., 2003) have generally done so with few spatial points, whereas we computed the wildlife value for multiple birds/guilds over thousands of points and across time.

To apply the wildlife models to the Habplan output for our study landscape, we developed an extension for ArcGIS 9.1 that automated the application of our logistic regression models to forested landscapes using standard procedures available in ArcGIS 9.1. We used the ArcGIS extension to apply our models to each simulated landscape in order to compute estimates of PD and PHR for a large number of sample points on the landscape for each 5-year increment under the seven scenarios. The tool computed, for each point on the map, the stand, neighborhood, and buffer variables used as input to the bird models (Table 1) and then for each point calculated the logistic regression p-value for species or guild from Eq. (1) (and Table 1). We used two methods to summarize the output: (1) mean p over the entire landscape and (2) percentage of the area above the geometric mean of the mean p-value and the maximum p-value.

2.7. Scenario evaluation

Economic valuation of scenarios was in terms of total harvested wood volume rather than net present value. Thus, we assumed that a decrease over time or between scenarios in total harvested wood volume reflected an economic ‘‘cost’’. All wood was considered to be pulp (saw logs or veneer from larger trees were not considered) which is reasonable for South Carolina. The rationale for using wood volume as our economic indicator without discounting or considering taxes is as follows. For land held to supply wood to a paper mill, the primary consideration is a steady wood supply. This restriction is covered by our even-flow constraint. For land under long-term contract to a mill, the same factor governs management. For governmental entities, tax issues do not apply and even flow of wood is again a major concern. Finally, we can view our analyses in terms of effects of management guidelines on wood supply. Thus we do not address the complications that result from assumptions about future stumpage prices, discount rates, and tax treatment.

In this study we were particularly interested in the economic cost (i.e., reduction in wood flow) of achieving increases in PHR and PD. We, therefore, plotted total wood volume harvested over the 40-year planning horizon versus PD for each species and PHR for each guild and for the total bird community. Wood volume was scaled to 1, with the maximum based on the unlimited cutting scenario. Wood volume was zero for the unmanaged scenario because no wood was harvested and wood volume on the road-closed scenario was slightly greater than 1 because wood was harvested from the replanted roads.

We compared costs and benefits by developing production frontier plots of PD and PHR at the end of the 40-year planning horizon versus total wood harvested over the 40 years. A production possibility frontier plot shows the response of the system to different levels of investment with diminishing returns being readily evident. For example, as more money is spent on fertilizer, corn yield increases but then levels off. The ideal management scenario for increasing wildlife habitat (defined as the amount of wildlife, in some sense, on that landscape) would be one in which we give up a small amount of wood production to gain large increases in PD, PHR, or other similar biodiversity metrics.

3. Results

For all guilds and species, changes in estimated PHR and PD were still occurring at year 40 (Fig. 4). For the total bird community (Fig. 4a), canopy nesters (Fig. 4b), cavity nesters (Fig. 4c), neotropical migrants (Fig. 4e), and the eastern wood-pewee (Fig. 4h), the unmanaged scenario produced an increase in PHR over time. However, for scrub-successional associates (Fig. 4d), it produced a decrease in PHR over time, and PD of Acadian flycatchers (Fig. 4f), common yellowthroats (Fig. 4g), and blue-gray gnatcatchers (Fig. 4i) declined over time. For the total bird community, canopy nesters, and cavity nesters, all scenarios caused a modest increase in PHR over time, although

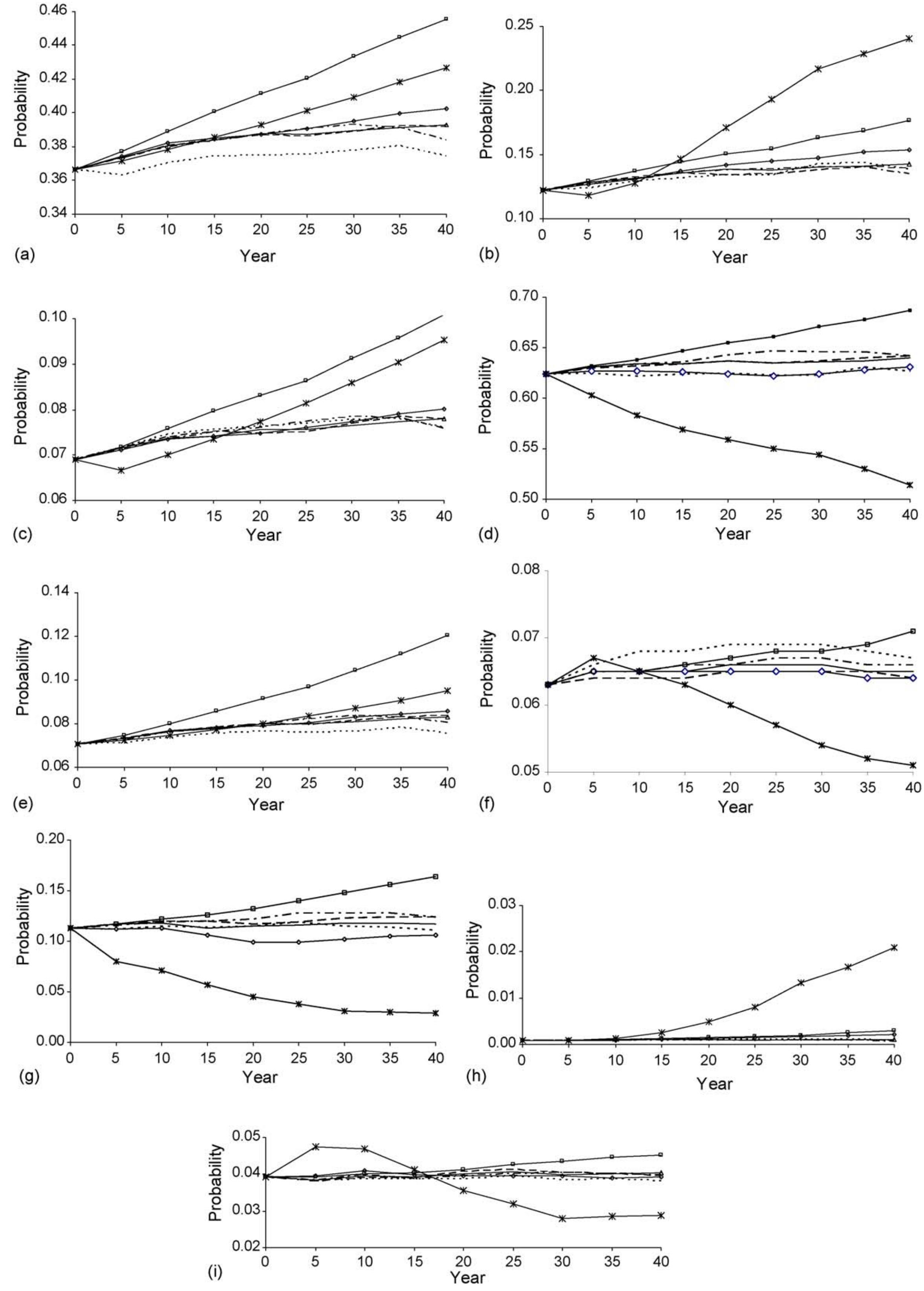

Fig. 4. Probability of high richness (all bird species and guilds) and probability of detection (species) over a 40-year planning horizon under seven different scenarios modeled for the Ashley-Edisto Districts, South Carolina. Legend: (◆) cut-120ac; (—) cut-180ac; (– – –) cut-nolim; (*) unmanaged; (□) setasides; (– – –) roadclosed; (· · ·) r50m. (a) All species; (b) canopy nesters; (c) cavity nesters; (d) shrub-successional; (e) neotropical migrants; (f) Acadian flycatchers; (g) common yellowthroats; (h) eastern wood-pewee; (i) blue-gray gnatcatcher.

not as great as for the unmanaged scenario. For the total bird community, cavity nesters, scrub-successional associates, neotropical migrants, Acadian flycatcher, blue-gray gnatcatchers, and common yellowthroats, the set-asides scenario produced the greatest increase in PHR or PD over time. It should be noted that some high-priority species used in this exercise were relatively rare on the study landscapes; three species (Acadian flycatcher, eastern wood-pewee, and blue-gray gnatcatcher) had probabilities of detection on a plot of <0.10.

For several species and guilds, the unmanaged scenario yielded the greatest improvement in richness but at the expense of 100% of the harvested wood volume (Fig. 5). The unmanaged scenario did not produce high landscape

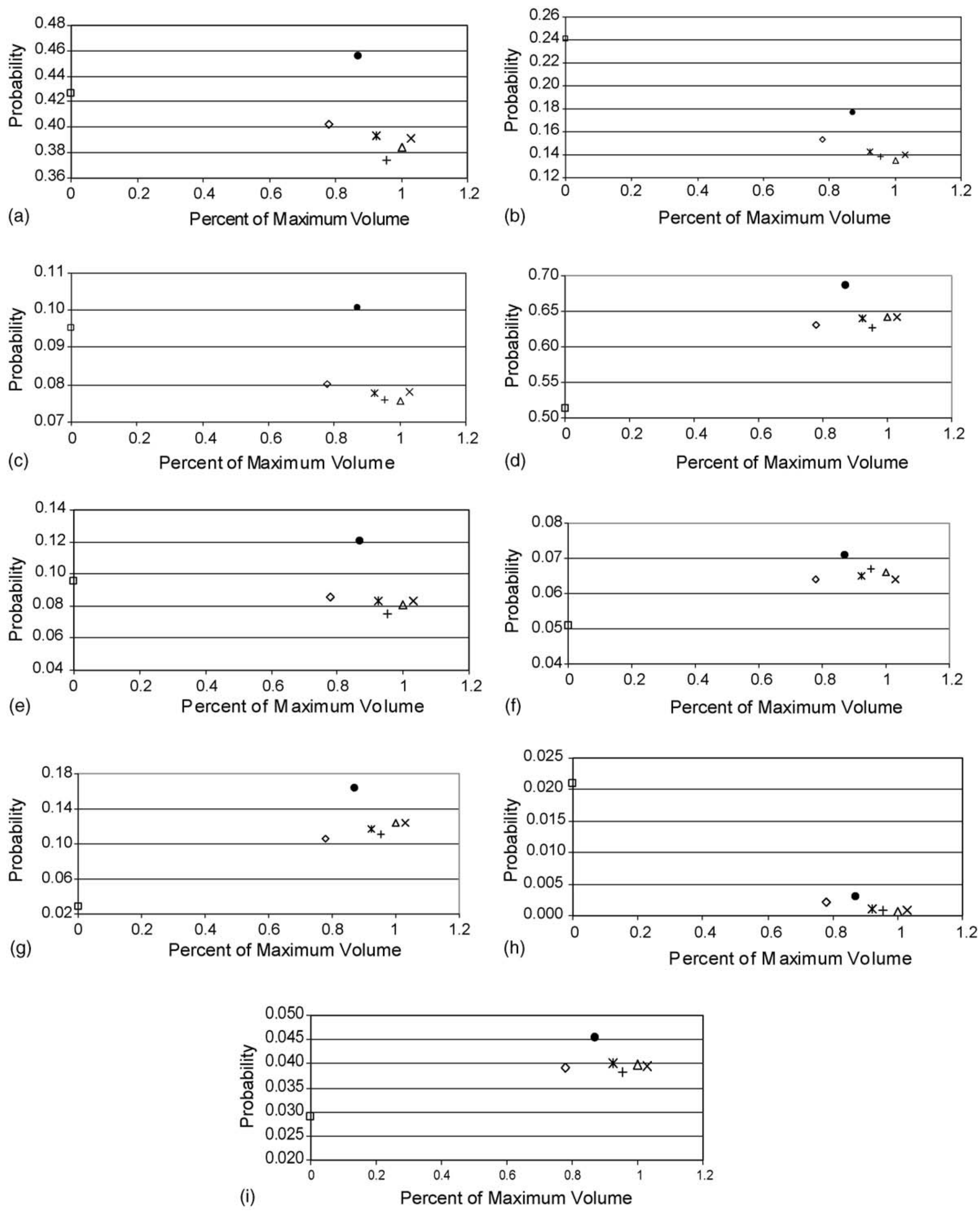

Fig. 5. Probability of high richness (all bird species and guilds) and probability of detection (species) vs. percent maximum wood production at the end of a 40-year planning horizon under seven different scenarios modeled for the Ashley-Edisto District, South Carolina. Legend: (◇) cut-120ac; (*) cut-180ac; (△) cut-nolim; (□) unmanaged; (●) setasides; (×) roadclosed; (+) r50m. (a) All species; (b) canopy nesters; (c) cavity nesters; (d) shrub-successional; (e) neotropical migrants; (f) Acadian flycatchers; (g) common yellowthroats; (h) eastern wood-pewee; (i) blue-gray gnatcatcher.

heterogeneity in this landscape and for four species/groups (Acadian flycatcher, common yellowthroat, scrub-successional associates, blue-gray gnatcatcher) the unmanaged scenario produced lower PD or PHR. In all cases, the set-asides scenario provided a favorable option for producing wildlife benefits that were greater than those of other scenarios but at the cost of a 14% reduction in wood volume. Smaller area in set-asides land would likely produce a lesser but still noticeable wildlife benefit. In most cases, the set-asides scenario was the only scenario that provided a benefit and it provided a benefit to all groups. For all species and guilds, riparian buffers had a largely neutral effect. The 48.6 and 72.9 ha restricted block size options had a small benefit for some groups, but at considerable cost, because these restrictions prevented some larger stands from being harvested (data not shown). The road conversion scenario did not have a large impact, indicating that edges caused by roads in our database did not unduly influence diversity, nor did roads *per se* cause either a positive or negative effect overall.

We also plotted for each scenario the percent of the landscape above the geometric mean p value (i.e., the percent of landscape with high index value in terms of probability of species or guild detection or density). The results of this analysis were very similar (not shown) to results described above, except that in all cases the benefit from set-asides was more dramatic than for mean habitat p values, indicating that there was an increase in the proportion of the highest index habitat. Under the set-asides scenario, neotropical migrants benefited most over the 40-year period in the lowland areas where hardwood forests were concentrated (as much of the older forest put into set-asides were in the lowlands).

4. Discussion

To date, evaluation of the biodiversity consequences of forest management has had certain limitations. Generally, studies have not considered spatial aspects of species response to habitat (e.g., Azevedo et al., 2005; Klaus et al., 2005), which we found to be significant for all species and guilds tested, or to spatial restrictions on management such as adjacency restrictions (e.g., Hynenen et al., 2005; Klaus et al., 2005; Wintle et al., 2005). When harvesting is simulated, only a few studies have considered economics (Hynenen et al., 2005) while most use a simulator such as LANDIS or HARVEST, which uses fixed regimes and makes no attempt to derive an optimal management regime (Klaus et al., 2005; Larson et al., 2004; Wintle et al., 2005). The only analysis we could locate that specifically simulated SFI® guidelines (Azevedo et al., 2005) used habitat models with no spatial component, a harvest simulator with no optimization capabilities, and did not consider any tradeoff of income versus biodiversity. Thus we believe our study improves upon the state of the art in at least four areas, including several recommended by Edenius and Mikusinski (2006). First, we utilized spatially explicit wildlife response models. Second, we used multiple measures of biodiversity (multiple species and guilds). Third, we used an optimizing harvest scheduler, Habplan, to represent realistic forest management in the context of operational restrictions (e.g., even flow of wood) and provisions of sustainable forestry certification programs. Fourth, we evaluated tradeoffs between measures of biodiversity and wood production, which is a key consideration for adoption of biodiversity goals by commercial forestry enterprises.

Our results suggest that managers could achieve some biodiversity-related objectives by increasing landscape age heterogeneity. The approach we used was extending rotations or setting aside a small portion of the landscape. This possible benefit of this strategy, particularly the benefit to all species and guilds, was unexpected. However, the habitat-relationship models for all species and guilds we used had positive coefficients for either stand age or age heterogeneity at some spatial scale (Mitchell et al., 2006). Analyses based on habitat models that include only stand-level habitat characteristics (e.g., Polasky et al., 2005) likely would not have identified this effect. Increased age heterogeneity can be achieved on a landscape at no cost to commercial forest operations when late-rotation public or nonindustrial private holdings or non-commercial lands (e.g., parks) are interspersed with commercial forest lands, even if these lands are managed for other purposes (e.g., recreation). Costs can be reduced for increasing age heterogeneity within commercial forest ownerships by managing selected areas for long-rotation, high-quality wood, if such an option exists.

In addition to protecting water quality, riparian buffers also can function as set-asides, even though in our study they did not achieve the status of "older" forest over our 40-year planning horizon. Furthermore, our riparian buffers were not equivalent to the set-asides because many of our set-asides were in pine. Regardless, riparian buffers in the South generally are dominated by older hardwood forests that provide many habitat features (e.g., large hardwood trees) not commonly found in pine-dominated landscapes (Melchiors and Cicero, 1987; Wigley and Melchiors, 1994). Riparian buffers can even be managed for high-value wood products in some cases. It is possible, of course, that our results may have differed for riparian buffers of different width, age structure, or species composition. In addition, in this landscape there were many small isolated wetlands, which likely obscured the distinction between riparian and upland forests (Turner et al., 2002). This may be why so few species showed a response to stream variables in the habitat models.

The other scenarios apparently provided little benefit to the breeding birds we modeled. For example, in contrast to expectations, the restricted block size scenarios (requiring smaller harvest units) did not generate any benefits. Thus, block size restrictions may be most appropriate for meeting aesthetic objectives rather than biological objectives. While complete cessation of management for 40 years benefited some species, our simulations suggested a negative impact on other species and guilds and clearly would not be economically viable for commercial forests. Of course, different results from these scenarios may accrue to other taxa (e.g., amphibians) or to bird species not modeled here.

Because the primary purpose of our study was to demonstrate an approach to forest planning that integrates economic and ecological considerations, we urge caution when interpreting our results. It may be best to view our results as raising questions rather than providing an exact test of alternative management guidelines. The scenarios we developed obviously are not exactly what would occur on a landscape. The bird models developed by Mitchell et al. (2006) provided acceptable to excellent discrimination among levels of richness or probabilities of detection, but no doubt failed to accurately capture all bird responses to habitat such as reproductive success and likely do not represent responses by some other taxa (e.g., amphibians). Additionally, the bird models were generated at a regional scale and were relatively insensitive to some changes that could occur within a single managed forest. Patterns in avian richness and distributions revealed in our analyses should be interpreted solely for their heuristic value in comparing management scenarios. We suggest additional studies before rigorous conclusions regarding relationships between biodiversity and forest management can be drawn.

However, our results do suggest that our approach to using wildlife-habitat relationship models in concert with output from harvest scheduling software is promising even though more work is needed. Habitat models that consider landscape-scale variables would be most useful to managers if incorporated into spatially explicit harvest schedulers where biodiversity metrics such as PD or PHR could be considered simultaneously with wood flow or economic variables (whereas we computed these metrics externally to Habplan). Such an integration would allow forest managers to directly assess tradeoffs and synergies between objectives for timber management and those for the conservation of wildlife, with the potential for arriving at optimal or near-optimal solutions. Achieving this integration, however, will require overcoming several important challenges. For example, adding components such as wildlife models into a spatially explicit harvest scheduler greatly increases the time needed to accomplish each iteration and scheduling problems can then easily overwhelm the capabilities of current hardware (Wigley et al., 2001). Thus, while not ideal, our approach is an important first step. The addition of population viability analyses (e.g., Larson et al., 2004; Wintle et al., 2005) would further enhance our approach but also would be very computationally demanding.

Acknowledgments

The project was funded by a grant from the National Commission on Science for Sustainable Forestry to the National Council for Air and Stream Improvement, Inc. We thank the many organizations that provided funding and logistical support during prior field studies, including Alabama Cooperative Fish and Wildlife Research Unit, International Paper Company, MeadWestvaco Corporation, National Council for Air and Stream Improvement, Inc., North Carolina State Museum of Natural Science, North Carolina State University, Oklahoma State University, University of Arkansas-Monticello, USDA Forest Service, Virginia Tech University, West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia Division of Natural Resources, West Virginia University, and Weyerhaeuser Company. Helpful comments were provided by Eric Gustafson and Thomas Spies.

References

Arthaud, G.J., Rose, D.W., 1996. A methodology for estimating production possibility frontiers for wildlife habitat and timber value at the landscape level. Can. J. For. Res. 26, 2191–2200.

Azevedo, J.C., Wu, X.B., Messina, M.G., Fisher, R.F., 2005. Assessment of sustainability in intensively managed forested landscapes: a case study in eastern Texas. For. Sci. 51, 321–333.

Barrett, T.M., Gilless, J.K., Davis, L.S., 1998. Economic and fragmentation effects of clearcut restrictions. For. Sci. 44, 569–577.

Baskent, E.Z., Jordan, G.A., 2002. Forest landscape management modeling using simulated annealing. For. Ecol. Manage. 165, 29–45.

Bertomeu, M., Romero, C., 2001. Managing forest biodiversity: a zero-one goal programming approach. Agric. Syst. 68, 197–213.

Bettinger, P., Johnson, D.L., Johnson, K.N., 2003. Spatial forest plan development with ecological and economic goals. Ecol. Modell. 169, 215–236.

Brender, E.V., Clutter, J.L., 1970. Yield of even-aged, natural stands of loblolly pine. Report No. 23. Georgia Forest Research Council.

Calkin, D.E., Montgomery, C.A., Schumaker, N.H., Polasky, S., Arthur, J.L., Nalle, D.J., 2002. Developing a production possibility set of wildlife species persistence and timber harvest value. Can. J. For. Res. 32, 1329–1342.

Carter, D.R., Vogiatzis, M., Moss, C.B., Arvanitis, L.G., 1997. Ecosystem management or infeasible guidelines? Implications of adjacency restrictions for wildlife habitat and timber production. Can. J. For. Res. 27, 1302–1310.

Crowe, K.A., Nelson, J.D., 2005. An evaluation of the simulated annealing algorithm for solving the area-restricted harvest-scheduling model against optimal benchmarks. Can. J. For. Res. 36, 2500–2509.

Edenius, L., Mikusinski, G., 2006. Utility of habitat suitability models as biodiversity assessment tools in forest management. Scand. J. For. Res. 21 (Suppl.), 62–72.

Gustafson, E.J., Rasmussen, L.V., 2002. Assessing the spatial implications of interactions among strategic forest management options using a Windows-based harvest simulator. Comput. Electron. Agric. 33, 179–196.

Hannon, S.J., Schmiegelow, K.A., 2002. Corridors may not improve the conservation value of small reserves for most boreal birds. Ecol. Appl. 12 (5), 1457–1468.

Harrison, W.M., Borders, B.E., 1996. Yield prediction and growth projection for site-prepared loblolly pine plantations in the Carolinas, Georgia, Alabama and Florida. PMRC Technical Report 1996-1. University of Georgia.

Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression, 2nd ed. John Wiley and Sons, Inc., New York, NY, USA.

Hummel, S., Calkin, D.E., 2005. Costs of landscape silviculture for fire and habitat management. For. Ecol. Manage. 207, 385–404.

Hynenen, J., Ahtikoski, A., Siitonen, J., Sievänen, R., Liski, J., 2005. Applying the MOTTI simulator to analyse the effects of alternative management schedules on timber and non-timber production. For. Ecol. Manage. 207, 5–18.

Kant, S., 2002. The marginal cost of structural diversity of mixed uneven-aged hard maple forests. Can. J. For. Res. 32, 616–628.

Klaus, N.A., Buehler, D.A., Saxton, A.M., 2005. Forest management alternatives and songbird breeding habitat on the Cherokee National Forests, Tennessee. J. Wildl. Manage. 69, 222–234.

Larson, M.A., Dijak, W.D., Thompson III, F.R., Millspaugh, J.J., 2003. Landscape-level habitat suitability models for twelve species in southern Missouri. General Technical Report, NC-233. USDA Forest Service, North Central Research Station, St. Paul, MN.

Larson, M.A., Thompson III, F.R., Millspaugh, J.J., Dijak, W.D., Shifley, S.R., 2004. Linking population viability, habitat suitability, and landscape simulation models for conservation planning. Ecol. Modell. 180, 103–118.

Li, H., Gartner, D.I., Mou, P., Trettin, C.C., 2000. A landscape model (LEEMATH) to evaluate effects of management impacts on timber and wildlife habitat. Comput. Electron. Agric. 27, 263–292.

Liu, G., Nelson, J.D., Wardman, C.W., 2000. A target-oriented approach to forest ecosystem design—changing the rules of forest planning. Ecol. Modell. 127, 269–281.

Loehle, C., MacCracken, J.G., Runde, D., Hicks, L., 2002. Forest management at landscape scales—solving problems. J. For. 100 (6), 25–33.

Loehle, C., Wigley, T.B., Rutzmoser, S., Gerwin, J.A., Keyser, P.D., Lancia, R.A., Reynolds, C.J., Thill, R.E., Weih, R., White Jr., D., Wood, P.B., 2005. Managed forest landscape structure and avian species richness in the Southeastern US. For. Ecol. Manage. 214, 279–293.

Maness, T., Farrell, R., 2004. A multi-objective scenario evaluation model for sustainable forest management using criteria and indicators. Can. J. For. Res. 34, 2004–2017.

Maurer, B.A., Villard, M., 1994. Population density: geographic variation in abundance of North American birds. Natl. Geogr. Res. Exploration 10, 306–317.

Melchiors, M.A., Cicero, C., 1987. Streamside and adjacent upland forest habitats in the Ouachita Mountains. Proc. Annu. Conf. Southeastern Assoc. Fish Wildl. Agencies 41, 385–393.

Metropolis, N., Rosenbluth, A., Rosenbluth, M., Teller, A., Teller, E., 1953. Equation of state calculations by fast computing machines. J. Chem. Phys. 21, 1087–1091.

Mitchell, M.S., Lancia, R.A., Gerwin, J.A., 2001. Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. Ecol. Appl. 11, 1692–1708.

Mitchell, M.S., Rutzmoser, S.H., Wigley, T.B., Loehle, C., Gerwin, J.A., Keyser, P.D., Lancia, R.A., Perry, R.W., Reynolds, C.J., Thill, R.E., Weih, R., White Jr., D., Wood, P.B., 2006. Relationships between avian richness and landscape structure at multiple scales using multiple landscapes. For. Ecol. Manage. 221, 155–169.

Nieuwenhuis, M., Tiernan, D., 2005. The impact of the introduction of sustainable forest management objectives on the optimization of PC-based forest-level harvest schedules. For. Policy Econ. 7, 689–701.

Ohman, K., 2000. Creating continuous areas of old forest in long-term forest planning. Can. J. For. Res. 30, 1817–1823.

Onal, H., Algozin, K.A., Isik, M., Hornbaker, R.H., 1998. Economically efficient watershed management with environmental impact and income distribution goals. J. Environ. Manage. 53, 241–253.

Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., Starfield, A., 2005. Conserving species in a working landscape: land use with biological and economic objectives. Ecol. Appl. 15 (4), 1387–1401.

Panjabi, A.O., Dunn, E.H., Blancher, P.J., Hunter, W.C., Altman, B., Bart, J., Beardmore, C.J., Berlanga, H., Butcher, G.S., Davis, S.K., Demarest, D.W., Dettmers, R., Easton, W., Gomez de Silva Garza, H., Iñigo-Elias, E.E., Pashley, D.N., Ralph, C.J., Rich, T.D., Rosenberg, K.V., Rustay, C.M., Ruth, J.M., Wendt, J.S., Will, T.C., 2005. The Partners in Flight Handbook on Species Assessment, Version 2005. Partners in Flight Technical Series No. 3. Rocky Mountain Bird Observatory website: http://www.rmbo.org/pubs/downloads/Handbook2005.pdf.

Rempel, R.S., Kaufmann, C.K., 2003. Spatial modeling of harvest constraints on wood supply versus wildlife habitat objectives. Environ. Manage. 32 (3), 334–347.

SAS Institute, 1990. SAS/STAT User's Guide, Version 6. SAS Institute, Cary, NC, USA.

Sustainable Forestry Board, 2005. Sustainable Forestry Initiative® (SFI®) Standard 2005–2009 Edition. Sustainable Forestry Board, Arlington, VA. , In: http://www.aboutsfb.org.

Turner, J.C., Gerwin, J.A., Lancia, R.A., 2002. Influences of hardwood stand size and adjacency on breeding bird communities in an intensively managed pine landscape. For. Sci. 48 (2), 323–330.

Van Deusen, P., 1996. Habitat and harvest scheduling using Bayesian statistical concepts. Can. J. For. Res. 26, 1375–1383.

Van Deusen, P., 1999. Multiple solution harvest scheduling. Silva Fennica 33 (3), 207–216.

Van Deusen, P.C., 2001. Scheduling spatial arrangement and harvest simultaneously. Silva Fennica 35 (1), 85–92.

Villard, M., Merriam, G., Maurer, B.A., 1995. Dynamics in subdivided populations of neotropical migratory birds in a fragmented temperate forest. Ecology 76, 27–40.

Wiens, J.A., 1995. Habitat fragmentation: Island vs. landscape perspectives on bird conservation. Ibis 137, S97–S104.

Wigley, T.B., Melchiors, M.A., 1994. Wildlife habitat and communities in streamside management zones: a literature review for the eastern United States. In: Proceeding of the Conference on Riparian Ecosystems in the Humid U.S.: Functions, Values and Management, National Association of Conservation Districts, Washington, DC, pp. 100–121.

Wigley, T.B., Mitchell, M.S., Van Deusen, P.C., Lancia, R.A., 2001. Tools for blending economic and ecological objectives on private forestlands. Trans. N. Am. Wildl. Nat. Resour. Conf. 66, 61–76.

Wikstrom, P., Eriksson, L.O., 2000. Solving the stand management problem under biodiversity-related considerations. For. Ecol. Manage. 126, 361–376.

Wintle, B.A., Bekessy, S., Venier, L.A., Pearce, J.L., Chisholm, R.A., 2005. Utility of dynamic-landscape metapopulation models for sustainable forest management. Conserv. Biol. 19, 1930–1943.

Zhou, W., Gong, P., 2005. Multiple-use tradeoffs in Swedish mountain region forests. For. Policy Econ. 7, 39–52.

Glossary

The suffix (n) indicates the scale of the measurement—1: 100 m, 2: 250 m, 5: 500 m, K = 1 km. Patches refer to operational stands.

AC5_n: Area of the neighborhood composed of forests 0–4 years old, including forests that had been harvested but not yet site prepared or planted.

AC30_n: Area of the neighborhood composed of forests 5–30 years old.

AGE_STD_n: Standard deviation of the mean age of forests in the neighborhood, weighted by area (m^2).

ASPECT: Aspect of the sample point (orientation in degrees towards north for the plot). Calculated from 30 m digital elevation model and surrounding pixels using the ''Aspect'' command of ESRI's ArcGIS 9.1 software. For univariate and logistic regression analyses, we transformed aspect according to Beers et al. (1966) using the following equation: transformed aspect = COS(45 × (PI(·)/180) − ASPCT × (PI(·)/180)) + 1. The transformed aspect ranged from 0 (225°) to 2 (45°).

CURV: Net curvature for the sample point, range −1: concave (collecting water) to 1: convex (shedding water). Calculated from 30 m digital elevation model and surrounding pixels using the ''pSurfaceOp.Curvature'' command of ESRI's ArcGIS 9.1 software.

DST2_RDS_A: Distance (m) to nearest road feature. This refers to all road features and uses 1:24,000 scale datasets derived from USGS topographic maps and/or supplied by landowners.

DST2_WTR_A: Distance (m) to nearest water feature. This refers to all water features and uses 1:24,000 scale datasets derived from USGS topographic maps.

DST2_WTR_C: Distance (m) to nearest water feature. This refers only to water features included in the US Census Bureau's hydrology coverage (1:100,000 scale).

EVNS_n: Evenness of landscape, using overstory classification and area (m^2).

FRGAC_n: Mean fragmentation of age class for the neighborhood calculated using a raster fragmentation formula. Age classifications—Class 1: 0–5; Class 2: 6–12; Class 3: 13–20; Class 4: 21–30; Class 5: >30. For age class ''ac'' and buffer size ''n'', the index is calculated as: Raster formula: $\text{FRGAC\_}n = 1 - \frac{s_{ac}}{N}$, where N is the total number of possible comparisons made at scale n, s the number of comparisons where neighboring pixels are similar for stand age class ''ac'' at scale n.

HARD_n: Area of the neighborhood classified as hardwood forest.

INTERCEPT: β_0 in the logistic equation.

IS_AGE: Individual stand age in years.

IS_AREA: Individual stand area (m^2 in the logistic regression equations) of the stand where the species count was conducted.

LANDPO_n: Landscape position. The relative position of the sample location on the landscape. LANDPO quantified the degree to which the observation location was exposed (ridge) or sheltered (valley) relative to the surrounding landscape, at various scales. Positive values indicate exposed and negative values indicate sheltered. It was estimated using the following equation: $\text{LANDPO\_}n = \frac{E}{\text{MA}+(E-\text{MA}/\text{Abs}(E-\text{MA})\times S)} - 1$, where E is the elevation at sample location, MA the mean elevation of an annulus around the sample location. The radius of this annulus varies with scale n. The term annulus refers to a hollow ring and S is the standard deviation, for the entire landscape, of MA + E.

M_AGE_n: Mean age of forests in the neighborhood.

MIX_n: Area of the neighborhood classified as mixed pine–hardwood forest.

NON_n: Area of the neighborhood classified as perpetual non-forest (agriculture, rights-of-way, etc.).

PFRGM_n: Fragmentation index based on forest type. PFRGM was calculated as the average of two fragmentation indices, PFRGA (fragmentation of forest type using relative patch area) and PFRGL (fragmentation of forest type using relative patch length to area ratios). We used an average of both indices to consider both variation in patch size and the complexities pertaining to the shape of the patches within a neighborhood. PFRGA (fragmentation index based on area) was computed using the following equation for s patches within a buffer: $\mathrm{PFRGA} = 1 - \frac{\sum_{i=1}^{s} \text{area of path}_i}{\text{total buffer area}}$. PFRGL (fragmentation index based on length/area ratios) was calculated using the following equation: $\mathrm{PFRGA} = 1 - \frac{\text{minimum buffer ratio}}{\text{buffer ratio}}$. Buffer ratio was computed as follows: $\text{buffer ratio} = 1 - \frac{\sum_{i=1}^{s} \text{length of path}_i + \text{perimeter length of buffer}}{2 \times \text{total buffer area}}$. Perimeter length of the neighborhood/buffer was derived by summing the perimeter length of each patch within the neighborhood. Because interior patches bordered each other, their length was counted twice. Therefore, we corrected by adding the perimeter length of the buffer and dividing by 2. Minimum buffer ratio was computed as follows: $\text{minimum buffer ratio} = \frac{\text{perimeter length of buffer}}{\text{total buffer area}}$. Because the neighborhoods are circular, we standardized the buffer ratio using the ratio of a simple Euclidean shape (a circle).

PINE_n: Area of the neighborhood classified as pine forest.

RL_BA_n: Road length based on 1:24,000 data.

RL_CEN_n: Road length based on US Census Bureau's road coverage. Approximately 1:100,000 scale, and includes all major and secondary roads as well as most larger access roads.

SL_BA_n: Stream length based on 1:24,000 scale datasets derived from USGS topographic maps. The dataset includes major tributaries and water bodies as well as small streams, ponds, and manmade canals.

SL_CEN_n: Steam length based on water features included in the US Census Bureau's hydrology coverage. The scale is 1:100,000 and includes major tributaries and water bodies.

SLOPE: Mean slope for the plot (bird sample location). Calculated from 30 m digital elevation model and surrounding pixels using the surface_operator.slope command that is available in ESRI's ArcGIS 9.1 software.