ELSEVIER

Computers and Electronics in Agriculture
27 (2000) 263-292

Computers
and electronics
in agriculture

www.elsevier.com/locate/compag

A landscape model (LEEMATH) to evaluate effects of management impacts on timber and wildlife habitat

Harbin Li [a,*], David I. Gartner [a], Pu Mou [b], Carl C. Trettin [a]

[a] *USDA Forest Service Center for Forested Wetlands Research, 2730 Savannah Highway, Charleston, SC 29414, USA*

[b] *Department of Forestry, Virginia Tech University, Blacksburg, VA, USA*

Abstract

Managing forest resources for sustainability requires the successful integration of economic and ecological goals. To attain such integration, land managers need decision support tools that incorporate science, land-use strategies, and policy options to assess resources sustainability at large scales. Landscape Evaluation of Effects of Management Activities on Timber and Habitat (LEEMATH) is a tool for evaluating alternative management strategies from both economic and ecological perspectives. The current version of LEEMATH emphasizes timber production and wildlife habitat in industrial forest landscapes. LEEMATH provides a framework upon which various models can be integrated. It is generic because it is designed to model stand growth, habitat attribute, and habitat suitability as they exist generally throughout the American Southeast. It is dynamic because it examines effects of management strategies on timber production and habitat quality over time, especially the balance between habitat loss and regrowth at the landscape scale. It is spatially explicit because it evaluates landscape configuration for its effects on habitat in terms of adjacency requirements and dispersal potential. It is heuristic because it simulates the dynamics of forest stands under different management scenarios and allows land managers to ask 'WHAT-IF' questions to explore management alternatives and their possible effects over time. In this paper, we discuss how to integrate different models into a decision-support system, and how to evaluate habitat suitability at the landscape level. We also discuss the gaps in our knowledge of landscape habitat assessment and the limitations of LEEMATH.

---

* Corresponding author. Tel.: + 1-843-7274271; fax: + 1-843-7274152.
E-mail address: lih@cofc.edu (H. Li)

0168-1699/00/$ - see front matter Published by Elsevier Science B.V
PII: S0168-1699(00)00088-0

Finally, we apply LEEMATH to a forested landscape on the coastal plain of South Carolina, USA, to demonstrate its usefulness in management planning with multiple interests. We show the effects of two management regimes on timber production, habitat attribute dynamics, and habitat quality of three target wildlife species at both the stand and the landscape scales. Published by Elsevier Science B.V.

Keywords: Ecosystem management; Landscape; Decision-support system; Sustainable forestry; Habitat attribute model; Habitat suitability

---

1. Introduction

Ecosystem management is a commonly perceived approach to ensuring the sustainability of natural resources (Franklin, 1993; Salwasser, 1994; Christensen et al., 1996). Managing forested landscapes for both ‘goods’ (timber, food, forage, game species) and ‘services’ (providing wildlife habitat, maintaining biogeochemical and hydrological cycles, generating and maintaining soil) is key to sustaining natural resources (Lubchenco et al., 1991; Christensen et al., 1996). While a consensus on its precise definition remains elusive, some basic tenets of ecosystem management have emerged (Salwasser, 1994; Berlyn and Ashton, 1996; Christensen et al., 1996; Lele and Norgaard, 1996; Grumbine, 1997). First, ecosystem management is based on ecological principles. These ecological principles describe how the physical (i.e. solar energy, water, climate) and biological (i.e. food chains, trophic levels, succession) components of ecosystems function and interact, and what potentials and consequences an ecosystem may reach as a result of a given set of management decisions (Salwasser, 1994; Christensen et al., 1996). Second, ecosystem management must consider values, social goals, and other socio-economic factors that translate into policies and, ultimately, management priorities and decisions (Salwasser, 1994; Lele and Norgaard, 1996; Haynes and Weigand, 1997). Third, ecosystem management requires that scientists, economists, land managers, and the public collaborate to set priorities that will balance the conflicting goals of a pluralistic society (Salwasser, 1994). Thus, ecosystem management decisions must be made in the context of ecological, economic, social, political, and legal parameters (Grumbine, 1997). Maser (1994, p. 309) provided an operational definition of ecosystem management: “[It is an] ecosystem approach to making, implementing, and evaluating decisions, by recognizing the interactions and interrelationships among different components (integrating parts), by understanding the relation between the system and its context, and by balancing the production and maintenance of ecosystem goods and services”.

Sustainable forest management will depend on successful integration of economic and ecological goals. Such integration can be a very complex process (Haynes and Weigand, 1997; Kohm and Franklin, 1997). It will require tools that integrate biophysical and economic systems to provide ecological and economic evaluations of forestry operations where timely information is necessary, but experimentation in the field or laboratory cannot be done because of time, money, scale, or ethics. Because of the increasing and often conflicting demands on a limited land base, land managers are asking: How can we manage forest landscapes to obtain maximum benefits while ensuring the integrity of the natural resources on which these benefits are based? Decision-support systems are tools that can help answer this question.

In this paper, we present Landscape Evaluation of Effects of Management Activities on Timber and Habitat (LEEMATH), a decision-support tool that has been designed to balance economic and ecological constraints in the management of forest resources. As a generic, spatially explicit, and dynamic model, LEEMATH simulates timber harvest and growth, habitat loss and regrowth, and habitat quality for birds, reptiles, and amphibians in managed forest landscapes in Southeastern USA. Such decision-support systems provide a new way to synthesize scientific information from multiple disciplines and to deliver necessary information to those who are charged to effectively manage natural resources for multiple objectives (Mower et al., 1997; Rauscher, 1999). The current version of LEEMATH deals only with timber production and wildlife habitat in managed landscapes, although other factors embraced in the ecosystem management concept will be considered in the future (e.g. detailed economic analysis, social values, water quality). This paper describes the modeling approaches and the model structure of LEEMATH, and, by means of a simulation experiment with an industrial forest landscape on the coastal plains of South Carolina, USA, shows how it can be used in land management planning. We also discuss some lessons learned, especially about the gaps in our knowledge of landscape habitat assessment.

2. Model description

2.1. Modeling approach

The central idea of LEEMATH is to bring both environmental and economic perspectives into forest management planning to assist decision-making (Fig. 1). In LEEMATH, we are developing a general framework upon which expert systems, empirical models, mechanistic models, and spatial analysis can be integrated to help implement the principles of ecosystem management.

LEEMATH has four major characteristics. It is generic because it is designed to model stand growth, habitat attribute, and habitat suitability as they exist generally throughout the American Southeast. It handles site-specific elements as input data, instead of as model parameters. The information flow between modules is minimized to reduce their dependence so that the stand and habitat models may be replaced by models better suited to specific conditions or applications. It is dynamic because it examines effects of management strategies on timber production and habitat quality in the whole landscape over time. At the stand scale, significant change may result from natural processes (e.g. stand growth, succession, wild fire) and management activities (e.g. thinning, fertilization). Habitat loss and habitat regrowth are associated with the processes of stand growth and succession. At the landscape scale, balance between habitat loss in some stands and habitat regrowth in others may be crucial to the long-term persistence of many wildlife species. It is spatially explicit because it evaluates landscape configuration for its effects on habitat in terms of adjacency requirements and dispersal potential. Most current landscape models do not consider landscape structure (i.e. nonspatial), even though some are coupled with geographic information systems (GIS) (Benson and Laudenslayer, 1986; Brand et al., 1986; Davis and DeLain, 1986; Burgman et al., 1994; Mower et al., 1997). We incorporate landscape structure into habitat evaluation and management planning in the model so that effects of the spatial configuration on wildlife habitats and timber production can be examined. It is heuristic because it simulates the dynamics of forest stands under different management scenarios (i.e. different simulation conditions) and allows land managers to ask 'WHAT-IF' questions to explore management alternatives and their possible effects over time. Thus, the model can be used as a tool to implement the ecosystem management concept.

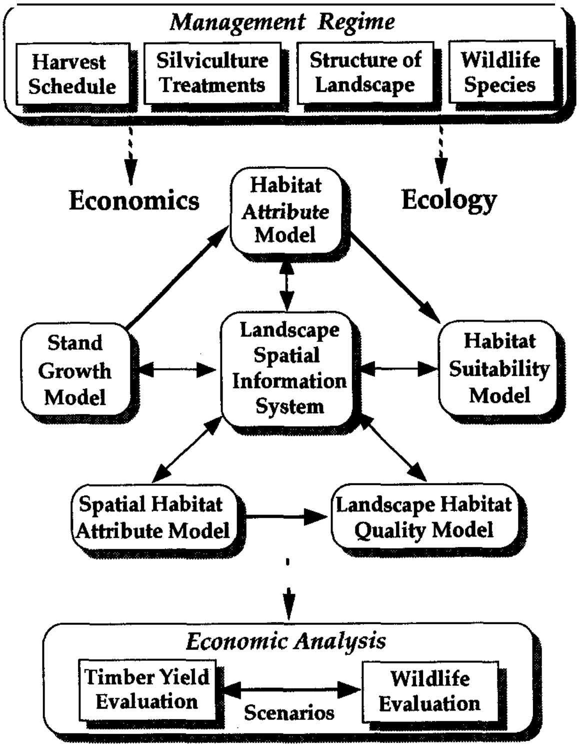

Fig. 1. The conceptual structure of a decision support tool (LEEMATH) for landscape evaluation of effects of management activities on timber and habitat.

2.2. Model structure and components

LEEMATH is composed of expert systems, empirical models, mechanistic models, and spatial analysis. It is coded in FORTRAN. Fig. 1 shows the conceptual structure, displaying its eight major modules, as well as the information flow among modules. We now describe each of the modules in detail.

2.2.1. Management regime

A management regime is a set of management objectives and activities that define possible management scenarios. In LEEMATH, this includes: (1) a harvest schedule, (2) a silviculture treatment plan, (3) a desired spatial distribution of stands, and (4) a target wildlife species list. The harvest schedule and the silviculture treatment plan are part of the traditional management planning. The harvest schedule is used to determine when, where, and how much timber can be harvested from the landscape (for example, Van Deusen, 1996). LEEMATH can use harvest schedules that are either a product of forest management planning or an output from a rule-based model. The silviculture treatment plan is used to consider what treatments (e.g. site preparation, thinning, burning, herbicide, fertilization) should be applied to a stand and when they should be applied. Like the harvest schedule, LEEMATH uses the output from rule-based models when a real silviculture treatment plan is not available. On the other hand, the desired spatial distribution of stands and the target species list are environmental considerations that constrain the planning process. The desired spatial distribution of stands is the landscape configuration that land managers may wish to implement to reflect the ecological perspectives on best management practices (Freemark et al., 1995; McCarthy and Burgman, 1995; Wiens, 1995; Hunter, 1997). Examples of the desirable landscape configuration include corridor systems (i.e. networks of linear habitat to facilitate species dispersal), stream-side management zones (i.e. protected buffer zones along streams), forest cutting patterns (i.e. systems to distribute clear cuts in the landscape), and the maximum cutting size of contiguous stands. The target species list enumerates those wildlife species selected for evaluation or protection.

Timber harvest is the major force that shapes vegetation change in a managed forest landscape, and vegetation change sets the context in which habitat dynamics for each wildlife species take shape. In LEEMATH, a simple model was developed as a default to generate harvest schedules for simulation when real, user-defined management plans are not available or when a heuristic examination of alternative harvest schedules is desirable. The model is rule-based with control variables on: (1) timber flow, (2) rotation age, and (3) adjacency. An even timber flow over time may be a desirable management output. However, the harvest scheduling model does not directly control timber flow, but, rather, the total harvest area (e.g. 600 hectares) at a given time. Rotation age is controlled for pine and hardwood stands separately (e.g. 30 years for pine and 60 years for hardwood stands). Adjacency is one of the factors that define the desired spatial structure of managed landscapes. The adjacency rule proposed in the Sustainable Forestry Initiative by the American Forest and Paper Association (1994) was adopted in the model. It states that, on average, a contiguous patch of clearcut stands should not exceed a certain size (e.g. 50 hectares) within a 3-year period.

2.2.2. Stand growth module

The current version of LEEMATH uses one pine model to represent all pine forests, one hardwood model to represent all hardwood forests, and the combination of the two models to represent mixed forests. LEEMATH has to deal with more than 14 forest types (Hamel, 1992; Wilson, 1995) but no growth models have been developed for many of them. This may cause problems in accurately predicting stand growth. A possible solution may be to use an individual tree model that can handle most of the common pine and hardwood species in a given region. The pine model in LEEMATH is for loblolly pine (*Pinus taeda)* plantations. It is a diameter distribution model created by Clutter et al. (1984) for unthinned loblolly pine plantations on the coastal plain of North and South Carolina, Georgia, and Florida. It uses stand age, basal area, and the Weibull probability density function to predict dominant tree height, density, and basal area for each diameter class. This model fits whole stand volume data reasonably well for the spacing most commonly used in loblolly pine plantations (ca. 3 m; Buford, 1991). The hardwood model in LEEMATH is for sweetgum *(Liquidambar styraciflua*), which is a whole stand model created by Kenney (1983) for piedmont bottomland hardwood stands with a large proportion of sweetgum in North and South Carolina, Virginia, Georgia, and Alabama. The sweetgum model uses site index, stand age, and the basal area at the previous year to predict dominant tree height, density, and basal area.

2.2.3. Habitat attribute module

Habitat attributes are those structural features that are related to food, shelter, and other physical habitat characteristics necessary for the reproduction and survival of wildlife species (Schamberger and O'Neil, 1986; Hamel, 1992). The habitat attribute module in LEEMATH projects habitat dynamics at the stand scale, considering habitat characteristics such as canopy closure, understory vegetation, snags, coarse woody debris, litter biomass, and vertical structure. These habitat characteristics are necessary components of habitat suitability models, but most are not available from stand growth models. To assess successfully the effects of forest management on wildlife habitats, we must be able to predict changes in habitat attributes at different developmental stages of stands and under different silvicultural treatments (Smith et al., 1981; Moeur, 1986; Urban and Smith, 1989; Teck et al., 1996). Few field studies have focused on this problem (Moeur, 1986), so we developed habitat attribute models using both empirical and mechanistic approaches to bridge gaps between growth and habitat suitability models (H. Li, P. Mou, unpublished manuscript). The empirical approach is based on relationships between habitat attributes and some stand characteristics (e.g. stand age, type, basal area) (Harmon et al., 1986; Tappe et al., 1992). The mechanistic approach is based on individually based and spatially explicit model of forest stand dynamics, REGROW (Wu et al., 1985; Mou and Fahey, 1993; Mou et al., 1993). Similar to

SORTIE by Pacala et al. (1993) and ZELIG by Smith and Urban (1988), REGROW focuses on the spatial distributions and dynamics of plant species, canopy cover, and various physical characteristics (e.g. light, soil water, nutrients) at a fine scale. The main advantages of the mechanistic approach are that it allows extrapolation of models in systems for which not many data are available, and that it can provide fine-scaled information necessary to habitat evaluation of some amphibians and reptiles.

2.2.4. Habitat suitability module

The habitat suitability module assesses a stand's habitat potential by comparing current habitat attribute conditions and the known habitat requirements by the species. Habitat requirements usually consist of observed species associations with certain habitat features (Schamberger and O'Neil, 1986). LEEMATH examines the structural characteristics of habitat, rather than species population dynamics or carrying capacity (Schamberger and O'Neil, 1986). This is because our current knowledge base about species habitat selection and movement is limited and highly uncertain (Wiens, 1995). We assumed that, given time, the populations of target species would recolonize stands when they became suitable habitat again.

The habitat suitability module in LEEMATH is based on two expert systems, developed and compiled by Hamel (1992) for 253 bird species, and by Wilson (1995) for 241 amphibian and reptile species in Southern USA. Each expert system consists of a database of individual species' habitat requirements and an evaluation scheme. The database is the habitat matrices that reflect known habitat requirements in four categories: (1) forest type and stand developmental stages, (2) vertical structure by birds, (3) physiographic features by amphibians and reptiles, and (4) specific habitat features. Such models are often referred to as wildlife habitat relationship models (Dedon et al., 1986). The successful use of LEEMATH will require updating these habitat matrices whenever new information becomes available. The evaluation scheme for determining habitat quality at the stand scale is based on ranking provided in the habitat matrices (Hamel, 1992; Wilson, 1995). First, a combination of the two principal factors, forest type and stand developmental stage, is used to determine the initial habitat rank of a stand for a given species (i.e. optimal, suitable, marginal, or nonhabitat). Then, additional factors (e.g. vertical structure, physiographic features, within-stand specific habitat requirements) are considered to determine the predicted habitat rank of the stand.

2.2.5. Spatial habitat attribute module

The spatial habitat attribute module was derived from the spatial heterogeneity analysis program for categorical maps, SHAPC (Li and Reynolds, 1994, 1995). The model consists of two sets of routines to calculate spatial characteristics of landscapes from GIS data: one to measure the characteristics of landscape configuration (e.g. edge density, patch size, distance to stream or wetland) and the other to calculate landscape indices (e.g. patchiness, contagion, fractal dimension). Many species require specific landscape configurations, and the degree to which those configurations are or are not present may exert great influence on habitat quality

(Hamel, 1992; Wiens et al., 1993; Freemark et al., 199.5; Hunter, 1997); for example, edge density represents the quality of ecotone habitat, patch size reflects the quality of interior habitat or home range, distance to water portrays the habitat quality for many amphibian and reptile species that require both forests and water bodies to complete their life cycles, and nearest-neighbor distance affects dispersal and metapopulation dynamics. Most landscape indices do not have unequivocal ecological meanings because they have complex and nonlinear relations to those real landscape variables and are insensitive to offsetting changes in different elements (Li and Reynolds, 1994). Nonetheless, some studies suggest that landscape indices may relate to wildlife habitat quality (O'Neill et al., 1988; Flather and Sauer, 1996). Because of their potential in providing a new way of habitat assessment at landscape or regional scales, landscape indices were included as part of spatial habitat attributes in LEEMATH.

2.2.6. Landscape habitat quality module

The landscape habitat quality module assesses overall habitat quality at the landscape scale, emphasizing landscape measures and spatial habitat requirements of species. This model is similar to the deductive GIS habitat suitability model discussed by Stoms et al. (1992). Considering landscape ecological principles, we designed two schemes to characterize habitat quality at the landscape scale (Turner, 1989; Freemark et al., 1995; Pickett and Cadenasso, 1995; Hunter, 1997). The first scheme is an expansion of the habitat matrices used to quantify habitat suitability at the stand scale (Hamel, 1992; Wilson, 1995), and examines species habitat requirements in 'edge' areas, minimum patch size, adjacency to water or wetland, and other landscape characteristics. The information on spatial habitat requirements is available for some wildlife species in the literature, although no database exists. The second scheme applies landscape analysis to the aggregated habitat maps rather than those original GIS maps (e.g. vegetation type map). LEEMATH simulation produces an aggregated habitat map for each target species at each time step, by aggregating adjacent stands with the same habitat rank predicted by the habitat suitability module. However, the user can choose to use original GIS maps with natural patches.

2.2.7. Landscape spatial information system

The landscape spatial information system (LSIS) is a set of tools and routines for GIS interface, input-output management, system variable updating and bookkeeping, and data reformatting. Data exchanges between the most recent version of LEEMATH and GIS are limited to the exporting of data from GIS for simulation, and the importing of simulation results into GIS for spatial displays. These input and output data can be in either map or table formats. In addition, real data come in many different formats and, sometimes, with essential data missing. Before LEEMATH can use these data, the user must estimate missing data and reformat all data. We developed programs in LSIS that assist the user in accomplishing these tasks. For example, tree density is an essential variable used to run the stand growth models, but tree density in hardwood stands is often not sampled or reported in the forest inventory database. To run LEEMATH for hardwood or mixed stands, the user must invoke the program to estimate tree density from a mean value for young stands, modified by stand age and current stocking of basal area. The uncertainty caused by such estimation routines must be acknowledged.

2.2.8. Economic analysis module

The economic analysis module is to assess implications of alternative management strategies on net profits from timber production under different economic and environmental constraints. Economic analysis is designed as an expert system with databases of timber revenues, annual growth rates, the discount rate, and operational costs (e.g. planting, bedding, fertilizing, burning, logging). It can be used to calculate opportunity costs associated with environmental protection alternatives, and evaluates the environmental and economic tradeoffs of forest management options. Valuation of ecosystem goods and services needs to be developed and incorporated into economic analysis (Haynes and Weigand, 1997). The current version of LEEMATH uses timber production as a surrogate of economic outputs; a comprehensive economic analysis is in the process of being developed.

2.3. Input to and output from LEEMATH

Input data necessary to run LEEMATH include five categories (Table 1). GIS maps and associated parameters (e.g. map dimensions, scale) help define the spatial context of the landscape for simulation. The forest inventory data are primarily used to drive the stand growth models. For better economic analysis, the proportions (in density or basal area) of hardwood and pine in each stand are also needed. All forest inventory variables are essential, although some can be estimated if they are not available. The habitat matrices define habitat requirements of individual wildlife species (Hamel, 1992; Wilson, 1995). These habitat matrices should be updated to reflect new information and the user’s experiences and observations. A few habitat attributes cannot be predicted by the models, including special attributes like isolated wetlands, ponds, grassy openings, rocky places, and earth banks (Hamel, 1992; Wilson, 1995). These special habitat attributes will not be considered in habitat evaluation if their existence in the landscape is not reported in the stand inventory data. The information on management regimes defines the management scenarios that the user wants to examine.

Output from LEEMATH includes many predictions that characterize various aspects of landscape dynamics (Table 1). LEEMATH predictions include three categories: (1) timber growth and harvest, (2) habitat attribute dynamics, and (3) habitat suitability of the target species. Each category of the output may be summarized at either the stand or the landscape scales. All the predictions are made by simulation year; some are made also by stand, by species, or by both.

Table 1
Major inputs and outputs of LEEMATH

Input	Output
A. GIS maps	*A. Timber growth and harvest*
Vegetation type	Total basal area
Soil type	Basal area growth
Stream network	Basal area harvested
	Dominant tree height
B. Forest inventory data	Tree density
Stand distribution map	Quadratic mean diameter
Forest type	Tree mortality
Stand age	
Basal area (by species)	*B. Habitat attributes*
Dominant tree height	Stand developmental stage
Tree density	Canopy closure
Site index	Woody plant percent cover
	Herbaceous plant percent cover
C. Habitat matrix	Snags by size classes
Forest type and stand stage	Coarse woody debris
Vertical structure	Litter biomass
Physiographic features	Edge density
Specific habitat features	Mean habitat patch size
Spatial habitat features	Distance to stream or wetland
D. Special habitat attributes	*C. Habitat suitability of a species*
Isolated wetlands	Habitat rank by stands
Grassy openings	Aggregated habitat maps
Rocky places	Average habitat rank
	Habitat rank frequency
E. Management regime	Total habitat area
Harvest schedule	Habitat loss
Silvicultural treatment plan	Habitat regrowth
Target wildlife species list	Landscape indices

3. LEEMATH simulation example

We applied LEEMATH to a forested landscape on the coastal plain of South Carolina, USA. This simulation example is a part of a cooperative research project sponsored by the National Fish and Wildlife Foundation, the National Council of the Paper Industry for Air and Stream Improvement, the National Audubon Society, the US Department of Agriculture Forest Service Center for Forested Wetlands Research, and the International Paper Company. It is important to note that the following management regimes were created for the sole purpose of demonstrating LEEMATH. This simulation should not be viewed, under any circumstances, as analysis for management policy development or planning by the International Paper Company. With this example, we wish to show that land managers can use LEEMATH to evaluate economic output and ecological considerations simultaneously in forest management planning.

3.1. Study site

The Woodbury Tract is at the confluence of the Little Pee Dee River and the Greater Pee Dee River, west of Georgetown, SC. The tract is about 12 000 ha. The vegetation types there include longleaf pine (*Pinus palustris*), loblolly pine, cypress-tupelo (*Taxodium* sp. and *Nyssa aquatica),* bottomland hardwoods, upland oak (*Quercus* sp.), mixed pine-hardwoods, and nonforest (Fig. 2). Forest inventory data include stand variables such as tree species, stand age, basal area, tree density, and soil types. The GIS data were provided by the International Paper Company, who owns and manages the tract.

3.2. Simulation set-up

We created two management regimes for this simulation experiment. The two management regimes differed only in harvest schedules generated by the rule-based harvest scheduling model. Harvesting schedule A used shorter rotation ages (i.e. 20 years for pine and 40 years for hardwood), while schedule B used longer rotation

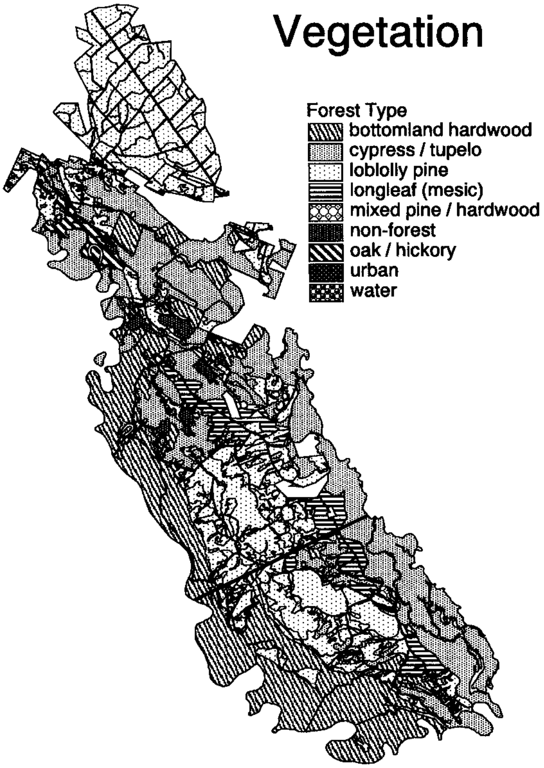

Fig. 2. The vegetation type distribution in the Woodbury landscape. Six forest types are present with a large proportion of hardwood forests. The GIS map also shows the stream systems.

Table 2
The habitat requirements of the three target species used in LEEMATH simulation with the Woodbury data (Hamel, 1992; Wilson, 1995)

Habitat attribute	Species habitat requirement[a]		
	Acadian Flycatcher	Bachman's Sparrow	Barking Treefrog
Forest type and stage			
Cypress			
Grassy			S[b]
Seedling	–		S
Pole timber	0	–	S
Saw timber	0	–	0
Loblolly			
Grassy	–	S	S
Seedling	–	0	S
Pole timber		M	S
Saw timber	–	–	0
Vertical structure			
Herbaceous		N, F, P[c]	
Shrub		N, F, P	
Midstory	N, F, P	P	
Overstory	N, F, P	P	
Physiographic features			
Sandhills			Yes
Flatwoods			Yes
Swamps			Yes
Carolina bays			Yes
Special habitat features			
Canopy closure ,	Closed	Open	Closed
Snags	215 cm		
Moist soil			Yes
Dead trees	Yes		
Water	Fresh		Pond

[a] Note that the list of habitat attributes is incomplete: only two of the 14 forest types are shown here, only the breeding season habitat requirements are included for the birds, and only some of the physiographic features and the special habitat features are included. Refer to Hamel (1992) and Wilson (1995) for the complete habitat matrices.

[b] The four habitat ranks are optimal (0), suitable (S), marginal (M), and nonhabitat (–).

[c] The three usage types for birds are indicated by the letters N (nesting), F (foraging), and P (perching).

ages (i.e. 30 years for pine and 60 years for hardwood). Both schedules used a 50 ha adjacency constraint and a 600 ha annual harvest limit. No silvicultural treatment was used. Three species were selected because they represent different functional groups (Table 2) (Hamel, 1992; Wilson, 1995). Acadian Flycatcher (*Empidonax virescens*) is a tree-nesting Neotropical migratory bird that requires moist deciduous forest with a moderate understory and generally near a stream.

Bachman's Sparrow *(Aimophila aestivalis)* is a ground-nesting resident bird that breeds in open (young) pine forest, especially where there is a thick cover of herbaceous understory. Barking Treefrog (*Hyla gratiosa)* lives in permanent ponds in pine flatwood or bottomland hardwood stands and overwinters by burrowing into the ground near ponds.

We ran LEEMATH for 150 simulation years under each of the two management regimes, using forest inventory data from the Woodbury landscape. We limited our use of the special habitat features to those that could be predicted by the models or derived from GIS maps (e.g. vegetation type, stream network). Because of a lack of information, we classified all stands in the physiographic region of flatwood. The spatial resolution of landscape maps used in this simulation was 0.5 ha.

4. Results

Results of the test simulation runs were summarized in three categories: timber production, habitat attribute dynamics, and habitat quality assessment for the three target species. Timber production was analyzed at the landscape scale. Fig. 3 shows the dynamics of timber harvest and growth under the two management scenarios. Both timber harvest and growth display a flat pattern with some fluctuations, representing the 'steady' economic outputs from the landscape, as defined by our simulation objectives.

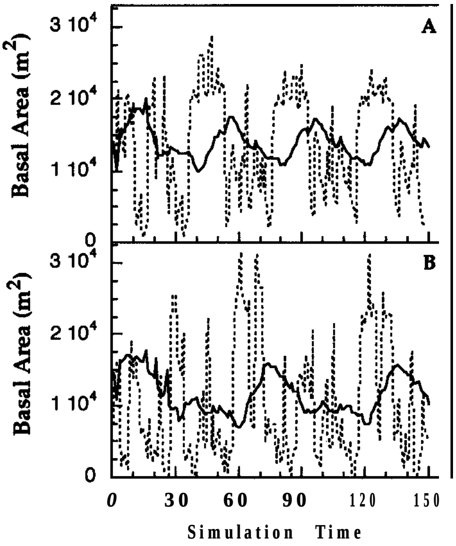

Fig. 3. The timber harvest (dash lines) and growth (solid lines) over the 150 years of simulation in the Woodbury landscape. (A) and (B), landscape conditions generated by harvest schedules A and B, respectively.

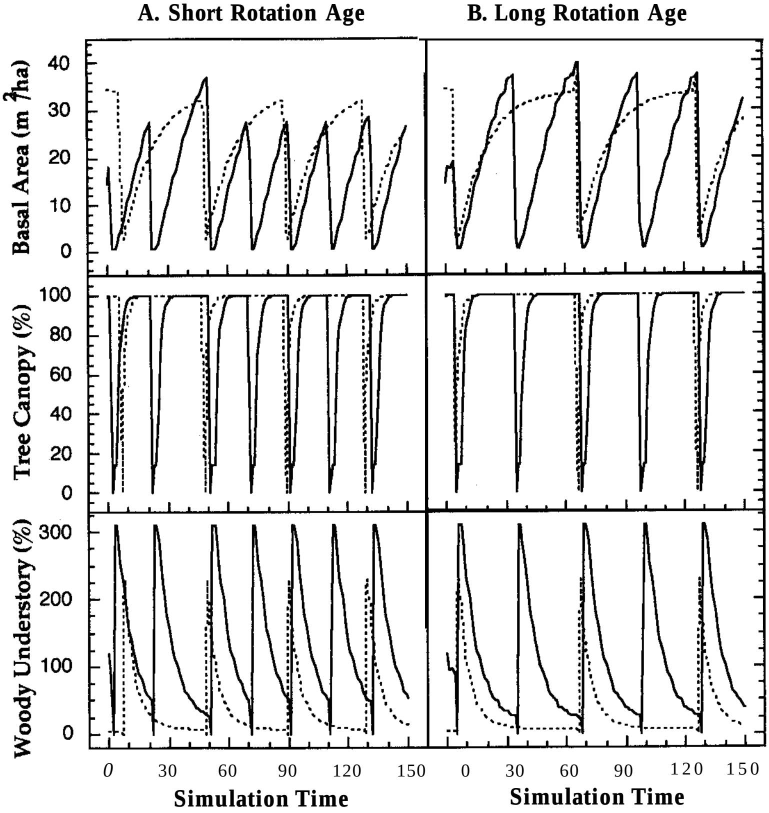

Fig. 4. The dynamics of three habitat attributes (i.e. basal area, canopy closure, woody understory vegetation percent cover) in two individual stand over the 150 years of simulation. In each panel, the solid line represents a loblolly pine stand and the dashed line represents a cypress-tupelo stand. The loblolly pine stand was harvested seven times under the short rotation regime (A panels), and five times under the long rotation (B panels), whereas the cypress-tupelo stand was harvested four and three times under the two regimes, respectively. Each harvest year is indicated by the lowest values of basal area. Notice the cyclic nature of habitat attribute dynamics produced by habitat loss and habitat regrowth.

The habitat attribute dynamics were examined at both the stand and the landscape scales. At the stand scale, the dynamics of three habitat attributes (i.e. basal area, canopy closure, woody understory vegetation) were presented for a loblolly pine stand and a cypress-tupelo stand (Fig. 4). Studying habitat attribute dynamics in individual stands is of interest because the analysis provides a way of examining in detail habitat changes at particular locations. This enables us to relate simulation results to field studies conducted at the same locations. The two stands were selected because they were among the stands in which wildlife field samplings were conducted in the Woodbury landscape. The cyclic nature of habitat loss and regrowth is clearly shown here (Fig. 4). The habitat attributes show clear differences in the temporal patterns between the two harvest schedules. These differences are due to the differences in the rotation age. At the landscape scale, the stand developmental stage is shown at the selected time steps (Fig. 5). The four-stage system (i.e. grassy, seedling, pole timber, and saw timber) is commonly used in forestry to characterize major changes in stand conditions. A clear difference between the two harvest schedules is that harvest schedule B displays some balance in the proportions of different stand-developmental stages, but harvest schedule A has few stands with the saw-timber stage after year 15 under the short rotation

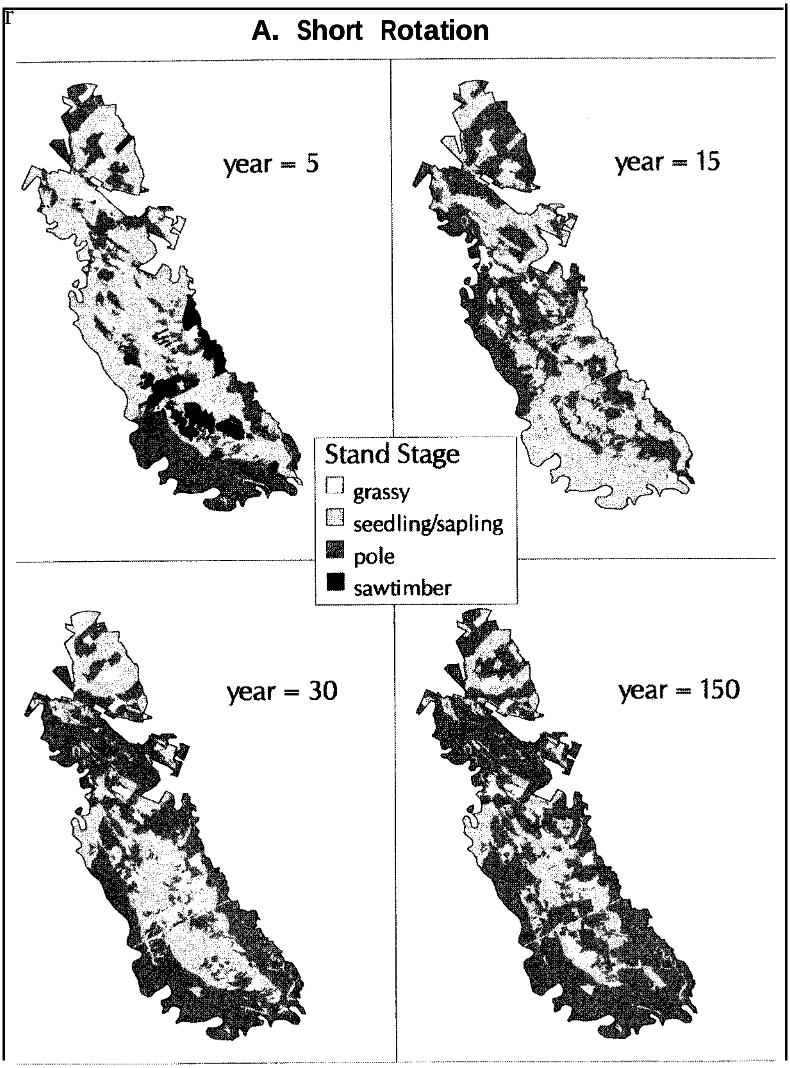

Fig. 5. The dynamics of a habitat attribute, the developmental stage of forest stands, in the Woodbury landscape under the two harvest schedules (A and B). The stand stage has four levels: grassy, seedling, pole timber, and saw timber, representing major changes in stand conditions. The landscape changes are displayed at four selected simulation times, i.e. 5, 15, 30, and 150.

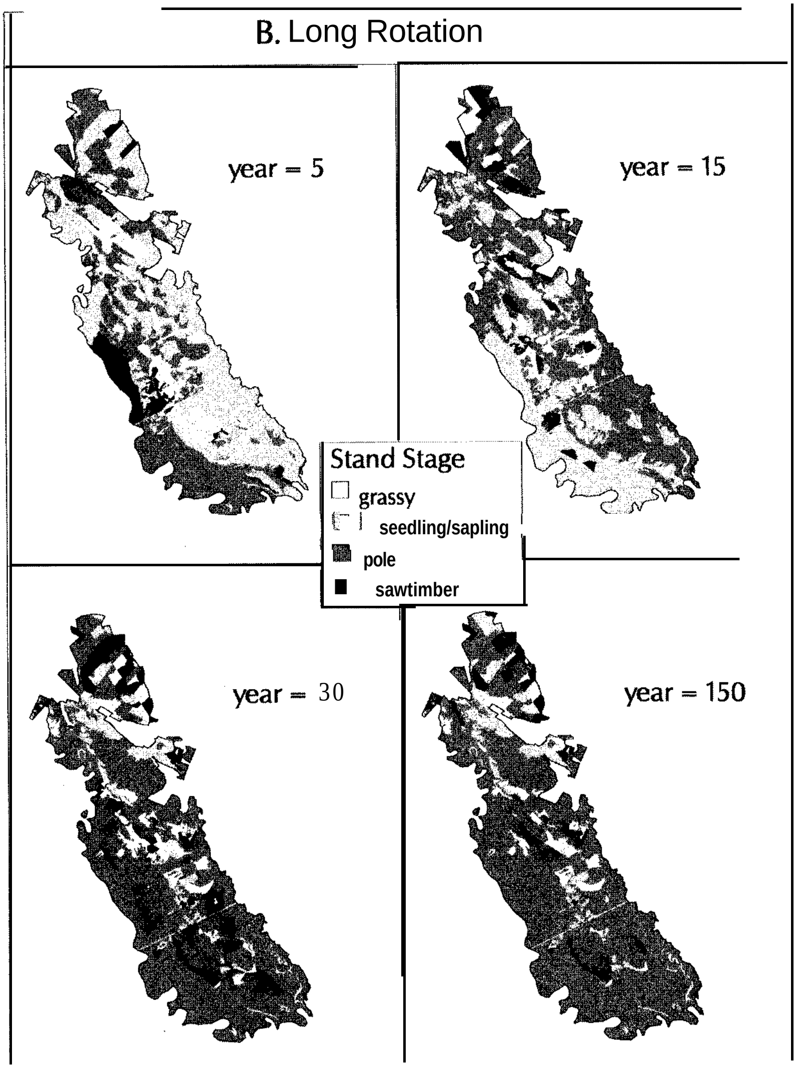

Fig. 5. *(Continued)*

regime. This will have great influence on habitat quality of the species that require mature stands.

Similarly, habitat suitability was also examined at the stand and landscape scales. At the stand scale, the dynamics of habitat ranking for the three species differ because of their different habitat requirements (Table 2). However, they closely follow the cyclic patterns of the habitat loss and regrowth in the two stands and under the two management regimes (Fig. 4). At the landscape scale, habitat quality for the three species is illustrated by the aggregated habitat maps (Figs. 668). These maps show the spatial distribution of species' habitat at the four selected years and under the two harvest schedules. From the habitat rank maps, we can assess management effects on habitat quality at the landscape level and over time for the target species, and identify potential 'hot spots' in management planning. For example, there are a few stands in the middle of the landscape that provide optimal habitat for Acadian Flycatcher earlier in the simulation (e.g. year 5, Fig. 6). Suitable habitat patches for Acadian Flycatcher are contiguous throughout the simulation years under both management regimes (Fig. 6). Some landscape habitat

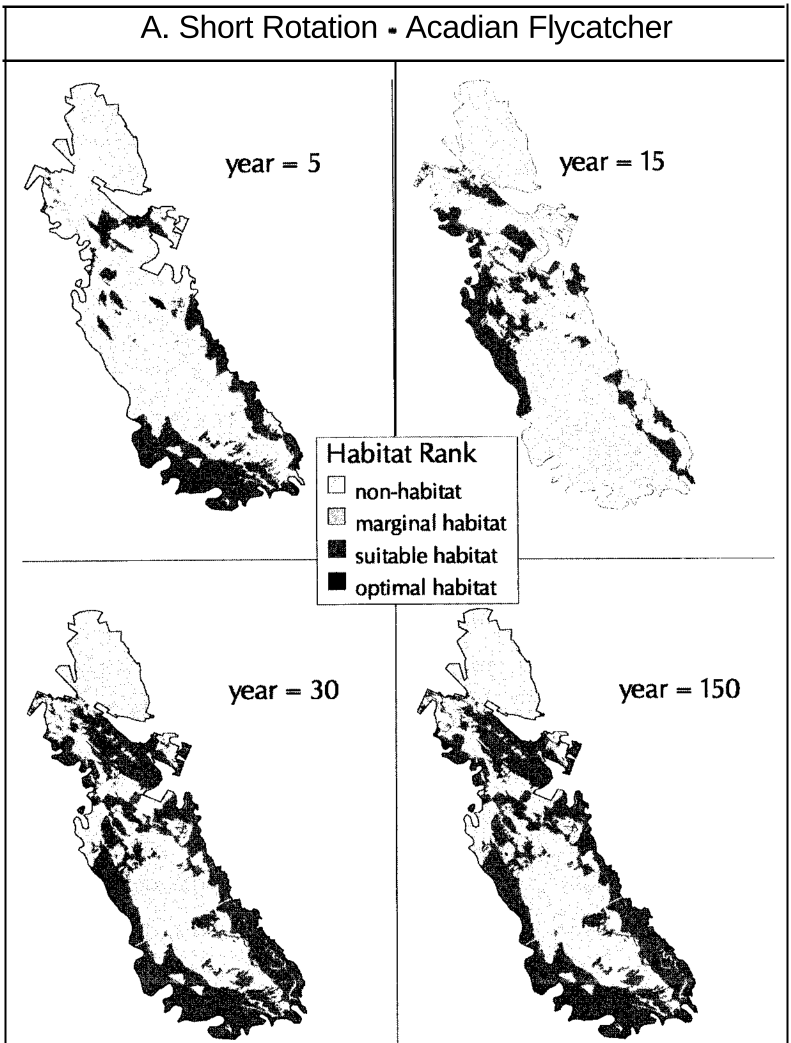

Fig. 6. A time series of habitat rank maps of Acadian Flycatcher in the Woodbury landscape at the four selected simulation times under the two harvest schedules (A and B).

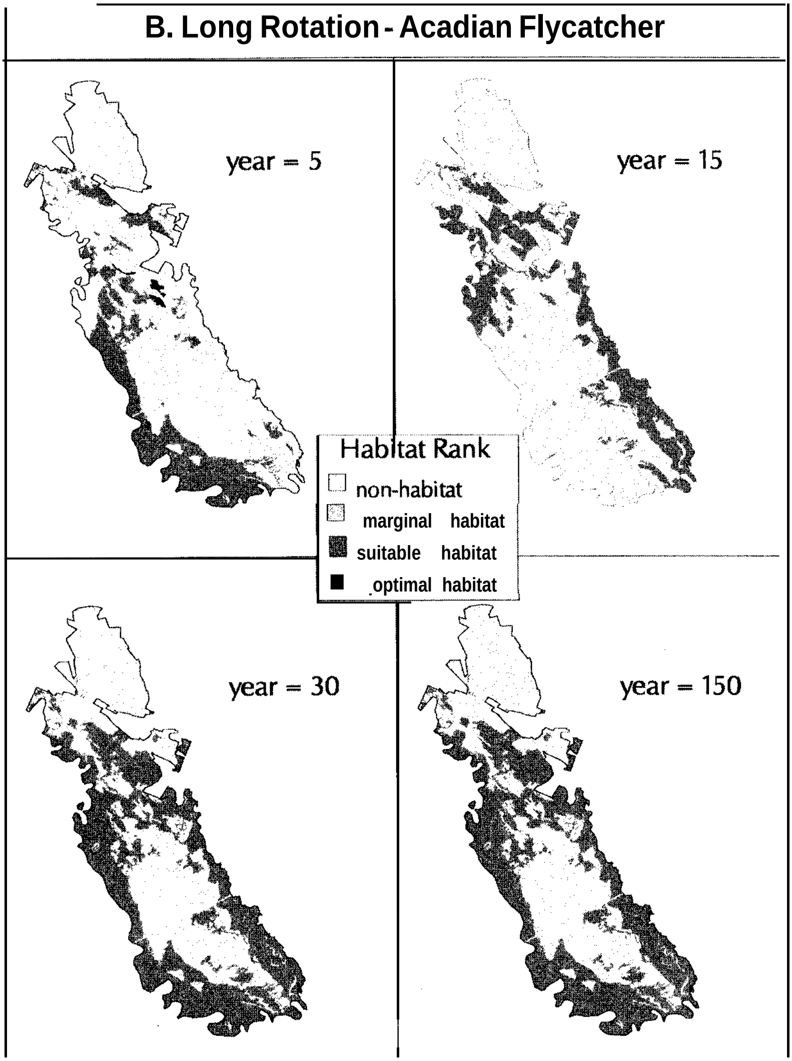

Fig. 6. *(Continued)*

variables were calculated from the aggregated habitat maps and are summarized in Table 3: total habitat area, habitat loss, and habitat gain of the three species. Total habitat areas fluctuate for Acadian Flycatcher and Bachman’s Sparrow, but show no change for Barking Treefrog. Bachman’s Sparrow shows balanced habitat loss and gain, whereas Acadian Flycatcher experiences spikes in habitat loss and gain over time. For Barking Treefrog, habitat ranks of stands change, but they never become nonhabitat. This lack of habitat loss and gain over time may indicate problems with the habitat suitability model of Barking Treefrog.

Table 3
Landscape habitat variables at the four selected years and under the two harvest schedules[a]

Harvest schedule	Year	Total habitat area (ha)			Habitat loss (ha)			Habitat gain (ha)		
		ACFL	BACS	BATR	ACFL	BACS	BATR	ACFL	BACS	BATR
A	5	3042.5	2299.5	7084.5	412.0	29.5	0.0	0.0	237.0	0.0
A	15	2674.0	3038.5	7084.5	130.5	92.0	0.0	1222.5	132.5	0.0
A	30	5896.5	3223.0	7084.5	40.5	193.5	0.0	0.0	138.5	0.0
A	150	5896.5	2202.0	7084.5	43.5	259.5	0.0	26.5	159.0	0.0
B	5	3266.0	2302.0	7084.5	340.0	29.5	0.0	0.0	148.0	0.0
B	15	3263.5	2062.5	7084.5	0.0	275.5	0.0	1081.0	323.5	0.0
B	30	6048.0	1072.5	7084.5	0.0	318.0	0.0	0.0	114.5	0.0
B	150	6048.0	1313.0	7084.5	0.0	227.5	0.0	0.0	114.5	0.0

[a] ACFL, Acadian Flycatcher; BACS, Bachman’s Sparrow; BATR, Barking Treefrog.

5. Discussion

5.1. Habitat analysis

Decision-support systems such as LEEMATH can provide rigorous analysis of habitat quality for a large number of wildlife species under various management regimes. LEEMATH can examine all 494 wildlife species contained in the habitat matrices, although only three species were selected for this demonstration. Thus,

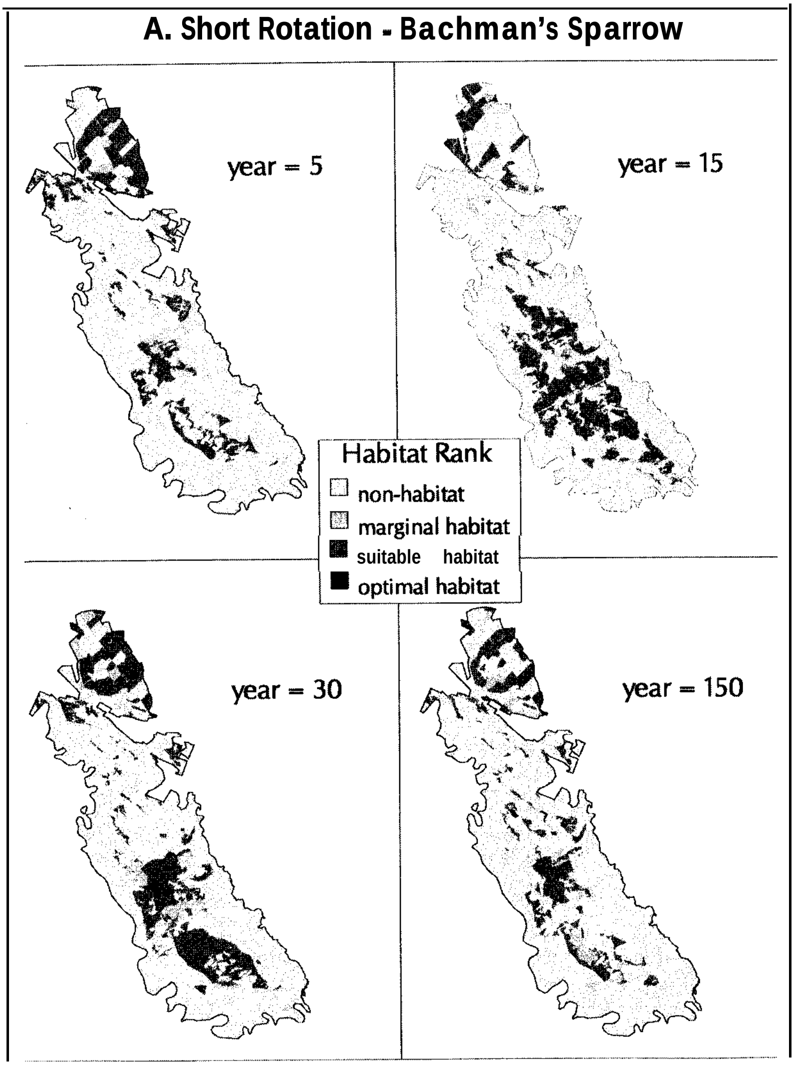

Fig. 7. A time series of habitat rank maps of Bachman's Sparrow in the Woodbury landscape at the four selected simulation times under the two harvest schedules (A and B).

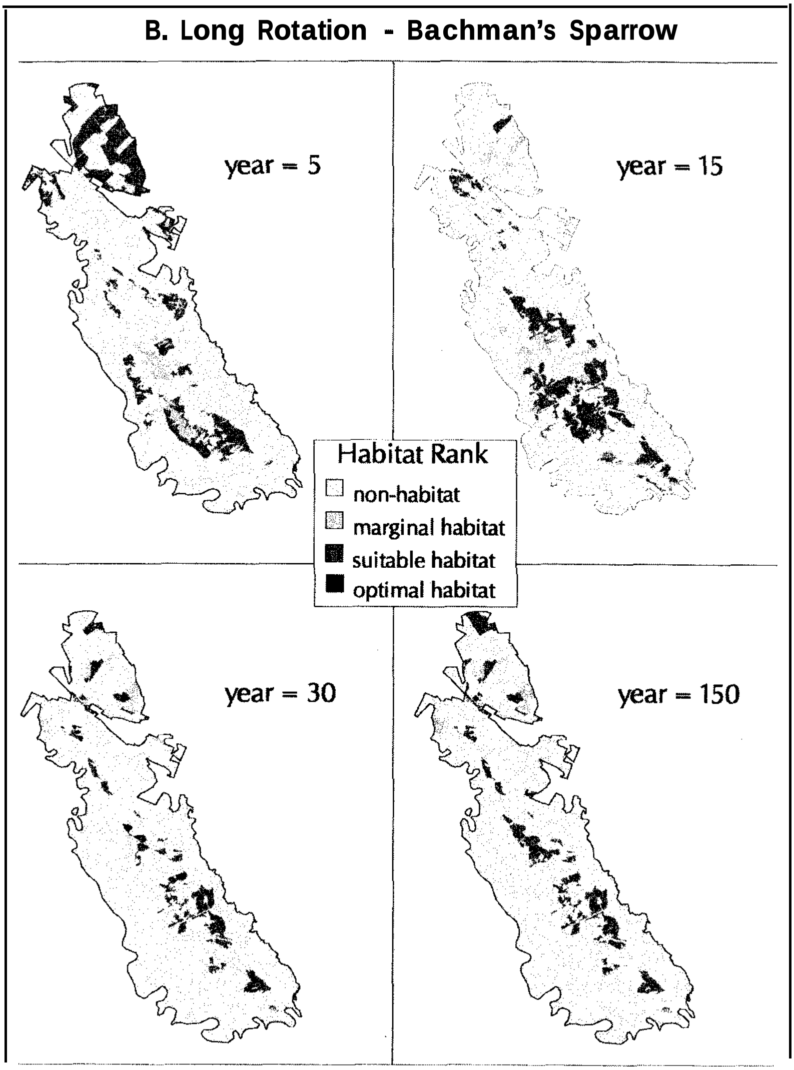

Fig. 7. *(Continued)*

LEEMATH has the advantage of flexibility and choice over single species based models. However, different species may respond differently to the same landscape. Management regimes that are good for one group of species may be bad for another group. The decision of what species to include on the target species list will have **great** impact on management planning. Therefore, criteria to select the target species must be clearly defined. Examples of selection criteria may include threatened species indigenous to the area, or species whose habitat needs are not met elsewhere in the region.

Successful predictions of habitat quality depend on incorporating wildlife habitat information at specific sites into habitat matrices of the habitat suitability models. The habitat suitability models in LEEMATH are expert systems, and the habitat matrices need to be updated with new knowledge of species. One can improve the accuracy and reliability of the model predictions by using the local habitat information of the target species, especially the forest type. While the habitat suitability models for avifauna have been tested (J. Kilgo, personal communication), the models for herpetofauna still need testing and improving as an assessment

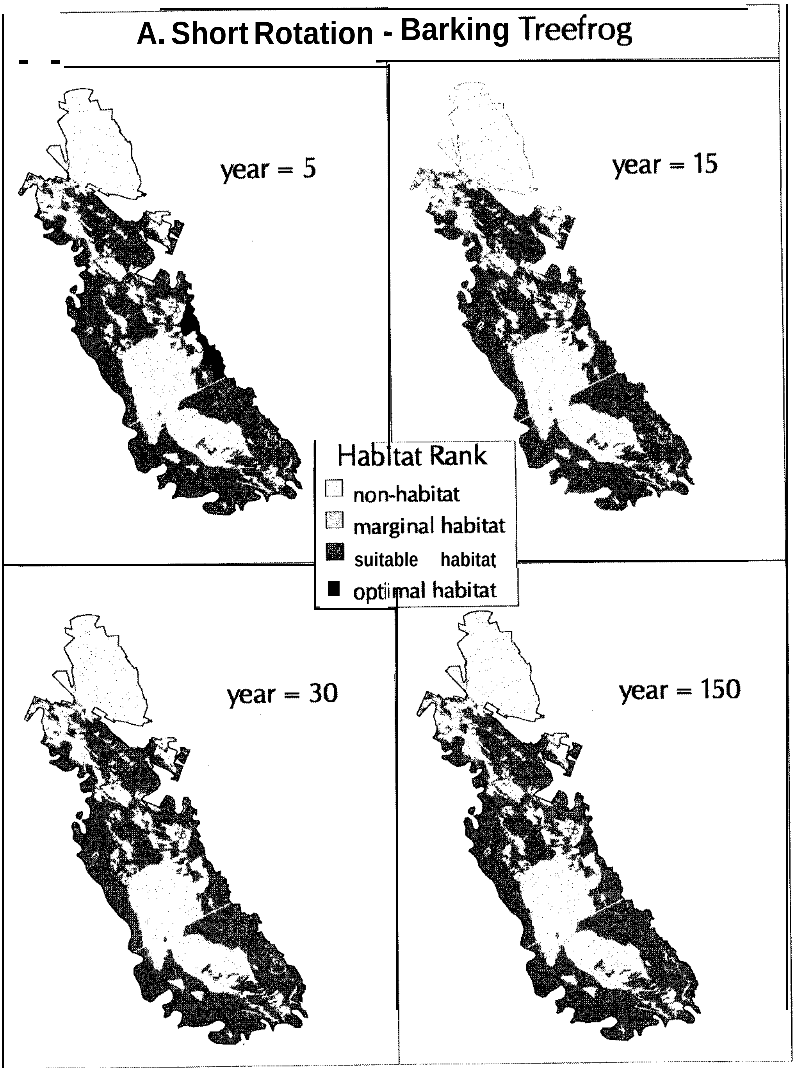

Fig. 8. A time series of habitat rank maps of Barking Treefrog in the Woodbury landscape at the four selected simulation times under the two harvest schedules (A and B).

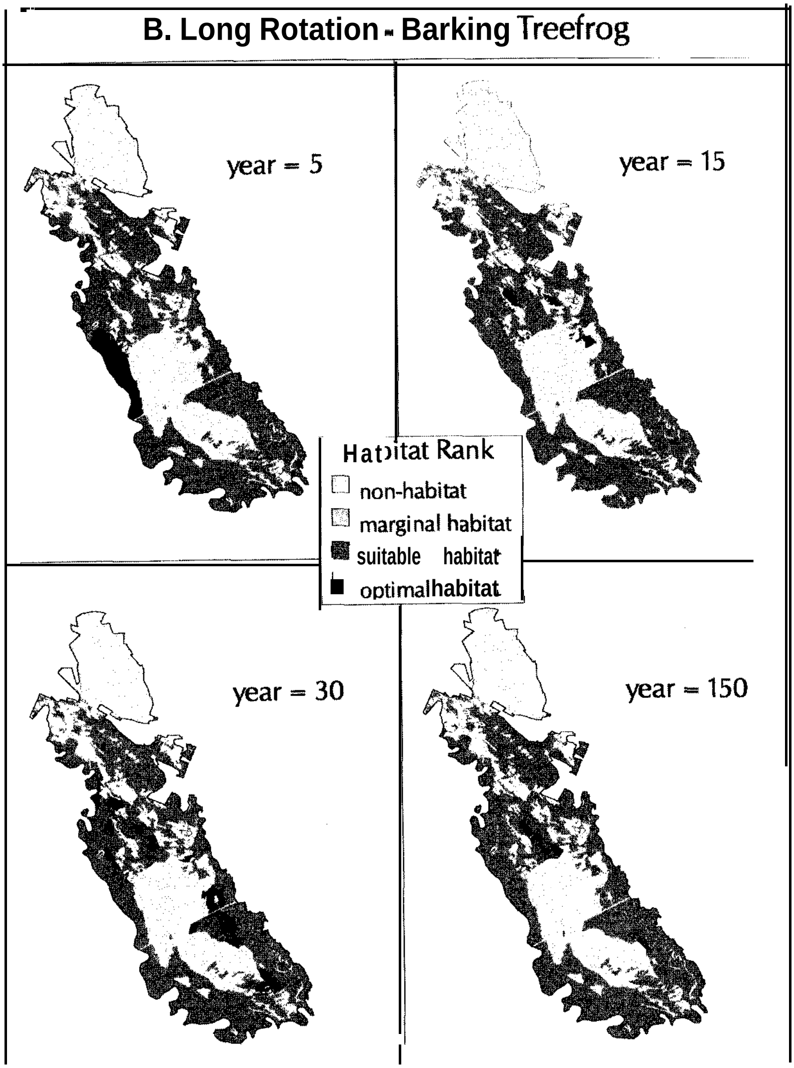

Fig. 8. (Continued)

tool of habitat quality. The LEEMATH simulation results indicate that the current habitat model for Barking Treefrog may have failed to detect habitat changes. The problem is probably common to many amphibian and reptile species. A possible cause of the problem **may** be that Herpetofauna species respond to **fine-scale** habitat features that are not predicted correctly by or built into the habitat attribute models. Thus, model improvement may focus on the prediction of fine-scale habitat features and their incorporation into the habitat suitability models.

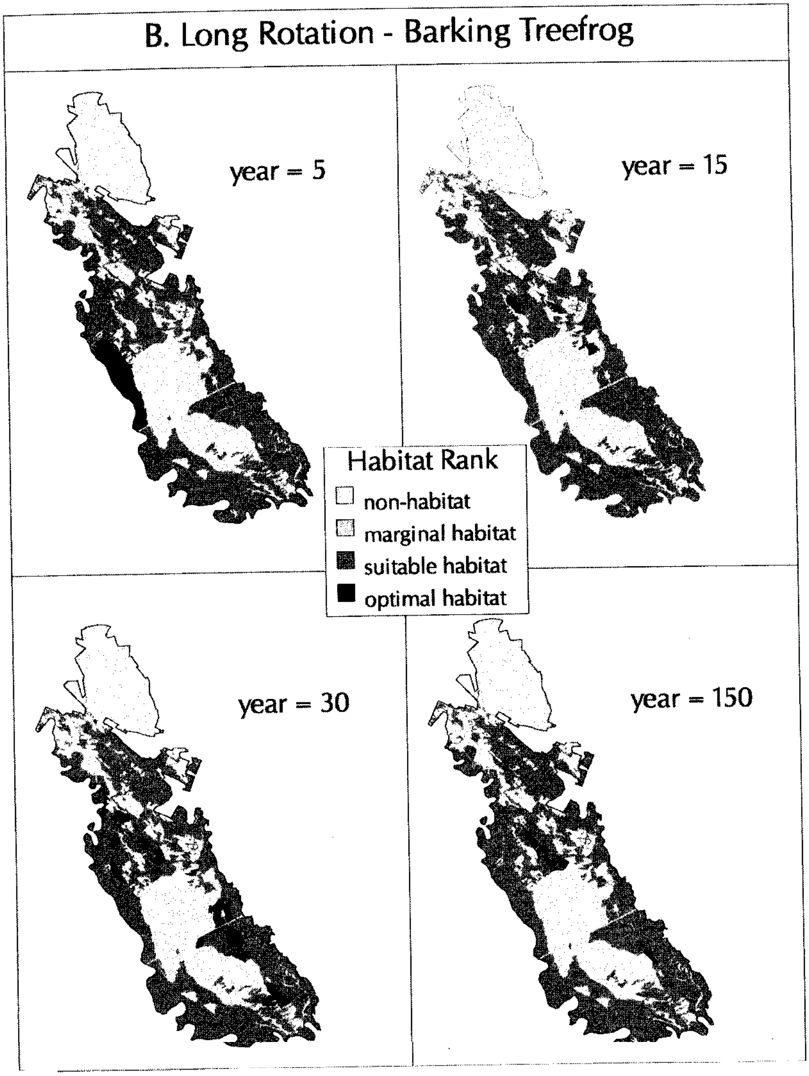

Fig. 8. (Continued)

tool of habitat quality. The LEEMATH simulation results indicate that the current habitat model for Barking Treefrog may have failed to detect habitat changes. The problem is probably common to many amphibian and reptile species. A possible cause of the problem may be that Herpetofauna species respond to fine-scale habitat features that are not predicted correctly by or built into the habitat attribute models. Thus, model improvement may focus on the prediction of fine-scale habitat features and their incorporation into the habitat suitability models.

Landscape habitat evaluation must focus on the ecological relevance of GIS data. Without ecologically relevant data, one cannot guarantee the validity of any analyses and, thus, achieve any meaningful results of landscape habitat evaluation. However, GIS data commonly used in landscape analysis may not be ecologically relevant, because such data are often collected for purposes other than to address ecological questions. The most important factor that determines the ecological relevance of the map data is the classification system used to create them. This is because the inclusion or exclusion of certain patch types in maps affects the structure of landscape mosaics, The question arises: What should be the standards by which landscape maps are to be generated for spatial analysis of habitat quality? Without such standards, it would be impossible to extrapolate any relationships obtained from spatial habitat analysis at one site to another. In LEEMATH, we are addressing the problem using the aggregated habitat maps generated by our spatial habitat attribute module. Aggregated habitat maps are ecologically relevant because they relate species habitat use to landscape structure. They reflect how wildlife species may view the landscape, and capture the differences of habitat quality that different species experience in the same landscape. The use of aggregated habitat maps in landscape habitat evaluation will strike a balance between species information and landscape analysis and provide a standard that makes extrapolation possible.

5.2. Model testing

The LEEMATH model is being tested with forest inventory data and limited wildlife data at selected sites. Model testing is important because it provides some measure of confidence in model predictions. However, testing complex, spatial, and dynamic models like LEEMATH is a difficult task because, in most cases, no long-term data of wildlife population dynamics and stand development are available at large spatial scales, and no comprehensive testing methods have been developed for such models. The current testing of LEEMATH emphasizes wildlife habitat predictions and is restricted to static evaluations that compare LEEMATH predictions with wildlife data of one or two sampling years. Preliminary tests with the Woodbury field observations of a dozen species, including Acadian Flycatcher and Barking Treefrog, show that LEEMATH predicts habitat quality of these species with high accuracy at the landscape scale (R. Lancia, W. Gibbons, H. Li, unpublished data). Regardless of the difficulties in testing LEEMATH, many of its component models have been tested in their initial development and subsequent applications, such as the stand growth models (Kenney, 1983; Clutter et al., 1984), the habitat attribute model based on forest stand dynamics (Mou et al., 1993), and the habitat suitability models for birds (J. Kilgo, personal communication). Many component models can also be evaluated with observations at the stand level, as demonstrated in the example. The confidence in the component models determines the confidence in LEEMATH

5.3. Knowledge gaps in large-scale habitat assessment

Theory and modeling have certainly surpassed the support of field studies in the realm of large-scale assessment of habitat quality. The LEEMATH project has highlighted the knowledge gaps in habitat quality assessment at the landscape scale, such as a lack of spatial habitat requirement data, a lack of established relationships between habitat quality and landscape indices, and omission of other land-use types (e.g. agriculture) in the forest inventory database. First, while speculation is abundant, data on spatial habitat requirements by species are scarce in the literature (Hamel, 1992; Freemark et al., 1995; Kareiva and Wennergren, 1995; Fahrig, 1997; Hunter, 1997). The only spatial habitat requirement available is the minimum habitat patch size for some birds (Hamel, 1992). Without knowledge of the spatial habitat requirements of species, we cannot study the effects of landscape configuration on habitat quality, which is an important objective of LEEMATH that distinguishes it from other forest planning models such as ECOSYM (Davis and DeLain, 1986) and FORPLAN (Burgman et al., 1994). The missing data are critical to any habitat quality evaluation at the landscape scale. We submit that this lack of spatial habitat requirement data may be partially responsible for the failure to detect fragmentation effects in previous field and simulation studies (McGarigal and McComb, 1995; Fahrig, 1997).

Second, the use of landscape indices to evaluate habitat quality can be traced to a doctrine of landscape ecology: Ecological processes not only affect, but are affected by, spatial patterns of ecological systems (Turner, 1989; Pickett and Cadenasso, 1995). However, few studies have demonstrated such relationships (Flather and Sauer, 1996; Gustafson, 1998). The lack of established relationships between habitat quality and landscape indices hinders habitat evaluation at the landscape scale. An important factor to this problem may be the ecological relevance of landscape indices and the map data used to calculate them. Ecologically relevant metrics and data are those that can functionally link the dynamics of ecological processes to landscape structure. Ecological relevance should be determined by our understanding of both the ecological processes under study and the quantitative methods that we use (Gustafson, 1998). In evaluating wildlife habitat, our challenge is to develop or identify those metrics related to food (e.g. quality versus quantity, foraging efficiency), shelter (e.g. energy conservation, escape from predation), reproduction (e.g. nesting sites, fecundity) and other population processes (e.g. dispersal, survival rates, competition) (Wiens, 1995). Only by using a combination of ecologically relevant map data and ecologically relevant landscape metrics can we obtain and extrapolate meaningful relationships between habitat quality and landscape indices.

Third, habitat assessment should consider the whole landscape, not just part of it. LEEMATH simulations are hindered by the lack of input data required for habitat evaluation, especially data that are not part of the traditional forest inventory database. An example is the omission of other land-use types (e.g. agriculture) in the database caused by political or ownership boundaries. The habitat related data in a full range of land-use types are essential to the proper assessment of habitat quality at the landscape scale. For example, adjacency of Neotropical migratory bird habitats to agricultural fields may degrade habitat quality because of nest parasitism by cowbirds (*Molothrus* sp.) (Robinson et al., 1995). Other examples include the presence of small isolated wetlands in forest stands, physiographic characteristics of stands (e.g. sandhills or flatwoods), and special habitat features (e.g. grassy openings, rocky places). These habitat variables must be added to the databases to ensure successful habitat assessment at large scales.

5.4. Decision-support systems for ecosystem management

Decision-support tools that incorporate science, land-use priorities, and policy options into assessments of forest resource sustainability at large scales are essential to the implementation of the ecosystem management concept. Ecosystem management is complex and must be science based (Kohm and Franklin, 1997; Rauscher, 1999). The most important function of decision-support systems like LEEMATH is to synthesize scientific information from various disciplines and deliver it to land managers in a readily usable form and a timely fashion. The LEEMATH simulation example suggests that LEEMATH can be an effective tool to deal with the complexity of scientific information, as well as the complexity of landscape dynamics over time and space. Ecosystem management is holistic and must consider the multiple objectives of natural resource management. The LEEMATH simulation example suggests that the management system (e.g. economics, values, decisions) and the biophysical system (e.g. growth, succession, habitat quality) can and should be combined in the planning process (Salwasser, 1994). Sustainable forest management, especially on industrial forest landscapes, must be ecologically sound and economically feasible (Rauscher, 1999). Thus, developing management plans that also produce better habitat for target wildlife species is imperative, because conservation cannot succeed in isolated reserves and wilderness areas alone, but in the vast matrix of managed landscapes (Franklin, 1993). Managed forest landscapes may provide good habitat for many species (for example, Wigley and Roberts, 1997), especially at the landscape scale, where the balance between habitat loss and habitat regrowth can be achieved. A systems perspective with the help of decision-support tools can manifest good stewardship and land ethics. Ecosystem management is adaptive and must reflect constant changes in scientific information, government policy, and value systems of the society. Decision-support systems like LEEMATH can facilitate such an adaptive approach by providing a framework for timely monitoring, re-evaluation, and adjustment. Simulation models focus on comparisons among the potential consequences of a range of management alternatives (for example, Thomas et al., 1990; Haynes and Weigand, 1997). With LEEMATH, we can ask ‘WHAT-IF’ questions to explore management alternatives and their possible effects on habitat quality. Our challenge is to find a management strategy that has the minimum impact on habitat quality while retaining a good level of economic outputs.

6. Future work

LEEMATH model development continues. We will improve different modules of LEEMATH, including the habitat attribute models for snags, coarse woody debris, litter biomass and depth, and understory vegetation, and the habitat suitability models for herpetofauna. We will complete the economic analysis module so that environmental constraints can be recognized in assessing the effects and the implications of alternative management strategies on net profits from timber production. We will compile a database for spatial habitat requirements so that LEEMATH can function in its full capacity. The success of LEEMATH and other similar models depends on such information. After testing and sensitivity analyses, we will deliver LEEMATH to field researchers and industrial land managers so that it can be assessed for its usefulness in resource management planning with realistic management scenarios. Finally, we will modify LEEMATH such that it may be used not only to assess management effects on habitat quality, but also to develop management regimes that meet the desirable habitat quality for selected target species. This modification is important because, in situations of managing public lands such as the national forests, environmental considerations may take higher priority than the economic. The challenge is enormous. However, we are confident that, with intense multidisciplinary efforts, we will be able to develop better decision-support systems and answer the question posed at the beginning of the paper: How can we manage forest landscapes to obtain maximum benefits while ensuring the integrity of the natural resources on which these benefits are based?

Acknowledgements

We thank Bill Harms, George Hess, and anonymous reviewers for constructive comments on early drafts of the paper, and International Paper and Westvaco for providing support and access to their forest inventory data. The project is partially supported by the National Council of the Paper Industry for Air and Stream Improvement, US Department of Agriculture (USDA) Forest Service Southern Research Station, and the Southern Global Change Program of USDA Forest Service. The opinions expressed by the authors do not necessarily represent the policy or position of the US Department of Agriculture or the Forest Service.

References

American Forest and Paper Association, 1994. Sustainable Forestry Principles and Implementation Guidelines. Approved by the American Forest and Paper Association Board of Directors, 14 October, 1994.

Benson, G.L., Laudenslayer, W.F., 1986. DYNAST: simulating wildlife responses to forest-management strategies. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), Wildlife 2000. University of Wisconsin Press, Madison, WI, pp. 351-355.

Berlyn, G.P., Ashton, P.M.S., 1996. Sustainability of forests. Journal of Sustainable Forestry 3, 77-89.

Brand, G.J., Shifley, S.R., Ohmann, L.F., 1986. Linking wildlife and vegetation models to forecast the effects of management. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), Wildlife 2000. University of Wisconsin Press, Madison, WI, pp. 3833387.

Buford, M.A., 1991. Performance of four yield models for predicting stand dynamics of a 30-year-old loblolly pine (*Pinus taeda* L.) spacing study. Forest Ecology and Management 46, 23-38.

Burgman, M., Church, R., Ferguson, I., Gijsbers, R., Lau, A., Lindenmayer, D., Loyn, R., McCarthy, M., Vandenburg, W., 1994. Wildlife planning using FORPLAN. Australian Forestry 57, 131-140.

Christensen, N.L., Bartuska, A., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, D.H., Turner, M.G., Woodmansee, R.G., 1996. The report of the Ecological Society of American Committee on the scientific basis for ecosystem management. Ecological Applications 6, 665-691.

Clutter, J.L., Harms, W.R., Brister, G.H., Rheney, J.W., 1984. Stand Structure and Yields of Site-Prepared Loblolly Pine Plantations in the Lower Coastal Plain of the Carolinas, Georgia, and North Florida. GTR SE-27. USDA Forest Service Southeastern Forest Experiment Station, Asheville, NC.

Davis, L.S., DeLain, L.I., 1986. Linking wildlife-habitat analysis to forest planning. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), Wildlife 2000. University of Wisconsin Press, Madison, WI, pp. 361–369.

Dedon, M.F., Laymon, S.A., Barrett, R.H., 1986. Evaluating models of wildlife-habitat relationships of birds in black oak and mixed-conifer habitat. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), Wildlife 2000. University of Wisconsin Press, Madison, WI, pp. 115-119.

Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61, 603-610.

Flather, C.H., Sauer, J.R., 1996. Using landscape ecology to test hypotheses about large-scale abundance in migratory birds. Ecology 77, 28-35.

Franklin, J.F., 1993. Preserving biodiversity: species, ecosystems or landscapes? Ecological Applications 3, 2022205.

Freemark, K.E., Dunning, J.B., Hejl, S.J., Probst, J.R., 1995. Landscape ecology perspective for research, conservation, and management. In: Martin, T.E., Finch, D.M. (Eds.), Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, pp. 381–427.

Grumbine, R.E., 1997. Reflections on 'what is ecosystem management?'. Conservation Biology 11 (1), 41–47.

Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1, 1433156.

Hamel, P.B., 1992. The Land Manager's Guide to the Birds in the South. The Nature Conservancy, Chapel Hill, NC, 367 pp.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 1333302.

Haynes, R.W., Weigand, J.F., 1997. The context for forest economics in the 21st century. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC, pp. 285–301.

Hunter, M.L., 1997. The biological landscape. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC, pp. 57-67.

Kareiva, P., Wennergren, U., 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373, 299-302.

Kenney, K.M., 1983. A growth and yield model for natural stands of piedmont bottomland hardwoods. Unpublished Masters Thesis. NC State University, Raleigh, NC.

Kohm, K.A., Franklin, J.F. (Eds.), 1997. Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC, pp. 475.

Lele, S., Norgaard, R.B., 1996. Sustainability and the scientist's burden. Conservation Biology 10 (2), 3544365.

Li, H., Reynolds, J.F., 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology 75, 24462455.

Li, H., Reynolds, J.F., 1995. On definition and quantification of heterogeneity. Oikos 73, 280–284.

Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Manson, P.A., Melillo, J.M., Mooney, H.A., Peterson, D.H., Pulliam, H.R., Real, L.A., Regal, P.J., Risser, P.G., 1991. The sustainable biosphere initiative: an ecological research agenda. Ecology 72, 371-412.

Maser, C., 1994. Sustainable Forestry: Philosophy, Science, and Economics. St. Lucie Press, Delray Beach, FL, pp. 373.

McCarthy, M.A., Burgman, M.A., 1995. Coping with uncertainty in forest wildlife planning. Forest Ecology and Management 74, 23-36.

McGarigal, K., McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. Ecological Monograph 65, 235–260.

Moeur, M., 1986. Predicting canopy cover and shrub cover with the Prognosis-Cover model. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), Wildlife 2000. University of Wisconsin Press, Madison, WI, pp. 151–155.

Mou, P., Fahey, T.J., 1993. REGROW: a computer model simulating the early successional process of a disturbed northern hardwood ecosystem. Journal of Applied Ecology 30, 676-688.

Mou, P., Mitchell, R.J., Jones, R.H., 1993. Ecological field theory model: a mechanistic approach to simulate plant-plant interactions in southeastern forest ecosystems. Canadian Journal of Forest Research 23, 2180–2193.

Mower, H.T., Barber, K., Campbell, J., Crookston, N., Dahms, C., Day, J., Laacke, J., Merzenich, J., Mighton, S., Rauscher, M., Reynolds, K., Thompson, J., Trenchi, P., Twery, M., 1997. Decision Support Systems for Ecosystem Management: An Evaluation of Existing Systems. GTR RM-296. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, SW., Dale, V.H., Graham, R.L., 1988. Indices of landscape pattern. Landscape Ecology 1, 153–162.

Pacala, S.W., Canham, C.D., Silander, J.A., 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Canadian Journal of Forest Research 23, 1980–1988.

Pickett, S.T.A., Cadenasso, M.L., 1995. Landscape ecology: spatial heterogeneity in ecological systems, Science 269, 331–334.

Rauscher, H.M., 1999. Ecosystem management decision support for federal forests in the United States: a review. Forest Ecology and Management 114, 1733197.

Robinson, S.K., Rothdtein, S.I., Brittingham, M.C., Petit, L.J., Grzybowski, J.A., 1995. Ecology and behavior of cowbirds and their impact on host populations. In: Martin, T.E., Finch, D.M. (Eds.), Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, pp. 428-460.

Salwasser, H., 1994. Ecosystem management: can it sustain diversity and productivity. Journal of Forestry 82, 6–10.

Schamberger, M.L., O'Neil, L.J., 1986. Concepts and constraints of habitat-model testing. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), Wildlife 2000. University of Wisconsin Press, Madison, WI, pp. 5–10.

Smith, T.M., Urban, D.L., 1988. Scale and resolution of forest structural pattern. Vegetatio 74, 1433150.

Smith, T.M., Shugart, H.H., West, D.C., 1981. Use of Forest Simulation Models to Integrate Timber Harvest and Nongame Bird Management. GTR RM-87. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Stoms, D.M., Davis, F.W., Cogan, C.B., 1992. Sensitivity of wildlife habitat models to uncertainties in GIS data. Photogram. Photogrammetric Engineering and Remote Sensing 58 (6), 843–850.

Tappe, P.A, Shelton, M.G., Wigley, T.B., 1992. Overstory-understory relationships in natural loblolly pine-hardwood stands: Implications for wildlife habitat. In: Proceedings of the Seventh Biennial Southern Silvicultural Research Conference, Mobile, AL, pp. 6133619.

Teck, R., Moeur, M., Eav, B., 1996. Forecasting ecosystems with the forest vegetation simulator. Journal of Forestry 84, 7–10.

Thomas, J.W., Forsman, E.D., Lint, J.B., Meslow, E.C., Noon, B.R., Verner, J., 1990. A conservation strategy for the northern spotted owl. Report of the Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl. US Government Printing Office, Washington, DC.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20, 171–197.

Urban, D.L., Smith, T.M., 1989. Microhabitat pattern and the structure of forest bird communities. American Naturalist 133 (6), 811-829.

Van Deusen, P.C., 1996. Habitat and harvest scheduling using Bayesian statistical concepts. Canadian Journal of Forest Research 26, 1375-1383.

Wiens, J.A., 1995. Habitat fragmentation: island v landscape perspectives on bird conservation. IBIS 137, S97–S104.

Wiens, J.A., Stenseth, N.C., Van Horne, B., Ims, R.A., 1993. Ecological mechanisms and landscape ecology. Oikos 66, 3699380.

Wigley, T.B., Roberts, T.H., 1997. Landscape-level effects of forest management on fauna1 diversity in bottomland hardwood. Forest Ecology and Management 90, 141-154.

Wilson, L.A., 1995. The Land Manager’s Guide to the Amphibians and Reptiles of the South. The Nature Conservancy, Chapel Hill, NC pp 324.

Wu, H., Sharpe, P.J.H., Walker, J., Penridge, L.K., 1985. Ecological field theory: a spatial analysis of resource interference among plants. Ecological Modelling 29, 2155243.