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ECOLECON: An ECOLogical–ECONomic model for species conservation in complex forest landscapes

Jianguo Liu
Institute of Ecology, University of Georgia, Athens, GA 30602, USA

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ABSTRACT

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An ECOLogical–ECONomic model (ECOLECON) has been developed to simulate animal population dynamics and economic revenues in response to different forest landscape structure and timber management scenarios. ECOLECON is a spatially-explicit, individual-based, and object-oriented program. It is coded in Borland C++ 2.0 and contains 14 classes or subclasses of ecological and economic information which are hierarchically interlinked. ECOLECON can generate artificial forest landscapes or can link with geographic information systems (GIS) to run simulations on real landscapes. The model predicts population dynamics, spatial distribution, extinction probability of a species under consideration as well as future landscape structure, and economic income from timber harvest based on current tax and timber market situation. The model outputs provide valuable information for balancing the conflicts between the generation of economic revenues and the conservation of endangered species. Because ECOLECON is interactive and easy to use, it is a useful tool for both research and education. This paper introduces the methods of model development, presents the model structure, demonstrates a sample simulation using the model, and discusses the validation and utilities of the model as well as means to expand the model in the future.

1. INTRODUCTION

Conservation of endangered and threatened species has recently become a high priority for many scientists, politicians and ordinary citizens throughout the world (Council on Environmental Quality and U.S. Department of State, 1980; Soulé, 1986; Office of Technology Assessment, 1987; Shaffer and Saterson, 1987; World Commission on Environment and Development,

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Correspondence to (present address): J. Liu, Harvard Institute for International Development, Harvard University, 1 Eliot Street, Cambridge, MA 02138, USA.

1987; May, 1988; Lubchenco et al., 1991). Although there are no accurate statistics about how many species have been lost, Harvard biologist E.O. Wilson (1988) has estimated that the rate of species extinction in rain forests due to human intervention is between 1000 and 10 000 times higher than the natural extinction rate. The major cause for the rapid extinction is the massive loss of habitats due to human economic activities such as deforestation (Ehrlich, 1988).

In the processes of evaluating ecological and economic consequences of human activities, ecologists and economists usually do not work together, and policy-makers are often in a dilemma because of the contradictory recommendations from these two sides. A well-known example is the heated argument about the impacts of timber harvesting on the Northern Spotted Owl (*Strix occidentalis*) and the economy in the Northwestern United States (Simberloff, 1987). Ecologists, as well as environmental activists and conservationists, have warned that continued logging of the old-growth trees will threaten the existence of the spotted owls (Doak, 1989), but some economists and the timber industry have argued that without the timber harvest, the negative impacts on job opportunities and regional economic developments would be tremendous (Dixon and Juelson, 1987; Salwasser, 1987). This debate has lasted years and it is very difficult for various interest groups to reach a compromise (Salwasser, 1987).

Conflicts between ecological and economic goals have called for simultaneous studies on ecological and economic impacts of human activities (World Commission on Environment and Development, 1987; Lubchenco et al., 1991). Accordingly, many ecologists and some economists have been very active in pushing the marriage of ecology and economics (e.g., H.T. Odum, 1971, 1973; H.T. Odum and E.C. Odum, 1981; Ma, 1983; Jansson, 1984; E.P. Odum, 1984; Costanza, 1989; Ehrlich, 1989; Norgaard, 1989; Daly, 1991). In 1988, the International Society for Ecological Economics was established. One year later, the society began to publish a journal called "Ecological Economics". In 1990, an international conference on ecological economics was held in Washington, DC, and 32 papers from this conference were compiled as a book (Costanza, 1991). Recently, the Ecological Society of America has released a historic document about future research (Lubchenco et al., 1991) and stated that there is "an urgent need (1) to forge new theory that explicitly incorporates economics as well as ecological principles, and (2) to conduct research on the economics of exploitation and conservation". This view has been shared by many others. For example, the president and president-elect of the British Ecological Society recently suggested "research that explicitly links ecology with economics... should rank high on any explicit list of priorities" (Grubb and May, 1991).

One of the most useful approaches for dealing with ecological and economic issues simultaneously is quantitative modeling (Braat and van Lierop, 1987; Costanza et al., 1991). With the aid of modern computer techniques and mathematical methods, some ecological–economic models have been established for a marine fishery (Grant et al., 1981; Krauthamer et al., 1987), regional land-use planning (Camara et al., 1986), the management of natural resources and policy analysis (Braat and van Lierop, 1987), and emergy analysis of natural resources (H.T. Odum and Arding, 1991). To my knowledge, however, no ecological–economic models of species conservation have been developed to date.

To meet the research need mentioned above, I have developed an ecological–economic model (ECOLECON) that simulates animal population dynamics and economic cash-flows in response to landscape structure and timber harvest in managed forests. ECOLECON is a spatially-explicit, individual-based and object-oriented program that contains both ecological and economic algorithms and information. The model has been parametrized using growth and yield functions for loblolly pines (*Pinus taeda*) and using ecological information of Bachman's Sparrow (*Aimophila aestivalis*), a species of management interest occurring in pine forests in the southeastern United States. Because Bachman's Sparrows breed in young and mature pine stands, quantitative and spatial changes in these habitat stands would affect the sparrow population dynamics and economics of forest management. In other words, the sparrow population dynamics is linked with forest economics through forest structure and management. Simulation of the sparrow population dynamics is largely based on the single-sex "grid" models for Mobile Animal Populations (MAP, Pulliam et al., 1992) and BACHMAP, the version of MAP parametrized for the Bachman's Sparrow (Pulliam et al., 1992). The economic components include the functions of growth and yield predictions for loblolly pines in the southeastern U.S. as well as cash-flow of timber harvest and forest management. The objective of ECOLECON is to search for good management schemes which coordinate species conservation and economic revenues.

In this paper, I will introduce the methods of model development, present the model structure, demonstrate a sample simulation using the model, and discuss the validation and utilities of the model as well as means to expand the model.

2. METHODS

In this section, I summarize key characteristics of major computer simulation languages, with emphasis on C++ and Borland C++ 2.0, which I used for coding the model. Then, I discuss the data sources for parametrizing the model.

2.1. *Three generations of computer simulation languages*

The evolution of computer languages can be divided into three stages: (1) unstructured, (2) structured, and (3) object-oriented. The unstructured computer languages tend to have spaghetti code, the untrackable interlinkages in a program because of heavy dependence on "GOTO" statements. They are difficult to read. The structured computer languages avoid spaghetti code and the overall program is logically and inherently structured through procedures (loop and branch control structures). Object-oriented languages have a hierarchical organization consisting of objects which are sections of code reflecting the characteristics and processes of different entities (e.g., trees and insects). Although an object has its own distinct properties, it inherits properties of higher-level objects since an object is one of the nodes in a network hierarchy.

The unstructured languages are the first generation of computer languages, such as the early versions of FORTRAN and BASIC. The initial FORTRAN was created in the mid-1950s and was the language of choice for the scientific and engineering community (Kerrigan, 1991).

The structured languages like PASCAL and C are the second generation of the computer languages. C was developed at Bell Laboratories as a system language in the 1970s. One decade later, use of C had exceeded that of FORTRAN because C is available on a wide range of hardware and is the predominant computer language learned by new programmers (Kerrigan, 1991). C is portable, fast, efficient, and has a structure that is easy to read and comprehend (Traister, 1987).

The third or the most advanced generation of computer languages is object-oriented programming (OOP) languages, which are currently heavily utilized in the area of artificial intelligence (Waterman, 1985). Polese and Goldstein (1991) suggested that "If there's one development paradigm that every software engineer should learn and understand, it's object-oriented programming". OOP languages (e.g., Smalltalk, LISP, and C + +) have modular structures which make data management very convenient. Functionally, OOP languages provide a straightforward way for handling concurrent and asynchronous operations. Coulson et al. (1987) and Rykiel (1989) think it would be more natural for ecologists to create models by using ecological objects. In ecology, an object may be an organism and ecological objects are generally hierarchically related. OOPs are built hierarchically and therefore they can adequately describe the hierarchical structures and relationships of ecology (Rykiel, 1989).

Object-oriented programming languages such as PC-Scheme, Smalltalk, and LISP have been used by several ecological modelers. Graham (1986) developed a prototype (HAREMS) in PC-Scheme for feral horse populations in heterogeneous habitats. In 1989, she expanded the HAREMS model to include more features. Because the model complexity increased, she had to shift the language from PC-Scheme to Smalltalk 80.

Another model (WASP, Makela et al., 1988) employed object-oriented programming techniques to simulate the population dynamics of an insect host–parasitoid system in a closed, heterogeneous environment (cotton fields) according to individual behaviors. Saarenmaa et al. (1988) presented a generic model of animal–habitat interaction and a specific model of moose (*Alces alces*) –forest interactions in Finland. Folse et al. (1989) demonstrated the use of object-oriented programming and rule-based decision procedures for modeling deer movements in a patchy brushland habitat. The model was developed in Franz Extended Common Lisp with Flavors (an object-oriented extension) on a small Sun Microsystems workstation. The model can simulate effects of patch size on deer movements and the deer's learning process about habitat structure. For a more detailed review about the application of object-oriented approach in ecological modeling, please see Sequeira et al. (1991).

Although OOP languages like PC-Scheme, LISP and Smalltalk have been introduced to ecological modeling, I have not seen any report using the most advanced OOP language, C + +, for ecological or ecological–economic studies. Therefore, I will briefly introduce the history and the most important features of C + +.

2.2. C + + language

The C + + language was designed and originally developed by Bjarne Stroustrup in the Computer Science Research Center at AT&T Bell Laboratories in Murray Hill, New Jersey. To create a simulation language with the features of object-oriented programming, Stroustrup decided to add object-oriented features to the well-established C language. C + + was developed as a translator program that processes C + + source code into C source language. The translated C source language could be then compiled on any computer architecture that supports C. Since 1985 the C + + language has been continuously extended and improved by other companies such as Sun Microsystems, Borland International in California, and Zortech Incorporated.

C + + programming language is a superset of C language because C + + has many improvements and extensions. Here, I just list a few examples: (1) C + + includes better comment style and input/output

TABLE 1

A sample class to exemplify encapsulation

```
class TREES{
    // data
  float height;
  int age;
    // functions
  float Calculate_average_height();
  int Search_for_the_oldest_tree();
  };
```

streams. (2) A C + + function prototype can declare default values for arguments. The C + + compiler substitutes the default values if the corresponding arguments are omitted when the function is called. (3) In C, all variables must be declared at the beginning of the block in which they have scope. C + + removes this restriction and allows a variable to be declared anywhere. This makes the code more readable because a variable's declaration is close to the section of code in which it is used. (4) C + + is object-oriented.

There are three major properties for the OOP feature in C + +: encapsulation, inheritance, and polymorphism. Encapsulation means the welding of data and functions that manipulate the data. This task is completed by a single entity which combines both functions and data and defines explicit relationships between them. In C + +, a class is a template which is used to define an object. Because the functions and data are components of the class, they are known as member functions and data members respectively. For example, class TREES has two data members and two member functions (Table 1). Tree height includes real numbers which are defined by data type **float**. Tree age is an integer which is represented by data type **int**. **Calculate_average_height**() is a function which uses height data to calculate average height of all trees. **Search_for_the_oldest_tree**() is a function which can find out which tree is the oldest one.

The class in C + + is very helpful for programmers to design, implement, maintain, and reuse programs. It is simpler to debug a C + + program because many errors can be quickly traced to one particular class. The C + + encapsulation also makes it easier to use the object's data since all actions take place through member functions.

Inheritance is the technique of inheriting characteristics from higher-level classes in the class hierarchies. Fig. 1 shows a partial taxonomy chart of

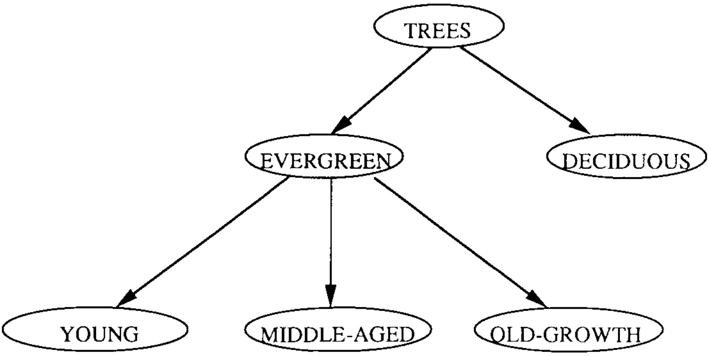


Fig. 1. A partial taxonomy chart of trees.

trees. At the first level (or base level), major characteristics of trees are defined. At a lower level, trees can be divided into two major categories: evergreen and deciduous. At the next hierarchical level, evergreen trees can be divided into young, middle-aged, and old-growth. Each level is more specific than the one above it and includes the characteristics of higher levels. Therefore C + + programmers may just need to write code for special properties in each class and do not need to rewrite codes for the features that higher-level classes have. This is a good way to reuse code.

Polymorphism in C + + lets programmers use many versions of the same function throughout a class hierarchy, with a specific version to be executed at run time. This offers programmers a high degree of flexibility and easy maintenance.

2.3. Borland C + + 2.0

The above are some common properties of C + + languages. Various software companies have developed C + + languages somewhat differently. At present, there exists no standard C + + language. The C + + compiler I used was Borland C + + 2.0 produced by Borland International, Inc. (1991). Borland C + + 2.0 has new releases of the C and C + + compilers, a program profiler, a stand-alone debugger, and the Turbo assembler. Besides, Borland C + + 2.0 includes the Whitewater Group's Resource Toolkit for creating and maintaining Window resources (e.g., menus, dialog boxes, and icons). The Integrated Development Environment (IDE) is very user-friendly and convenient for editing, compiling and debugging programs. I implemented Borland C + + 2.0 on a Zenith 386 computer with a math coprocessor.

2.4. Data collection

All the data for the parametrization of the model ECOLECON were collected from the field or from relevant references. For ecological and biological information of Bachman's Sparrow, the major references were Haggerty (1986), Dunning and Watts (1990), and Pulliam et al. (1992). John B. Dunning, Bryan D. Watts, Brent Danielson, René M. Borgella, Jr. collected field data about the Bachman's Sparrow at the Savannah River Site (South Carolina) during the past five years. Borders et al. (1990) and Souter (pers. commun., 1991) were the primary sources for the growth and yield functions for loblolly pines in the southeastern United States. Cubbage et al. (1991) provided a basis for financial analysis, while Norris (1990), Cubbage (pers. commun., 1991) and Dubois et al. (1991) supplied information about timber market price and cost of managing forests.

As mentioned above, the animal species I used to parametrize the model was Bachman's Sparrow. It is a potentially threatened species (Dunning and Watts, 1990; Pulliam et al., 1992), and the range of this species has shrunk significantly since the 1930s (Haggerty, 1986). The sparrows breed in young and mature pine stands in the southeastern United States. At a field study site, the Savannah River Site, the pine plantations are usually mosaics of even-aged stands of different management practices. The decline of the sparrow's range may be due to local and regional changes in the availability of suitable habitats (Dunning and Watts, 1990). For the model (ECOLECON) I have developed, the demographic and dispersal characteristics of Bachman's Sparrows as well as changes in habitat suitability were considered to be factors that impact the population dynamics.

In the southeastern United States, there are three major pine species: loblolly pines (*Pinus taeda*), longleaf pines (*Pinus palustris*), and slash pines (*Pinus whiteveris*). Since the functions of growth and yield projection for longleaf and slash pines are not as complete as those for loblolly pines (Borders et al., 1990), I assumed that the forest landscapes in the simulations were composed of loblolly pines.

3. MODEL STRUCTURE

Ecological–economic systems consist of both ecological and economic components. ECOLECON incorporates ecological and economic information pertaining to species conservation in complex forest landscapes. The ecological and economic objects are hierarchically interlinked as shown in Fig. 2. The source code of the model is available upon request from the author or from Institute of Ecology, University of Georgia, Athens, GA 30602. In the following, I will first describe some of the inputs and then discuss the structures of classes and subclasses.

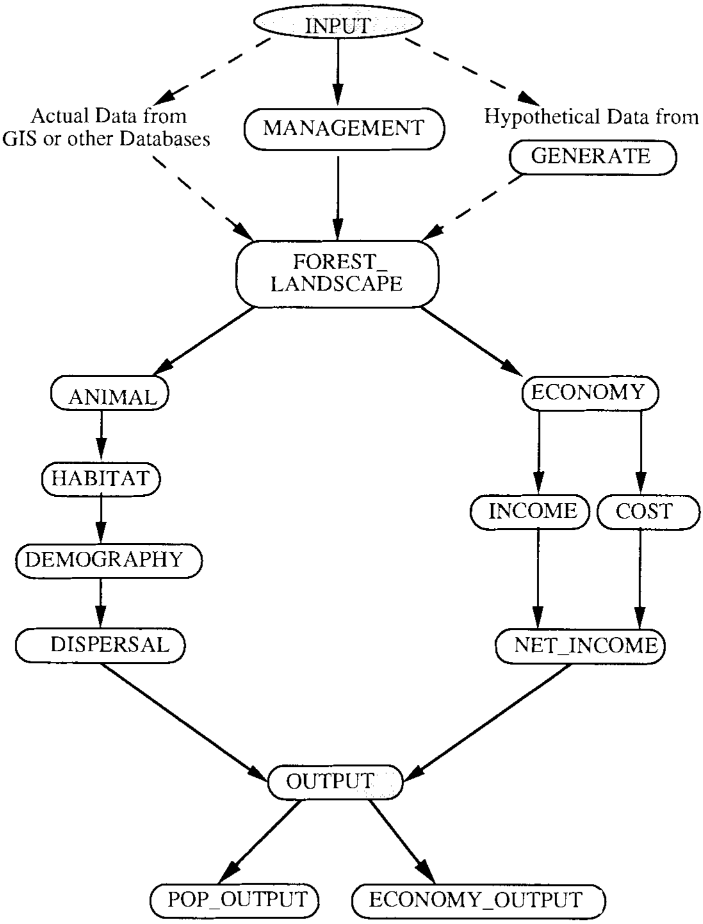


Fig. 2. A diagram outlining the hierarchical structure of ECOLECON.

3.1. Model input

ECOLECON is a man–machine dialogue system. In other words, to run the model users simply need to answer some questions by typing in desired numbers or letters (e.g., Yes or No). The options included in ECOLECON are:

(1) Options for the number of replicates and the simulation length (number of years) for each replicate. As I will discuss below, some processes of the ECOLECON are stochastic, so an adequate number of replicates is required to obtain averages and variances for statistical analyses.

(2) Choice of either creating hypothetical landscapes or linking ECOLECON with real landscapes from geographic information systems (GIS) or other databases. A detailed description of the link between the model and

GIS can be found in Liu (1992) and Liu et al. (1993b). To produce an artificial landscape, users can select different landscape shapes, sizes, composition, and configurations. If there is a lack of data about animal abundance and distribution pattern from field investigation, the model will ask users to initialize animal populations.

(3) Variable demographic parameters. The user is asked to supply demographic information, such as survivorship for adults and juveniles. This allows the model to simulate population dynamics for any species for which the information is known or can be estimated.

(4) Habitat selection rules. For juvenile and adult dispersal, a user can decide what types of habitat a disperser prefers, how far an disperser can search, and from how far a disperser can identify the patch quality.

(5) Economic variables. The user is asked to supply economic information, such as discount rate, unit prices for three types of timber (pulpwood, chip-and-saw, and sawtimber), cost for regeneration (site preparation, seedling and planting), maintenance cost and tax.

(6) Result output options. The outputs can be examined on a computer screen and are stored in designated files. For example, users can decide whether or not to see annual abundance and spatial distribution of animals. The users also can see where juveniles disperse and the fate of the dispersal (e.g., whether the disperser settles down in a suitable habitat, fails to find a suitable habitat, or dies). The detailed dispersal processes can be displayed with sound and colorful animation effects. At the end of simulations, annual dynamics of population sizes and net income as well as the averages over a selected period of time are shown on a computer screen.

The input procedure is hierarchically organized and rule-based; that is, the questions asked later are determined by the preceding answers. For example, if I use actual landscapes from GIS, all questions about how to create artificial landscapes are omitted.

3.2. Classes and subclasses

In the model ECOLECON, there are 14 classes and subclasses which are hierarchically structured (Fig. 2). MANAGEMENT and GENERATE are the base classes from which the class FOREST_LANDSCAPE is derived. If information is available on the actual abundance and distribution of the species, ECOLECON can use this information for the initialization of the model. If this information is not available, ECOLECON will generate initial conditions based on random probabilities that any given suitable site is occupied. The classes ANIMAL and ECONOMY are dependent on FOREST_LANDSCAPE. Class ANIMAL transfers information to HABITAT, DEMOGRAPHY, DISPERSAL, and ultimately to

OUTPUT. Class ECONOMY consists of the subclasses INCOME and COST, which together pass values to NET_INCOME. Class OUTPUT also accepts results from NET_INCOME. Population dynamics and extinction information are stored in POP_OUTPUT (a subclass of OUTPUT), while another subclass ECONOMY_OUTPUT contains information about net cash flows, net present value and expectation value of the forest landscapes, and average net revenues.

In the following, I will describe these classes in more detail, including some functions and parameters for the model.

3.2.1. GENERATE

Class GENERATE is used to create an artificial forested landscape and to generate initial animal population abundance and spatial distribution. This class consists of functions and data which create forest landscapes of different sizes, shapes, composition (forest age structure) and configurations. The basic unit in the forest landscape is a hexagonal cell (Fig. 3), which is designated as an animal territory (2.5 ha for Bachman's Sparrow, see Pulliam et al., 1992). A stand is an aggregation of cells of similar structure. It can be as small as one hexagonal cell or can be made of two or more adjacent cells of the same age. Initial population abundance ($Y1$) is treated as a linear function of the number of initial suitable habitats ($X1$), $Y1 = \alpha X1$, where α is a value between 0 and 1, and is determined by the users. For Bachman's Sparrow, suitable habitats are young (1–5 years) and mature (80 + years) stands (Dunning and Watts, 1990; Pulliam et al., 1992; Liu, 1993). Initial animals are randomly distributed onto the suitable habitats. The generated forest and animal information is stored in designated disk files.

3.2.2. MANAGEMENT

The class MANAGEMENT consists of source code that specifies different forest harvest strategies such as rotation length and which forest stands are scheduled to be harvested. Harvest schemes are divided into two general categories: regular and irregular harvest. The former refers to the forest being cut at regular rotations of a fixed length. In other words, when a stand reaches a certain age, it is cut and one year later the area is regenerated using seedlings. For irregular harvests, forest managers have the flexibility of cutting all the trees in any stand at any time. In either case, seedlings are planted one year after the area is harvested.

3.2.3. FOREST_LANDSCAPE

In the class FOREST_LANDSCAPE there are three functions that obtain information either from a geographic information system or from

(a)

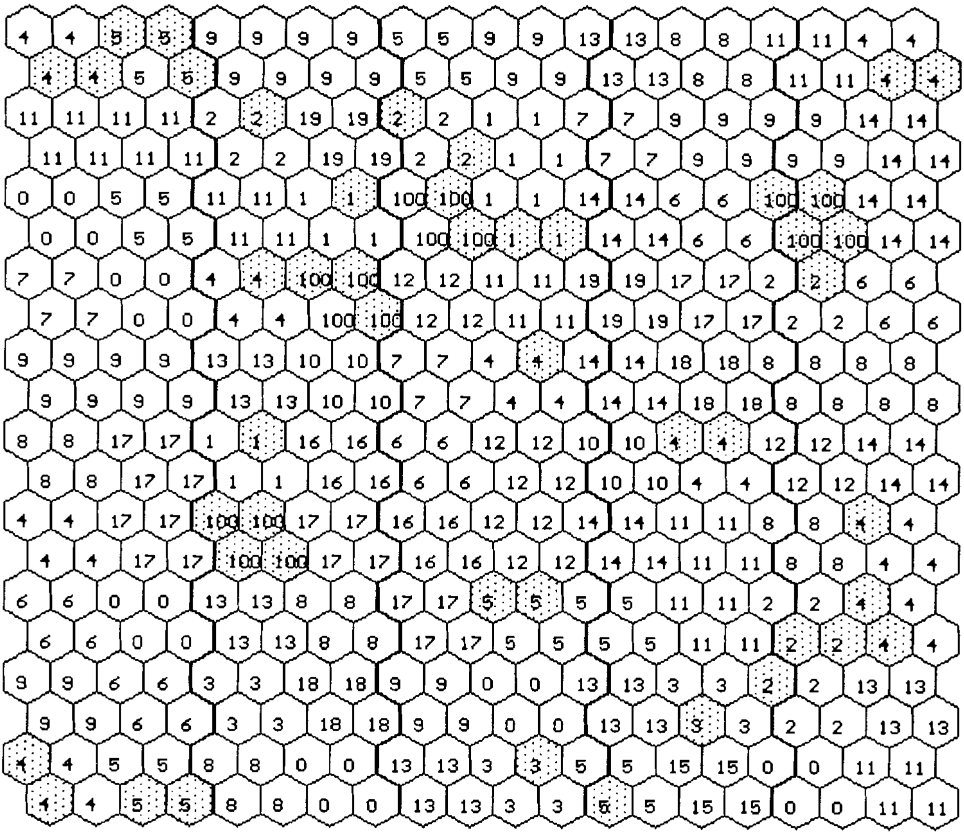


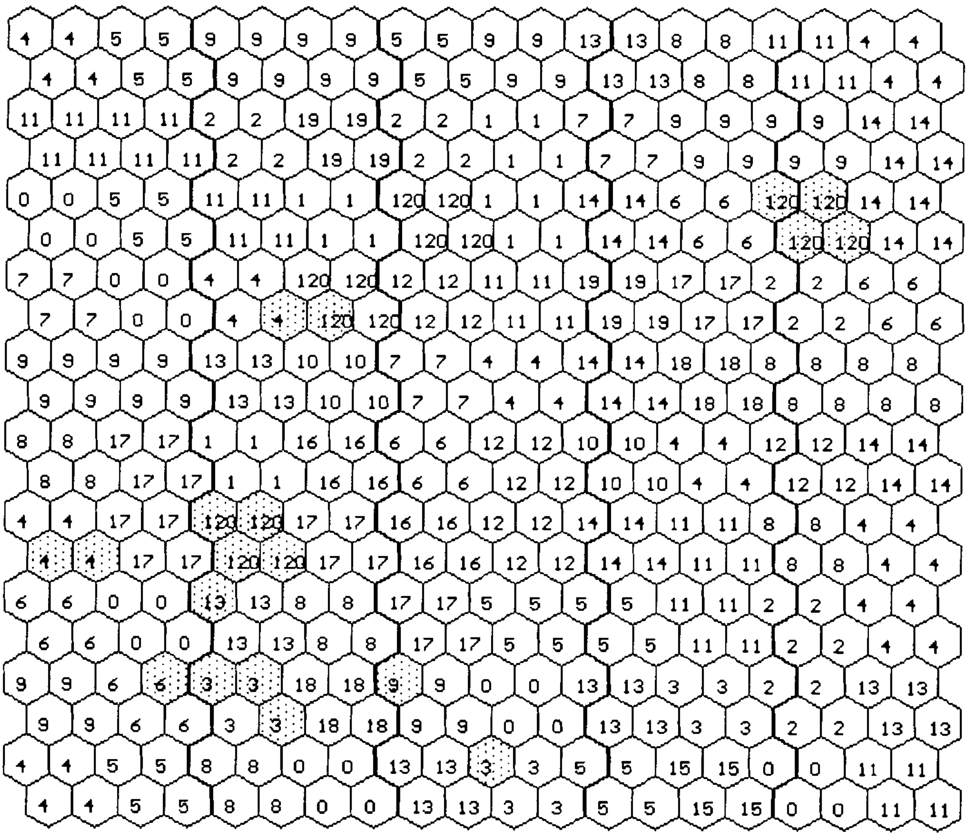
Fig. 3a. Spatial distribution of Bachman's Sparrow at the beginning of a sample simulation. Each hexagonal cell is designated as a territory for a pair of Bachman's Sparrow. Numbers inside each hexagonal cell refer to the age of pine stands. Mature stands are 100 years old. Shaded cells indicate the occupation by the sparrows.

databases that are created in class GENERATE. The information includes patch location, and initial age for each patch. Since patch age changes over time, one function is written to trace the age dynamics. A display function can draw landscapes showing the ages of stands on a computer screen.

3.2.4. ANIMAL

The class ANIMAL obtains information about the initial abundance and distribution of animals in landscapes. Functions of this class calculate population sizes in different habitats and in the whole landscape. Animal occupation in each cell is stored in a database. Spatial and temporal distribution of animals across landscapes can be displayed on a computer screen in colors, indicating presence and absence. For the Bachman's

(b)



4	4	5	5	9	9	9	9	5	5	9	9	13	13	8	8	11	11	4	4
4	4	5	5	9	9	9	9	5	5	9	9	13	13	8	8	11	11	4	4
11	11	11	11	2	2	19	19	2	2	1	1	7	7	9	9	9	9	14	14
11	11	11	11	2	2	19	19	2	2	1	1	7	7	9	9	9	9	14	14
0	0	5	5	11	11	1	1	120	120	1	1	14	14	6	6	120	120	14	14
0	0	5	5	11	11	1	1	120	120	1	1	14	14	6	6	120	120	14	14
7	7	0	0	4	4	120	120	12	12	11	11	19	19	17	17	2	2	6	6
7	7	0	0	4	4	120	120	12	12	11	11	19	19	17	17	2	2	6	6
9	9	9	9	13	13	10	10	7	7	4	4	14	14	18	18	8	8	8	8
9	9	9	9	13	13	10	10	7	7	4	4	14	14	18	18	8	8	8	8
8	8	17	17	1	1	16	16	6	6	12	12	10	10	4	4	12	12	14	14
8	8	17	17	1	1	16	16	6	6	12	12	10	10	4	4	12	12	14	14
4	4	17	17	120	120	17	17	16	16	12	12	14	14	11	11	8	8	4	4
4	4	17	17	120	120	17	17	16	16	12	12	14	14	11	11	8	8	4	4
6	6	0	0	13	13	8	8	17	17	5	5	5	5	11	11	2	2	4	4
6	6	0	0	13	13	8	8	17	17	5	5	5	5	11	11	2	2	4	4
9	9	6	6	3	3	18	18	9	9	0	0	13	13	3	3	2	2	13	13
9	9	6	6	3	3	18	18	9	9	0	0	13	13	3	3	2	2	13	13
4	4	5	5	8	8	0	0	13	13	3	3	5	5	15	15	0	0	11	11
4	4	5	5	8	8	0	0	13	13	3	3	5	5	15	15	0	0	11	11

Fig. 3b. Spatial distribution of Bachman's Sparrow at the year 20 of a sample simulation. Note the mature stands are now 120 years old. The ages of other stands are the same as in Fig. 3a because all stands have gone through a complete rotation. Most of the individuals are in mature stands and population size is much smaller than the initial population size shown in Fig. 3a.

Sparrow example, the population size and distribution are based on censuses at the start of the breeding season (see the life cycle paradigm in Pulliam (1988) and Pulliam et al. (1992)).

3.2.5. *HABITAT*

The class HABITAT includes functions that identify habitat types utilized for reproduction by the animals.

3.2.6. *DEMOGRAPHY*

This class contains information and functions about reproductive success and survivorship of adults and juveniles. Reproductive success is habitat specific. In other words, it depends on the habitat type where breeding occurs. For example, Bachman's Sparrow breeds in three habitat types: mature stands ($\geqslant 80$ years), young stands of 1–2 years old and 3–5 years old. In Pulliam et al. (1992) a pair of Bachman's Sparrow was assumed to produce 1.5 female offspring in mature stands and 1–2-year stands, but only 0.5 female offspring in lower quality, 3–5-year-old stands. No reproductive success was given in other age classes (i.e., stands older than 5 years and younger than mature stands) (Dunning and Watts, 1990; Pulliam et al., 1992). These values were derived from estimates of the total reproductive success (Haggerty, 1986; Dunning and Watts, 1990) and the assumption that the sex ratio was 1 : 1 (Pulliam et al., 1992). For simplicity, ECOLECON simulated dynamics of a single sex (female) of Bachman's Sparrow (Pulliam et al., 1992).

On the basis of literature and field investigation (see Haggerty, 1986; Dunning and Watts, 1990; Pulliam et al., 1992), ECOLECON assumed adult survivorship of Bachman's Sparrow to be 60% and the juvenile survivorship 40% in all patches in most simulation studies.

3.2.7. DISPERSAL

The DISPERSAL class consists of functions that implement the juvenile and adult dispersal processes. Juveniles and adults may follow very different dispersal strategies. The juvenile dispersal process modeled in ECOLECON allows for inheritance of the natal patch and search for new patches. If the parents have died, one female juvenile may stay in the natal patch. The remaining female juveniles move out in order to find suitable patches. Before deciding which way to move, a dispersing juvenile detects the quality of the "neighboring patches" (patches immediately adjacent to the focal patch) and determines if one of them is suitable. If there is one or more suitable neighboring patches, then the juvenile randomly moves into one of them and detects if it is occupied. I presume that the juvenile moves on if the patch is already taken. If no neighboring patches are suitable, the disperser randomly moves into one of them and looks again for a neighboring suitable patch. This dispersal process continues until the juvenile finds a suitable and unoccupied patch, or until the disperser dies. A disperser has a fixed mortality probability each time it moves from one patch to another (Pulliam et al., 1992).

For an adult dispersal, if the occupying patch becomes unsuitable for reproduction, and if there are suitable neighboring patches, the adult moves to one of the suitable adjacent patches. Otherwise, adults do not move to new locations.

In Pulliam et al. (1992), a disperser could identify the quality only of immediately adjacent neighboring patches. To provide a greater range of variability in dispersal rules, ECOLECON has relaxed this restriction. This

TABLE 2

Functions of yield and growth prediction for loblolly pines (adapted from Borders et al., 1990)

Variables	Equations	Parameters	
Initial dominant height (IHD)	$IHD = \exp(c1/iage + c2 * (\ln(SI) + c3) * \exp(c4/iage))$	$c1 = -35.3202$ $c3 = 1.4128$	$c2 = 0.85152$ $c4 = 4.01832$
Dominant height (HD)	$HD = \exp(c1/age + c2 * (\ln(SI) + c3) * \exp(c4/age))$	SI = 60 (site index) iage = 10 years (initial stand age) age = age of interest (in years)	
Trees per acre (TPA)	$TPA = c1 + ((ITPA - c1)^{c2} + c3 * (HD/c4)^{c5} - (IHD/c4)^{c5})^{c6}$	$c1 = 25$ (year) $c3 = 0.00047$ $c5 = 4.08722$ ITPA = 600 (initial trees per acre)	$c2 = -1.45382$ $c4 = 100$ $c6 = -1/1.45382$
Basal area per acre (BAPA)	$BAPA = \exp(c1/age) * HD^{(2c + c3/age)} * TPA^{(C4 + c5/age)}$	$c1 = -51.13703$ $c3 = 5.23322$ $c5 = 4.84386$	$c2 = 0.81396$ $c4 = 0.28078$
Volume per acre (VPA)	$VPA = \exp(c1) * HD^{c2} * TPA^{c3} * BAPA^{c4}$	$c1 = -1.74685$ $c3 = 0.05221$	$c2 = 1.20281$ $c4 = 0.96452$
Relative spacing (RS)	$RS = ((c1/TPA)^{c2})/HD$	$c1 = 43560$	$c2 = 0.5$
Quadratic mean diameter (D)	$D = ((BAPA/TPA)/c1)^{c2}$	$c1 = 0.00545$	$c2 = 0.5$
Volume over 3.5 inches of DBH	$VPA35 = VPA * \exp(c1 * (c2/D)^{c3} + c4 * RS^{c5} * (DBH35/D)^{c6})$	$c1 = 0.51428$ $c3 = 3.76584$	$c2 = 4$ $c4 = -0.33752$
Volume over 7.5 inches of DBH	$VPA75 = VPA * \exp(c1 * (c2/D)^{c3} + c4 * RS^{c5} * (DBH75/D)^{c6})$	$c5 = -0.12110$ DBH35 = 3.5 (inches)	$c6 = 5.49547$
Volume over 11.5 inches of DBH	$VPA115 = VPA * \exp(c1 * (c2/D)^{c3} + c4 * RS^{c5} * (DBH115/D)^{c6})$	DBH75 = 7.5 (inches) DBH115 = 11.5 (inches)	
Pulpwood volume (PVPA)	PVPA = VPA75-VPA35		
Chip-and-saw volume (CVPA)	CVPA = VPA115-VPA75		
Sawtimber volume (SVPA)	SVPA = VPA115		

allows the user to consider how differences in the ability to detect more distant patches influence dispersal of individuals and, ultimately, population dynamics. The detection ability of an individual is represented by how many surrounding "rings" of neighboring patches in which the disperser can distinguish habitat quality. The first ring of neighboring patches are those immediately adjacent to the occupied patch; the second ring of neighboring patches are those one patch away from the disperser; the third ring is two patches away, etc.

3.2.8. ECONOMY

This class includes the growth and yield functions for loblolly pines in southeastern coastal regions. ECOLECON simulates tree growth based on an index of site quality and initial tree density. Site index is a measurement of timber production potential of a site for a particular tree species (Clutter et al., 1983). It is usually expressed by the average heights of dominants and codominants at a specified reference age. The simulations presented here assume that (1) average site index is 60 feet (or 18.3 m) at base age of 25 years and (2) initial tree density is 600 trees per acre (4047 m^2) where initial age is 10 years. All functions are adapted from Borders et al. (1990) and (Souter, pers. commun., 1991) (Table 2) and they are suitable for trees which are 10 years or older. The steps to make a growth projection and a yield prediction are as follows:

(1) Calculate the initial dominant height (IHD) and the dominant height (HD) using the age of interest for each particular prediction.
(2) Calculate the surviving trees per acre (TPA).
(3) Calculate the basal area per acre (BAPA).
(4) Calculate the total timber volume per acre (VPA).
(5) Calculate the relative spacing (RS).
(6) Calculate the quadratic mean diameter (D).
(7) Calculate the timber volumes for pulpwood, chip-and-saw and sawtimber.

The criterion to define the above three categories of timbers is the diameter at breast height (DBH, in inches, 1 inch = 2.54 cm): pulpwood ($3.5 \leqslant \text{DBH} < 7.5$), chip-and-saw ($7.5 \leqslant \text{DBH} < 11.5$), sawtimber ($\text{DBH} \geqslant 11.5$). Before obtaining timber volume in each category, it is necessary to calculate timber volume with three DBH values (11.5, 7.5, and 3.5 inches). The timber volume with DBH = 3.5 (VPA35) consists of all the trees whose DBHs are $\geqslant 3.5$ inches. Similarly, timber volume with DBH = 7.5 (VPA75) includes timber whose DBHs are > 7.5 inches; and timber volume with DBH = 11.5 inches (VPA115) covers timber whose DBHs are > 11.5 inches. The harvest volume is the sum of all of these, assuming the timber is clear-cut.

3.2.9. INCOME

This class deals with the algorithms to calculate timber income. The algorithms must be specific to both the region being considered and the timber crop. Based on the stumpage price published by Timber Mart–South, Inc. in North Carolina (Norris, 1990), I chose timber prices for Area 2 (Piedmont–Savannah) in Georgia. The prices for the above three categories of timbers are 0.42 $\$/\mathrm{ft}^3$ (pulpwood; 1 $\mathrm{ft}^3 = 28317\ \mathrm{cm}^3$), 0.75 $\$/\mathrm{ft}^3$ (chip-and-saw), and 0.91 $\$/\mathrm{ft}^3$ (sawtimber). Therefore, the total timber income per acre (TIPA) (dollars per acre) is:

$$\mathrm{TIPA} = 0.42 * \mathrm{PVPA} + 0.75 * \mathrm{CVPA} + 0.91 * \mathrm{SVPA}.$$

Incomes from all forest stands are summed every year to estimate annual income in the entire forest.

3.2.10. COST

The class COST includes costs for forest regeneration and annual property tax and administration (Cubbage et al., 1991; Dubois et al., 1991). I assume a tax and administrative cost of $6 per acre per year, and an average regeneration cost of $176.53 per acre (including $125 for site preparation, $21 for seedlings and $30.53 for planting). Timber buyers pay the cost of cutting trees, but forest owners will obtain lower income if a tract is less than or equal to 60 acres (or 242 820 m^2). Harvest on small tracts are less profitable due to the fixed costs of moving equipment, etc. This is accounted for in the model by an "income deduction" (ID, $ per acre) for small tracts. The following models of calculating income deduction are constructed using the information provided by Cubbage (pers. commun., 1991).

For pulpwood:

$$\mathrm{ID} = 0.01 * (17.702 - 9.9114 * \log(\mathrm{tract\_size})) * \mathrm{PVPA}.$$

For chip-and-saw:

$$\mathrm{ID} = 0.01 * (17.702 - 9.9114 * \log(\mathrm{tract\_size})) * \mathrm{CVPA}.$$

For sawtimber:

$$\mathrm{ID} = 0.01 * (10.606 - 5.854 * \log(\mathrm{tract\_size})) * \mathrm{SVPA}.$$

Where PVPA, CVPA, and SVPA are respectively the volume of pulpwood, chip-and-saw, and sawtimber in one acre.

Costs for each forest stand are summed each year to estimate annual costs for the entire forest of interest.

3.2.11. NET_INCOME

Functions of class NET_INCOME calculate the difference between annual incomes and annual costs and report this difference as the annual net income. Class NET_INCOME also provides two other financial criteria: net present value (NPV) and land expectation value (LEV). Net present value is the summation of net annual income within a rotation discounted to year 0 at a certain discount rate (Cubbage et al., 1991). The formula is given as

$$\mathrm{NPV} = \sum_{t=0}^{n} \frac{R_t - C_t}{(1+i)^t}$$

where t is the number of years in the future with a given reference year 0; n is the number of years in a rotation; R_t is the benefits in year t; C_t is the costs in year t; and i is the discount rate.

Land expectation value (LEV) is the total value of a management scheme maintained in perpetuity at a given discount rate. The formula to calculate land expectation value is

$$\mathrm{LEV} = \mathrm{NPV} + \left\{\mathrm{NPV}/\left[(1+i)^n - 1\right]\right\},$$

where NPV is the net present value; n is the number of years in a rotation; and i is the discount rate.

Both NPV and LEV are common criteria for financial investment decisions. If NPV and LEV are positive, the management scheme is generally considered financially acceptable, otherwise, it is unacceptable. Note that the calculation of LEV is based on NPV. It is useful to use LEV when rotation lengths are not the same under different management regimes (Cubbage et al., 1991).

3.2.12. OUTPUT

This class contains functions to store simulation results in disk files and draw the resulting population dynamics and annual changes in net income on a computer screen. POP_OUTPUT is a subclass of OUTPUT. Functions in this subclass store the results in databases for more detailed analyses. Databases consist of population dynamics (including extinction time) in different patches for each replicate as well as average population size and extinction rate during a period of time for all replicates.

ECONOMY_OUTPUT is another subclass of OUTPUT, which saves economic outputs to disk files. The files store annual net income, net present value and land expectation value for each replicate, and averaged values of the above three economic indexes over all replicates.

4. A SAMPLE SIMULATION

The results of applying ECOLECON and sensitivity analyses are demonstrated in Liu (1992, 1993) and Liu et al. (1993a,b). In order to demonstrate how ECOLECON works, this paper just shows a simple case simulating Bachman's Sparrows in a hypothetical forest consisting entirely of pine stands. The sample simulation has 10 replicates with 100 years of simulation for each replicate. The hypothetical forest consists of 400 hexagonal cells (Fig. 3), each of 2.5 ha (or 25 091 m^2); therefore the whole forest is 1000 ha in size. Each forest stand is 10 ha and made of 2 × 2 adjacent cells. There are four mature stands which are randomly distributed in the forest and are never harvested. Besides the mature stands, there are 20 other types of randomly distributed stands in the forest representing 20 age classes (0–19 years) of trees in a 20-year rotation.

I assume that cells of mature stands, 1–2-year stands and 3–5-year stands have initial probabilities of 0.8, 0.5, and 0.3, respectively, of being occupied by Bachman's Sparrow. Dispersing individuals continue searching until they find an unoccupied suitable patch. Each disperser has a mortality of 0.02 when it moves from one patch to another. From a specific cell, a disperser can only identify the quality of immediately adjacent patches and it chooses randomly among suitable neighboring patches. Annual abundance and distribution can be seen for each replicate (Fig. 3a and b).

Fig. 4 shows the average simulation results of ten runs. Because annual population size changes dramatically during the first rotation, I calculate the average population size using the annual population size during the last four rotations of each replicate. Since the initial distribution of stands is random, the number of stands in each age class is not exactly the same. Therefore, annual net income is not constant between years.

As shown in Table 3, the population in the whole landscape is about 21 individuals, and about half of the individuals are found in mature stands. In this example, no populations go extinct and, therefore, extinction probability is 0. Average annual net income is \$166 401, while net present value and land expectation value are about \$2 million and over \$3 million, respectively.

5. CONCLUSIONS AND DISCUSSION

The model has been validated using field data. Many validation processes are still under away (Dunning and Pulliam, pers. commun., 1992). Fig. 5 shows an example of validation results. There is no significant difference between the observed and predicted distribution of Bachman's Sparrow in different ages of stands ($\chi^2 = 0.837$, d.f. = 6).

The model ECOLECON is useful in three major aspects: research, education, and forest management. First, it is an important research tool for testing hypotheses, guiding collection of field data, predicting future changes of landscapes, population dynamics, and financial cash flows. Like

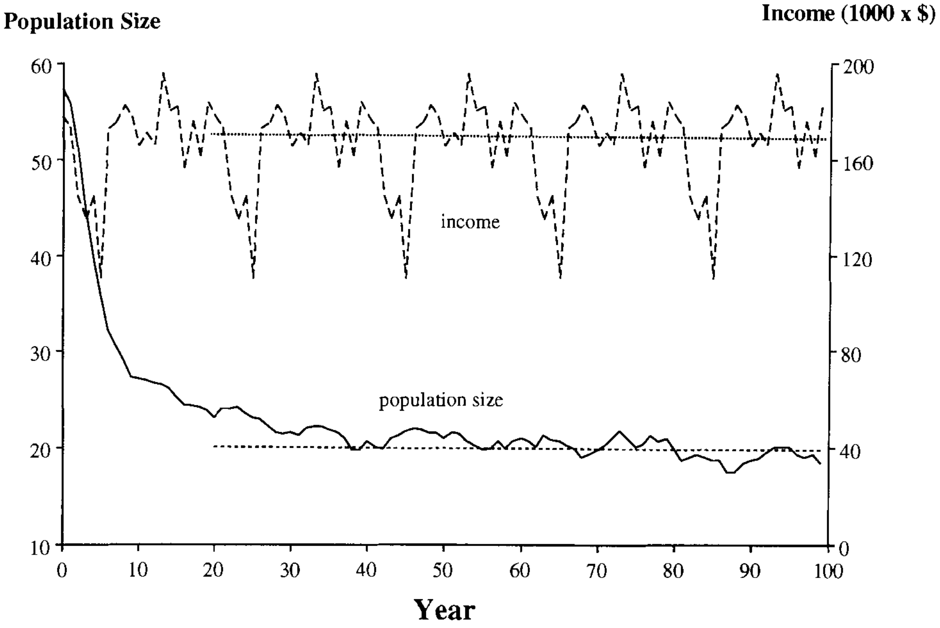


Fig. 4. Population dynamics (solid line) and annual changes of net income (dashed line) of the sample simulations. The population size decreases significantly in the first rotation (20 years) and then remains relatively stable. The net income exhibits cyclic changes. The average net income and average population size over the last 80 years (4 rotations) are indicated by horizontal lines.

BACHMAP (Pulliam et al., 1992), ECOLECON can be a powerful tool to determine where to place emphasis in field work using sensitivity analysis. There are many factors influencing population dynamics, and it is impossible to investigate the roles of all the variables. By changing values of various parameters in the model and determining how much the results are changed, I can see which variables in the model have the highest sensitivi-

TABLE 3

Population sizes and economic revenues from sample simulations

I. Average population size	
Total population size	20.60
Population size in mature stands	10.74
Population size in other stands	9.86
II. Economic revenues (discount rate = 0.05)	
Annual net income ($)	166401
Net present value ($)	2149679
Land expectation value ($)	3449916

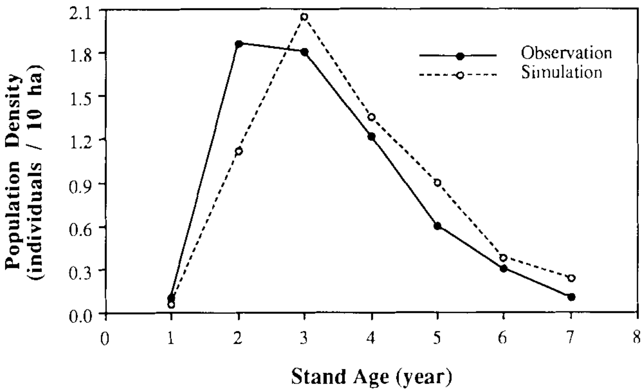


Fig. 5. Distribution of Bachman's Sparrow in different ages of stands. The field data were collected at the Savannah River Site, 1991, by John B. Dunning, Jr. and René M. Borgella, Jr. The simulations were done on an artificial forest of 40×20 hexagonal cells (2000 ha). Each stand consisted of four adjacent cells (2×2). There were eight mature stands and the remaining stands were with equal probability divided into 21 age classes (year 0 to year 20). All the stands were randomly distributed. It was assumed that annually a pair of adults produced 1.5 female offspring in 1–2-year stands and mature stands, and 0.5 female offspring in 3–5-year stands. Adult and juvenile mortalities were set at 60% and 40% respectively. A dispersing juvenile could search for 50 cells or patches (expected value) and settled down in 1–2-year or mature stands only. The forest was harvested at rotations of 21 years each. Each simulation was run for 105 years (5 rotations). The population size was the average of the last 4 rotations over 10 simulations.

ties to small changes in the values of the parameters of interest. These would be the key variables which the field work should emphasize.

ECOLECON is being modified for other species. Modifications may include changes in some functions and parameters, such as demographic variables and dispersal functions. Establishment of function and parameter libraries suitable for different species in various forest landscapes will result in a more general model.

The second major aspect of the model that has proven useful is its potential as a heuristic educational tool. For example, the model has been used for teaching undergraduate and graduate students.

The third aspect of ECOLECON's utility will be as a valuable tool for management of biodiversity of forest landscapes. As demonstrated in Liu (1992) and Liu et al. (1993a,b), once fully parametrized, the model should be helpful for forest managers balancing the conflicts between economic and environmental goals. Liu (1992) studies the effects of forest structure and configurations as well as rotation length on economic income and population dynamics of Bachman's Sparrow. The simulation results have significant implications for forest design and management. Through linkage to a geographic information system (GIS), Liu (1992) also simulates some population and economic consequences of the "Savannah River Site Wildlife, Fisheries, and Botany Operation Plan" at the Savannah River Site, South Carolina (Savannah River Forest Station, 1992). The results show that although the Operation Plan might realize the long-term objective for maintaining Bachman's Sparrow, there is a long transition period when the population size is far below the minimum management goal. The management goals of generating economic income and maintaining the sparrow population are affected differentially by different harvest strategies. If the eligible stands are cut in clusters, it is most beneficial to the sparrow population. Harvesting the oldest stands first results in maximum gross income. When the eligible stands are harvested randomly, both the average economic revenue and population size are the lowest, and the sparrow population never reaches the minimum management objective. ECOLECON provides a method of balancing these two management goals.

In its present version, ECOLECON deals with one species of animal occupying forest plantation of one species of trees. It is feasible, however, to expand the model so that multiple species of animals and trees can be incorporated.

Timber price and site index of forests as well as some other variables in ECOLECON are treated as constants. In reality these variables are changing all the time. If information about these changes is known, the dynamic characteristics can be easily added to the model. Alternatively, ECOLECON can be linked to other models which attempt to predict these trends in parameters.

It is my hope that the approach used in constructing ECOLECON and the model itself would be beneficial to other researchers, conservationists, forest managers, business executives, policy-makers, students, and general citizens who face the conflicts between conservation and economic development.

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