Ecological and economic effects of forest landscape structure and rotation length: simulation studies using ECOLECON

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Abstract

ECOLECON is a spatially-explicit, object-oriented computer simulation model that simulates animal population dynamics and economic yield from timber harvests based on forest landscape structure and timber management schemes. The model has been parameterized to simulate the population dynamics and extinction probability of Bachman's Sparrow (*Aimophila aestivalis*), a species of management concern in southeastern pine forests. Simulations with ECOLECON have shown that forest landscape structure and management options such as rotation lengths influence both population sizes of the sparrows and economic returns from timber harvests. Sparrow population size and economic income were often maximized by different management strategies. For example, land expectation value reached a maximum when a rotation length was 20 years; however, whenever harvest rotation length was shorter than 80 years, sparrow population size had a negative linear relationship with rotation lengths. As the amount of mature pine habitat increased, sparrow population size increased, but annual net income decreased. Fragmentation of landscapes with only a small amount of mature habitat caused lower population sizes, but fragmentation of landscapes with a large amount of mature habitat resulted in a larger population size. Differences in placement of the mature habitat within the landscapes resulted in large differences in population size. Larger stand sizes produced higher economic revenues, but the effect of stand size on population size was confounded by the amount of mature habitat. Simulation models such as ECOLECON provide a potentially powerful tool for balancing wildlife population needs and economic revenues through designing and managing forested landscapes.

Key words: Bachman's Sparrow; ECOLECON; Forest management; Modelling

1. Introduction

Advances in technology and the management of exploited ecosystems have resulted in a more efficient human economy, but at the same time have caused serious ecological problems, including the rapid extinction of species (May, 1988).

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The rate of species extinction in some forests because of human interference is now estimated to be between 1000 and 10000 times higher than the natural extinction rate (Wilson, 1988). Although great efforts have been taken to conserve endangered and threatened species around the world (Council on Environmental Quality and U.S. Department of State, 1980; Soulé, 1986; Shaffer and Saterson, 1987; World Commission on Environment and Development, 1987), there still exist many challenges for conservation research and practice (Office of Technology Assessment, 1987; Lubchenco et al., 1991; Brussard and Ehrlich, 1992). Since the major cause for species extinction is the destruction of habitats due to human economic activities (Ehrlich, 1988), one of the biggest challenges is to reduce the conflict between economic development and species conservation (Dixon and Juelson, 1987; Salwasser, 1987).

Coordination of the economy and conservation may be achieved by applying theories and methods of the emerging field of ecological economics, which is an interdisciplinary science of the relationship between ecology and economics (Costanza et al., 1991). From the long-term point of view, it is essential to balance conservation and economic development because conservation and economic welfare are interdependent. Species conservation cannot be realized without financial support and development of new technology (Conway, 1980, 1988; Cade, 1988); the human economy cannot be sustained without natural resources and the life-supporting environment, including biological diversity (Norton, 1988; Plotkin, 1988; Balick and Mendelsohn, 1992; Costanza and Daly, 1992).

Debates about how to protect or manage forested landscapes and conserve endangered species are increasing (Dixon and Juelson, 1987; Marcouiller and Ellefson, 1987). Some of these disagreements focus on differences in personal values; some focus on inadequate biological and economic information. Most interest groups rely on ecological and economic studies and criteria when disputing appropriate management actions. The research disputes are largely due to a lack of systematic and integrative studies, since land-scape ecologists have been focusing their attention on ecological effects of landscape structure (e.g., Risser et al., 1984; Forman and Godron, 1986; Addicott et al., 1987; Pulliam and Danielson, 1991; Turner and Gardner, 1991; Dunning et al., 1992), while forest economists have been studying the economic impacts of management options such as rotation lengths (e.g., Clark, 1976; Clutter et al., 1983; Buongiorno and Gilless, 1987; Davis and Johnson, 1987; Gregory, 1987; Newman, 1988; Huntley, 1990; Neher, 1990). More integrated and simultaneous studies on the ecological and economic consequences of landscape structure can help reduce scientific uncertainty about the effects of forest management (Costanza, 1991). Better information can help reduce scientific disagreements among interest groups about resource management, and perhaps suggest more acceptable management methods (Seagle et al., 1987; Halbert and Lee, 1990; Lubchenco et al., 1991).

Modeling is a powerful tool for predicting ecological-economic phenomena (Costanza et al., 1991). Existing ecological-economic models have proven useful in predicting ecological and economic impacts (Braat and van Lierop, 1987; Costanza, 1991) in such diverse cases as 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 (Odum and Arding, 1991). To our knowledge, however, no landscape models explicitly combining economic yields and species conservation have been developed prior to ours.

In this paper, we explore both the ecological and economic impacts of forested landscape structure and rotation lengths by the application of ECOLECON, an ECOLogical-ECONomic computer simulation model which can simulate animal population dynamics and economic revenues in response to various landscape structures and timber management scenarios (Liu, 1992). We will begin with an introduction to the simulation methods, then present simulation results, and finally discuss implications of the results for balancing the conservation of endangered species

and the generation of economic revenues through designing and managing forests.

2. Methods

2.1. The model ECOLECON

ECOLECON is a spatially-explicit model for the study of the relationships between species conservation and economic yields in forested landscapes (Liu, 1992). The model consists of both economic and ecological components that are hierarchically interlinked. Economic information includes forest growth and yield, income, cost, and net income. Ecological components incorporate animal habitat selection, demography, and dispersal processes. The model predicts animal population dynamics, spatial distribution, and extinction probability, as well as future landscape structure and economic income from timber harvest (Liu, 1992). ECOLECON was programmed in Borland C + + 2.0 (Borland International, 1991) and can be implemented on IBM or IBM-compatible computers.

ECOLECON is an individual-based grid model (Fahrig, 1988) since it follows each individual in the population through its annual cycle of birth, dispersal, and reproduction (Pulliam, 1988). Landscapes are represented in the model as grids of hexagonal cells. Each cell is the size of a territory used by a breeding pair of the animal species under consideration. Habitat succession is mimicked by increasing the age of habitat in each grid cell at the end of each simulated annual cycle. Forest stands (clumps of cells of the same age) are harvested when they reach an appropriate age specified in the timber management regimes.

2.2. Forested landscapes

ECOLECON can operate on forested landscapes of any size. The results reported in this paper were from landscapes consisting of an array of 20 × 20 hexagonal cells (1000 ha). At the start of each simulation, the cells were usually assigned to 20 age classes (holding trees from 0 to 19 years) in addition to mature stands ($\geqslant 80$ yr). Unless mentioned otherwise, each forest stand consisted of four adjacent cells (2 × 2), totalling 10 ha. All stands were randomly distributed on the landscape. Stands of the 0-year age class were just harvested. It was assumed that mature stands were never harvested and always provided suitable habitat for Bachman's Sparrow.

2.3. Bachman's Sparrow

For the simulations presented in this paper, we set the parameters of ECOLECON to be suitable for Bachman's Sparrow (*Aimophila aestivalis*) in loblolly pine (*Pinus taeda*) forests. Bachman's Sparrow is a potentially threatened species and of management concern in the southeastern United States (Dunning and Watts, 1990) because the range of this species has been declining for several decades (Haggerty, 1986; Hunter, 1990). Bachman's Sparrow prefers habitats with relatively dense ground vegetation, but an open understory, such as is found in young pine stands (1–5 years) and mature ($\geqslant 80$ years) pine stands that are frequently burned (Dunning and Watts, 1990). The sparrows are territorial with average territory size of about 2.5 ha (Haggerty, 1986; Pulliam et al., 1992), thus each grid cell of appropriate habitat can hold one pair of the sparrows.

Since the information on the sparrows' ecology and biology is incomplete, we made some assumptions on reproductive success, survivorship, and dispersal. All parameter values were based on information from field investigations (Haggerty, 1986; Dunning and Watts, 1990; Hunter, 1990). Pulliam et al. (1992) described how the best estimates for each parameter were obtained for Bachman's Sparrow. For parameters which were most uncertain, Pulliam et al. (1992) performed a detailed sensitivity analysis choosing combinations of parameters from the entire feasible range. The results showed that population dynamics were most sensitive to demographic parameters (adult and juvenile survivorship), but relatively insensitive to variation in dispersal parameters. Field efforts to improve the parameter estimates are currently focusing on obtaining bet-

ter measurements for the most sensitive parameters.

In all simulations, annual adult survivorship of Bachman's Sparrow was assumed to be 60% and juvenile survivorship (prior to dispersal) was set at 40%. The sex ratio was assumed to be about 1:1 (Pulliam et al., 1992). We modeled the sparrow population dynamics using female individuals only so that the model complexity was reduced.

Reproductive success was assumed to vary among habitat age classes: 1.5 female offspring per pair per year in 1–2-year and mature patches, 0.5 female offspring in 3–5-year patches, and 0.0 female offspring in all other age classes (Liu, 1992). These values were averages for each habitat category. In the model, the actual reproductive success for a given territory in a given year was a random variable chosen from a distribution based on field observations.

It was assumed that dispersing juveniles searched until they found suitable patches or died. Dispersal mortality was set so that the expected number of patches searched by each dispersing juvenile before dying was 50. We further assumed that there were no immigrants and the dispersing juveniles never moved off of the simulated landscape. When the dispersing juveniles reached a landscape edge, they moved back into the landscape, i.e., the landscape boundaries were reflective. (This assumption is appropriate for forested landscapes surrounded by uninhabitable lands such as croplands or water.) Detailed rules for juvenile and adult dispersal can be found in Liu (1992) and Pulliam et al. (1992). To initialize the simulations, the sparrows were randomly assigned to half of the suitable patches (1–5-year and mature patches).

2.4. Economic information and criteria

Growth and yield data for loblolly pines were used as the basis for estimating forest stand volumes. The management regime analyzed was an even-aged silvicultural system. Stands were assigned an initial volume based on their initial age, and their timber volume was increased as age increased until harvest. Harvest volumes were estimated using equations from Borders et al.

(1990) and Souter (1991, pers. commun.; see Liu, 1992, 1993a). After the clear-cut harvest, stands were regenerated in the following year.

Economic incomes were generated through harvesting loblolly pines and selling the timber. The prices for three types of timber, pulpwood ($8.9 \leqslant DBH < 19.1$ cm), chip-and-saw ($19.1 \leqslant DBH < 29.2$ cm), and sawtimber ($DBH \geqslant 29.2$ cm), were set at $0.42, $0.75, and $0.91 per cubic foot ($0.0283$ m^3), respectively (Norris, 1990; Liu, 1992). (DBH = diameter at breast height; the metric units are conversion from English units in the forestry literature.) The costs included outlays for stand regeneration, annual property tax, and administration (Cubbage et al., 1991; Dubois et al., 1991). Taxes and administrative cost were set at $6.00 per acre (1 acre = 0.4046 ha) per year, and average regeneration cost was set at $176.53 per acre (including $125 for site preparation, $21 for seedlings, and $30.53 for planting) (Dubois et al., 1991; see Liu, 1992). We also assumed that timber buyers paid the cost of cutting trees, but forest owners obtained lower income if a tract was less than or equal to 60 acres (about 24 ha). Harvests 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 are the equations used for calculating income deduction (Liu, 1992):

For pulpwood:

$$ID = 0.004046 * (21.5969 - 9.9114$$
$$* \log(\text{tract\_size})) * PVPA.$$

For chip-and-saw:

$$ID = 0.004046 * (21.5969 - 9.9114$$
$$* \log(\text{tract\_size})) * CVPA.$$

For sawtimber:

$$ID = 0.004046 * (12.9054 - 5.854$$
$$* \log(\text{tract\_size})) * SVPA.$$

PVPA, CVPA, and SVPA are, respectively, the volume of pulpwood, chip-and-saw, and sawtimber in 1 ha.

Besides annual net income, we used net present value (NPV) and land expectation value

(LEV) as financial criteria. 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

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

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 benefit in year t; C_t is the cost 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

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

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). To estimate net present values and land expectation values, we assumed that the discount rate was 0.05.

2.5. Simulations

All simulations were run for 100 years. Population sizes were averaged over the last 80 years of simulation because the populations usually fluctuated drastically during the first 20 years due to
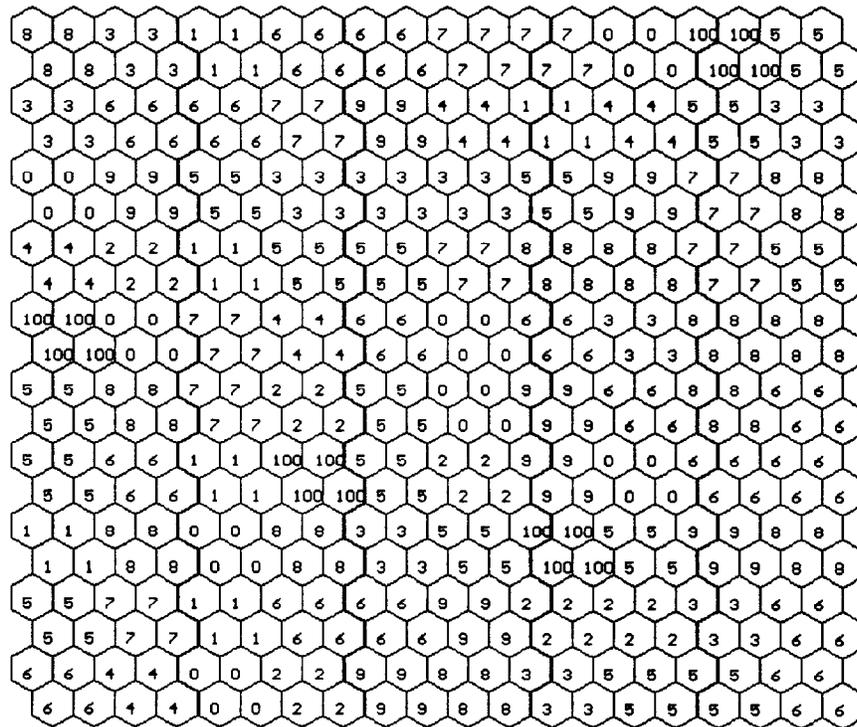

Fig. 1. An initial landscape with 0-9-year stands and four mature stands (age = 100 years). All the stands were randomly distributed. Each stand was made up of four adjacent cells (2 × 2), and each cell was 2.5 ha in size. Numbers inside each hexagonal cell refer to the tree ages.

the initialization of sparrow population sizes. Each simulation run had 10 or more replicates. Each of the points in Figs. 3–9 was based on the average of the runs for a given initial forest structure or a management regime. To test for significance of differences, we used two-tailed t-tests.

In the following, we describe the simulation methods for the effects of rotation lengths and landscape structure on population dynamics of Bachman's Sparrow and economic revenues.

Rotation length. In one set of the simulations, we varied rotation length (the number of years between two harvests) and monitored the population and economic consequences. We set up initial landscapes containing stands assigned to one of 10 age classes (0–9 years), in addition to four mature stands (Fig. 1). Each stand contained four adjacent 2.5-ha cells. Rotation length (RL) varied from 10 to 100 years. A stand was harvested when the stand age was (RL – 1) years. All harvested areas were regenerated 1 year after clear-cutting.

Landscape structure. In another set of simulations, we varied landscape structure to determine the effects on the sparrow dynamics and economic income. Landscape structure has two components, landscape composition and landscape physiognomy (Turner, 1989; Dunning et al., 1992). Landscape composition is the relative amount of each patch type within a landscape, while landscape physiognomy indicates the geometrical arrangements of patches within a landscape (Dunning et al., 1992). We tested the effects of landscape physiognomy by varying the size and placement of critical patches. In these simulations, the landscapes contained the 0- to 19-year-old age classes of patches plus the mature stands, with rotations of 20 years each. We explored the effects of stand sizes and spatial distributions as well as amount, fragmentation and location of mature habitat.

In the simulations that tested the effects of stand size, we varied stand sizes from 2.5 ha (1 cell, 1 × 1), 5.0 ha (2 cells, 1 × 2), 10 ha (4 cells, 2 × 2), 20 ha (8 cells, 2 × 4) to 40 ha (16 cells, 4 × 4). All stands were randomly distributed. Ma-

ture habitat accounted for 8% (32 cells) or 32% (128 cells) of the entire landscape.

Previous modeling studies have suggested that mature stands are one of the most important factors determining population dynamics for Bachman's Sparrow (Pulliam et al., 1992; Liu, 1993b). We studied the impacts of mature stands further with the following simulations:

(a) The percentage of mature stands was varied from 0% to 100% of the 1000-ha landscapes.

(b) All cells of mature habitat (80 ha) were placed as one large block (no fragmentation), or mature habitat cells were divided into four or more equal fragments (fragmented conditions).

(c) The mature stands (160 ha) were placed in the center, on one corner, or randomly distributed on the landscapes.

3. Results

3.1. Forest rotation length

Both population dynamics and annual net income exhibited recurring cycles related to rotation length. In each rotation, population size increased after some stands were harvested and regenerated, then decreased following periods when no stands were cut and regenerated. The magnitudes of the population and income cycles depended on the initial conditions of forest stand age structure and the harvest schedule. If, for example, a 20-year rotation was used and the initial age structure consisted of approximately equal representation of stands ranging from 0 to 19 years old, the cycles were not very pronounced because every year approximately the same amount of timber was harvested and approximately the same amount of habitat became newly suitable for the sparrows.

Fig. 2 shows two examples of simulations with pronounced cycles. In each example, the initial landscape consisted of approximately equal representation of young stands ranging from 0 to 9 years old. In Fig. 2a, rotation length was set at 20 years; accordingly, there was no harvest for the first 10 years of each rotation period and sparrow populations initially declined due to lack of new
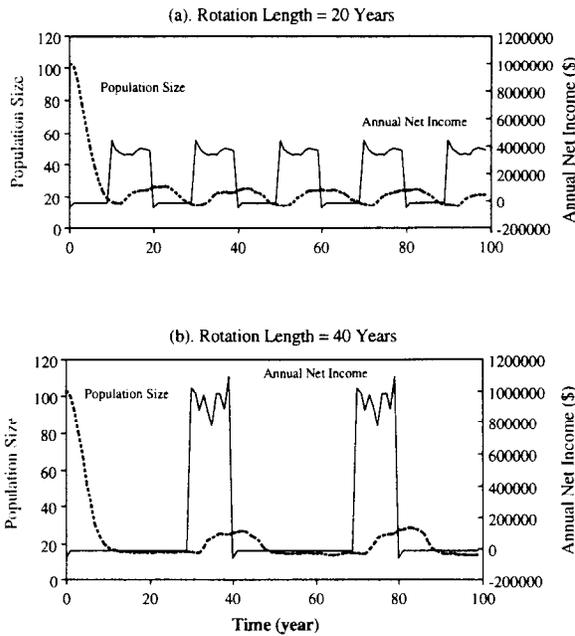
Fig. 2. (a) Dynamics of population size and annual net income. Rotation length was 20 years. (b) Dynamics of population size and annual net income. Rotation length was 40 years.

Fig. 3. The effects of rotation length on population size and land expectation value.

habitat becoming available. As soon as some stands reached 20 years of age, harvesting began and net income rose sharply. Sparrow populations increased after harvesting began, but only after a time lag of a few years. Fig. 2b is similar to 2a except that the rotation length is set at 40 years resulting in a longer period between harvests and, consequently, a longer period between peaks in sparrow population size.

As shown in Fig. 3, land expectation value (LEV) reached a maximum value when rotation length was 20 years. When rotation length was less than 10 years or more than 100 years, LEVs were negative. As rotation length increased from
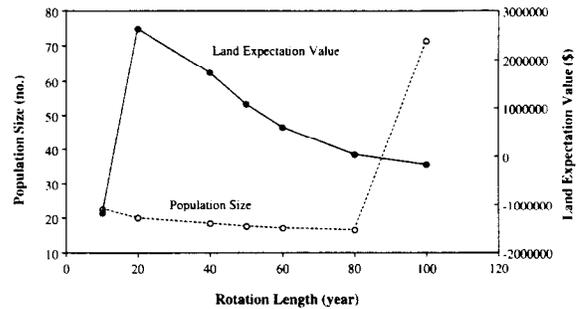
10 to 80 years, population sizes decreased slightly; however, the population size jumped to a very high level on a 100-year rotation due to the fact that the sparrows can breed in stands greater than 80 years old.

3.2. Landscape structure

Stand size. As shown in Fig. 4, annual net income increased significantly with increasing stand size. All the correlation coefficients were significant at a level of $p < 0.01$. This relationship held for both landscapes relatively poor in mature habitat (8% of the entire landscape) and landscapes relatively rich in mature habitat (32% of the entire landscape). Annual net income and net present value (NPV) were logarithmic functions of stand size (Table 1).

In a forest landscape with 8% mature stands, the population size was maximum when stands were 20 ha in size (Fig. 4a), i.e., stand sizes larger or smaller than 20 ha resulted in lower population sizes. For example, the population size for 20-ha stands was significantly higher than that with 40-ha stands or 10-ha stands ($p < 0.0001$

Table 1

Parameters and correlation coefficients (R^2) for functions of annual net income (Y) and net present value (NPV, Y) with stand sizes (X), $Y = a + b * \log(X)$, where a and b are the intercept and slope, respectively

Percentage of mature patches	Annual net income ($)			NPV ($)		
	a	b	R^2	a	b	R^2
8%	143070	25609	0.974	1878200	318670	0.975
32%	101110	19781	0.977	1317500	246380	0.970

and $p < 0.0031$, respectively). Stands of 2.5 ha and 5 ha generated both low economic revenues and small population sizes.

When mature stands accounted for 32% of a forest landscape, 5-ha stands had the highest population size (Fig. 4b). Population sizes decreased as stand sizes became bigger or smaller than 5 ha. Stands of 2.5 ha resulted in approximately the same population size as 10-ha stands ($p = 0.7654$).

Amount of mature habitat. The percentage of mature habitat in a landscape is a key factor in determining population sizes of Bachman's Sparrow (Liu, 1993b). Pulliam et al. (1992) found that in landscapes containing 0-4% mature stands, population sizes increased with increasing mature stands. In the simulations reported here, we varied mature habitat from 0% to 100%. The simulation results were consistent with the conclusions of Pulliam et al. (1992) and Liu (1993b). Popula-

Fig. 5. Annual net income and population size as functions of the percentage of the mature pine habitat. As amount of mature stands increased, population size increased but annual net income decreased.

tion sizes were a 3rd-order polynomial function of percentage of mature stands (Fig. 5), given by the following relationship:

$$P = -8.6269 + 8.7551M - 0.0848M^2 + 0.0038M^3,$$

where P is the population size, and M is the percentage of mature habitat cells ($R^2 = 0.99$, $n = 6$). When there was no mature habitat present in the landscape, sparrow populations always went extinct before the end of simulations and the population size at the end of simulations was zero (Fig. 5). When a landscape consisted entirely of mature habitat, the average population size (399.9) was essentially the same as the number of cells in the landscape (400); that is, virtually all of the landscape was occupied by Bachman's Sparrow.

As the percentage of mature habitat in a landscape increased, the annual net income was exactly inversely proportional according to the following function:

$$Z = 173950 - 1887.8M,$$

where Z is the annual net income and M is the percentage of mature habitat cells. When the whole forest landscape was mature, the net income was negative since there was no economic revenue from harvesting trees, but some money was spent for forest maintenance. From Fig. 5, when mature habitat covered about 92% of the landscape, the income from timber harvest just offset the management cost, and therefore the net income was zero.
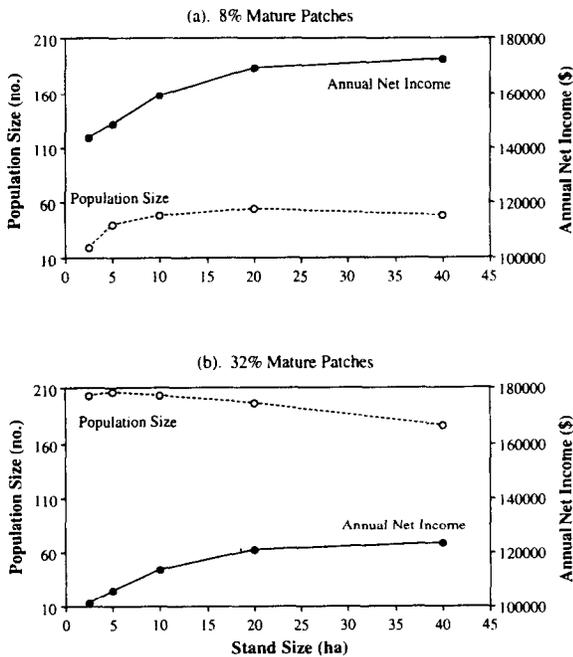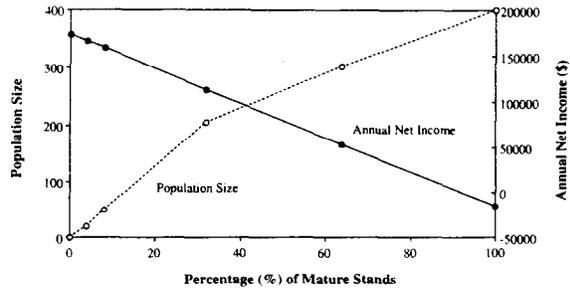

Fig. 4. The effects of stand sizes on population size and annual net income, (a) when 8% of the landscape was mature cells, and (b) when 32% of the landscape was mature cells.
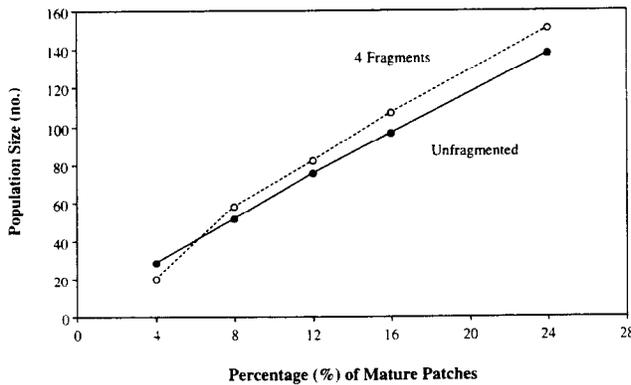
Fig. 6. The effects of fragmentation of mature stands on population size. The population sizes resulting from fragmentation and non-fragmentation were significantly different ($p < 0.01$).
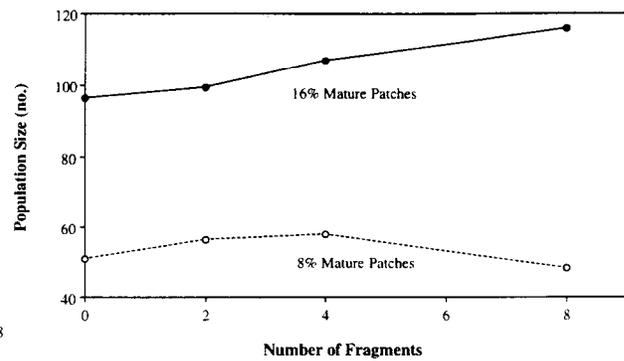

Fig. 7. The relationship between population size and degree of fragmentation of mature habitat in landscapes containing either 8% or 16% mature pine habitat.

Fragmentation of mature habitat. In the model, mature pine stands were the best habitat for Bachman's Sparrow because they allowed the highest reproductive success and were suitable for breeding every year. To test for the importance of fragmentation of mature habitat in the landscape, we chose different amounts of mature habitat divided into either one (unfragmented) or four equal fragments. With 4% mature stands in the landscape, fragmentation caused lower population sizes than non-fragmentation (Fig. 6). However, fragmentation of larger amounts of mature stands resulted in larger population sizes.

Mature stands in the simulations discussed above were only divided into four fragments. We also explored the consequences of different degrees of fragmentation by varying the number of fragments from 2 to 8 (Fig. 7). When the mature stands accounted for 16% of the landscape, higher population sizes were maintained in the more fragmented landscapes. The relationship between fragmentation and population size was more complicated when 8% of the landscape was mature habitat. If the mature habitats were divided into 2 or 4 fragments, the resulting population sizes were significantly higher than those with no fragmentation. When the mature cells were divided further into 8 fragments, the population size was significantly lower than with moderate

fragmentation (4 fragments) ($p < 0.01$) but was not different from that in the unfragmented landscape ($p = 0.4613$).

Location of mature stands. The location of the mature stands within a landscape influenced population sizes significantly (Fig. 8). If all of the mature stands were grouped as a square cluster, placing them on the landscape center and on one corner resulted in the largest and the smallest population sizes, respectively. Random distribution of the cluster resulted in an intermediate population size.
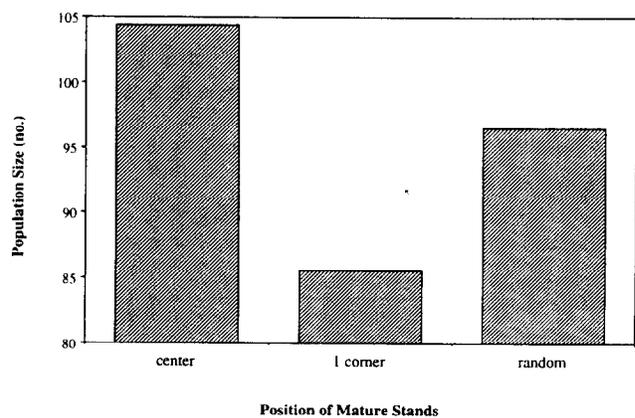

Fig. 8. The impacts of location of mature stands within the landscapes on population size.

4. Discussion and conclusions

After forest stands were harvested, they were regenerated and became temporarily suitable habitat for Bachman's Sparrows until they were older than 5 years but younger than 80 years (age of mature stands). Total population size was periodic and followed harvest cycles with a time lag of several years (Fig. 2a). When the initial landscape consisted only of stands 0–9 years old, there was positive net income from harvesting only during the last 10 years in each rotation. During the initial 10 years of each rotation there was negative net income because no income was generated, but some money was spent for maintenance and taxes. Since the number of stands in each age class was not exactly the same due to initial random assignments, economic net income fluctuated during the 10 years of harvesting in each rotation (Fig. 2b).

The effects of rotation lengths on population sizes were determined by the breeding biology of the species of concern. In particular, Bachman's Sparrows only breed in 1–5 and 80 + year pine stands. When rotation length was between 10 and 80 years, sparrow population size decreased as rotation length increased because longer rotations caused patches to be unsuitable for a longer period. When rotation length was longer than 80 years, some or all of the initial stands became mature and suitable for the sparrows 70 years after the beginning of the simulations, and therefore population size increased substantially (Fig. 3).

The effects of stand sizes on both economic yields and animal population dynamics have sig-

nificant implications for designing forest landscapes. Small tracts, less than 60 acres (about 24 ha), require extra efforts in harvesting and, consequently, reduce profits for forest owners. When mature stands accounted for 8% of the landscape (Fig. 4), the population sizes in landscapes with 10-ha stands were not different than those in landscapes with 40-ha stands ($p = 0.8567$), but economic income was higher on landscapes with 40-ha stands. In this case, a forest landscape consisting of 40-ha stands is beneficial with respect to both economic yields and population viability. Twenty-hectare stands resulted in a higher population size and a lower net income than 40-ha stands. Accordingly, the choice between 20-ha stands and 40-ha stands is not so clear and will depend on the priorities of the managers, who may prefer maintaining a higher population size or generating a higher income. When 32% of the landscape was mature stands, stands of 2.5 ha produced the lowest economic revenue and therefore would probably not be adopted (Fig. 4). Among the remaining stand sizes, population sizes decreased while economic revenues increased with increasing stand sizes. The decision to choose a stand size would depend on the importance of population sizes versus economic revenues. If a low population size satisfies conservation goals, forest managers could design the forest with a bigger stand size in order to obtain higher economic profits.

In simulations with only a small amount of mature habitat in the landscape there was a smaller population size when the mature stands were fragmented (Fig. 6). This result is consistent with the conventional belief about the conse-

Table 2

Population size (average number of the sparrows ± SE) due to fragmentation of mature stands. p is the significance level of two-tailed t-tests for differences in means of population sizes

Percentage of mature stands	Population in mature stands			Population in other stands		
	fragmentation	non-fragmentation	p	fragmentation	non-fragmentation	p
4%	10.19 ± 1.09	15.75 ± 0.02	0.0009	9.85 ± 1.14	12.59 ± 0.47	0.0668
8%	30.52 ± 0.10	31.82 ± 0.02	0.0001	27.23 ± 0.49	19.23 ± 1.32	0.0006
12%	47.46 ± 0.04	47.89 ± 0.01	0.0001	34.75 ± 1.13	27.94 ± 1.34	0.0141
16%	63.45 ± 0.07	63.89 ± 0.01	0.0001	43.35 ± 1.19	32.62 ± 2.21	0.0027
24%	95.64 ± 0.08	95.85 ± 0.03	0.0374	53.45 ± 1.57	42.08 ± 2.91	0.0023

quences of habitat fragmentation on animal population size (Harris, 1984; Quinn and Hasting, 1987; Small and Hunter, 1988; Saunders et al., 1991). However, in simulations where the percentage of mature stands in the landscape was high, there was a higher population size when the mature habitat was divided into four equal parts than when the mature habitat was unfragmented. The seemingly contradictory consequences of habitat fragmentation for landscapes with low versus high representation of mature stands make sense in light of the ability of dispersing individuals to find and occupy stands of different ages. As shown in Table 2, there were more individuals in unfragmented mature stands than in fragmented ones ($p < 0.05$) in all landscapes. When mature stands were 4% of the total area, more individuals were found in younger stands on landscapes with non-fragmented mature habitat than were found in younger stands on landscapes with fragmented mature habitat ($p = 0.067$). However, when mature stands comprised 8% or more of the total area, fragmentation resulted in many more individuals in other stands than were found in landscapes with unfragmented mature habitat ($p < 0.05$). This is because fragmentation in these landscapes increased the chances of surplus offspring produced in mature stands to disperse into habitats of other age classes. In contrast, fragmentation of a small amount of mature habitat (4%) resulted in a much lower population size in mature habitat. The number of surplus offspring produced in the mature habitat was smaller and therefore there were fewer immigrants from the mature habitat to habitat of other age classes.

The differences in population sizes under various locations of mature stands (Fig. 8) were mainly due to the impact of location on the ability of searching juveniles to find suitable breeding habitat. When the mature stands were in the center and on one corner, they conferred, respectively, the highest and the lowest chances for surplus juveniles to disperse and settle in other stands (Table 3). While mature stands were randomly distributed on a landscape, they might be sometimes on the center, sometimes on a corner, and sometimes on or close to landscape edges. Therefore, random distribution of mature stands

Table 3

Population size (average number of the sparrows ± SE) under different locations of mature stands. Letters a, b, and c indicate whether two population sizes are significantly different at 5% level. Comparisons are made within each column. If two numbers have different letters, they are significantly different

Location of mature stands	Population in mature stands	Population in other stands
center	63.84 ± 0.02 [a]	40.54 ± 0.02 [a]
1 corner	63.88 ± 0.01 [a]	21.71 ± 0.39 [b]
random	63.89 ± 0.01 [a]	32.62 ± 2.21 [c]

brought intermediate chances for surplus juveniles produced in mature stands to emigrate into other habitats.

Simulations using ECOLECON or similar models may result in useful rules of thumb for forest managers. In Fig. 9, we show population sizes plotted against land expectation values (LEV, $) from 55 simulations with different forest landscape structures and rotation lengths. We arbitrarily divided both population sizes (POP) and land expectation values (LEV) into three levels: Low (L, $0 \leqslant POP < 50$; $-1\,000\,000 \leqslant LEV < 1\,000\,000$), Moderate (M, $50 \leqslant POP < 150$; $1\,000\,000 \leqslant LEV < 3\,000\,000$), and High (H, $150 \leqslant POP$; $3\,000\,000 \leqslant LEV$). Thus Fig. 9 shows
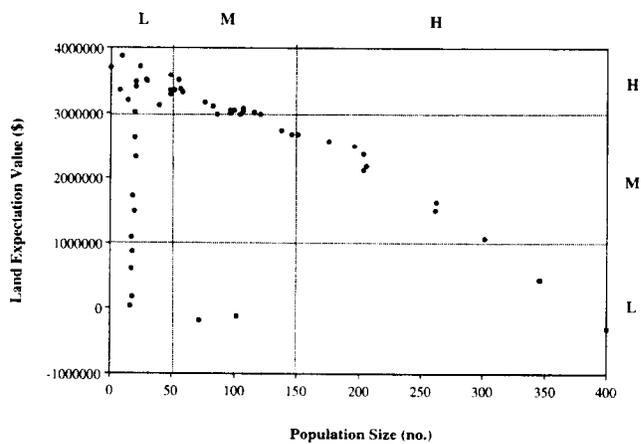

Fig. 9. Population size and land expectation value in response to various forest rotation lengths, composition and configurations. Both population size and land expectation value are arbitrarily divided into three levels: Low (L), Moderate (M), and High (H).

qualitatively the tradeoffs between economic yields and the population levels expected for a species of management concern. Information of this sort could help forest managers minimize the conflicts between economic and conservation goals and, thereby, avoid the worst scenarios. The landscape structures and/or management regimes that resulted in low LEV and low population size should certainly be excluded from consideration. The ideal case is to gain high economic revenues and high population sizes simultaneously, but this did not occur in any of the conditions simulated. Among the remaining scenarios, there were three relatively balanced options: high LEV and moderate population size, moderate LEV and moderate population size, moderate LEV and high population size. Choices between these scenarios would depend upon priorities for population management and economic profits.

Although it is hard to fully parameterize and validate models such as ECOLECON, these models could be helpful for research and adaptive management (Walters, 1986), and they can be continuously updated and improved as more information becomes available.

ECOLECON is currently a model for forests of a single tree species and a single animal species, but it can be expanded to include multiple tree and animal species. In fact, many multi-species population models have been developed by expanding single-species population models (e.g., Hutchinson, 1978). Expansion of the current model will increase the model complexity because interactions (e.g., competition and predation) among species should be incorporated. Ultimately it could be possible to provide useful insights for preserving biological diversity at community and landscape levels.

In the present paper the model was only used to simulate the ecological and economic impacts at a scale of 1000 ha over a period of 100 years, but it is feasible to run simulations at desirable (larger or smaller) scales because conservation and forest management may take place at various spatial and temporal scales (see Norton, 1992). In the beginning of a simulation, a user of this model can decide the size of the area to be simulated and the length of the simulation. We

have already run models of this sort on landscapes of more than 10000 ha, and we are now experimenting with parallel processors which can simulate much larger landscapes more efficiently.

Although net present value (NPV) and land expectation value (LEV) have been widely used in financial analysis as long-term investment criteria (Cubbage et al., 1991), their use in decision-making for conserving biological diversity may be controversial. One major issue is how to choose a proper discount rate to calculate NPV and LEV (see Liu (1992) for the formulae) (Norgaard and Howarth, 1991). In the simulations, we assumed the discount rate to be 0.05, a typical rate used in many financial analyses. A higher discount rate means discounting the future dollar value more. This would preferentially give support to management plans which harvest earlier. Conservationists normally prefer low discount rates which favor the management of slow-growing trees and preservation of biological diversity (Norgaard and Howarth, 1991). Furthermore, NPV and LEV in financial analysis only consider the market values (dollar values) of commercial products or projects. Natural resources such as forests, however, have both market and non-market values. For example, besides supplying timber, forests contribute to clean air and water, and help maintain ecosystem functions such as energy flow and nutrient cycling (Ehrenfeld, 1988; Hanenmann, 1988; Norton, 1988). Evaluation of non-market values of forests is a complicated task, but incorporation of the non-market values into ecological economic models will provide more objective information for decision-makers. In order to make wiser long-term decisions, it is essential that ecologists and economists collaborate to evaluate market and non-market values of forests for present and future generations.

ECOLECON can serve as a prototype for similar modeling efforts in other forest ecosystems. Combining the model with a geographical information system (GIS) allows users to simulate the effects of various management schemes in real forest landscapes (Liu et al., 1994). Computer simulations are a useful tool for providing valuable information and insights for policy making

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and analysis. Our results suggest that simultaneous ecological and economic studies could provide better information to reduce public debates and clarify management impacts.

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