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ECOSYSTEM MANAGEMENT WITH MULTIPLE OWNERS: LANDSCAPE DYNAMICS IN A SOUTHERN APPALACHIAN WATERSHED[1]

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Abstract. Ecosystem management is emerging as an organizing theme for land use and resource management in the United States. However, while this subject is dominating professional and policy discourse, little research has examined how such system-level goals might be formulated and implemented. Effective ecosystem management will require insights into the functioning of ecosystems at appropriate scales and their responses to human interventions, as well as factors such as resource markets and social preferences that hold important influence over land and resource use. In effect, such management requires an understanding of ecosystem processes that include human actors and social choices. We examine ecosystem management issues using spatial models that simulate landscape change for a study site in the southern Appalachian highlands of the United States. We attempt to frame a set of ecosystem management issues by examining how this landscape could develop under a number of different scenarios designed to reflect historical land-cover dynamics as well as hypothetical regulatory approaches to ecosystem management. Scenarios based on historical change show that recent shifts in social forces that drive land cover change on both public and private lands imply a more stable and a more forested landscape. Scenarios based on two hypothetical regulatory instruments indicate that public land management may have only limited influence on overall landscape pattern and that spatially targeted approaches on public and private lands may be more efficient than blanket regulation for achieving landscape-level goals.

Key words: ecosystem management; land-cover dynamics; landscape ecology; simulation modeling; southern Appalachians; spatial analysis.

INTRODUCTION

Ecosystem management is emerging as a systems level approach to protecting essential ecological function of the biosphere. It can be viewed in part as a response to the limited effectiveness of the reactive approach to species protection afforded by the Endangered Species Act (ESA) of 1973 (e.g., Rohlf 1991). The ESA focuses on the protection of individual species, but only after they are threatened. Accordingly, the ESA does not work to anticipate and discourage endangerment and, under the act, endangerment can trigger interventions that may be extremely costly in terms of human enterprise and welfare (e.g., the Northern Spotted Owl, *Strix occidentalis,* in the U.S. Pacific Northwest). By taking an ecological-health perspective, ecosystem management has the potential to maintain ecological functions, thereby preventing the endangerment of dependent species.

While clearly the focus of discussion and debate within natural-resource professions, public land management agencies, and policy-making bodies, ecosystem management has yet to be clearly defined in operational terms. It is perhaps best to view it as an emerging professional philosophy or ideology and not yet as a set of rules or guidelines. However, substantial federal initiatives—in the form of the National Biological Service in the Department of Interior and the ecosystem management program within the U.S. Department of Agriculture (USDA) Forest Service (e.g., Overbay 1992, Slocombe 1993)—indicate a significant impetus for change in how public lands and natural resources are managed.

This article examines various approaches that could be taken to implement ecosystem management. It focuses especially on the spatial nature of ecological functions and the concomitant need to address ecosystem functions across broad landscapes often occupied by a collection of different landowners. Ecosystem management suggests a set of social goals that are defined at a landscape level and a set of strategies that are spatially explicit. In implementation, then, lands with different "locational" qualities might be treated

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differently, and the activities of different landowners, even private landowners, must be considered in the assessment of ecosystem management approaches on public lands.

We explore different broad approaches to managing ecosystems in a setting with both public and private landowners. Through use of an integrated modeling framework, we simulate land use decisions and their implications for landscape structure and ecosystem integrity. Our starting point is a set of historical simulations that project the continuation of observed land cover dynamics. Historical simulations can, alone, provide crucial insights into ecosystem management by defining what and where problems may arise at the landscape level if historical trends persist. We then impose different management strategies and regulations on these models and simulate the consequent development of landscapes. This approach therefore allows us to sketch out the ecological implications of a range of hypothetical management approaches, contrasting (1) the exclusive use of public lands to effect ecosystem goals, (2) spatially explicit regulation of land uses on public and/or private land, and (3) blanket prohibitions of activities on public and/or private land. While several other approaches might be considered (and the scenarios considered here are by no means prescriptive), these relatively straightforward scenarios allow us to raise and examine a set of important questions for ecosystem management in general.

Engineering land use and land management to effect ecosystem goals is a difficult and fundamentally complex problem taken on in an environment of uncertainty (e.g., Ludwig et al. 1993). An important source of uncertainty is that ecological functions are not well understood. The degree of uncertainty is high at small scales—where, for example, most small fauna have not been cataloged (Raven and Wilson 1992)—and is magnified as scale approaches the landscape level (Franklin 1993). [While this high degree of uncertainty is often emphasized, it is also argued that the extent of existing knowledge about ecological-resource interactions is neither well appreciated nor well used in resource and land-use decision making (Holling 1978).] This fundamental lack of information has suggested to some that ecosystem management strategies focus on defining "safe minimum standards" that explicitly account for the inherent uncertainty of ecological responses to human endeavors (Bishop 1978, Toman 1992). This study focuses on the eventual landscape structure that would emerge from alternative land use choice models and regulation. It therefore provides the kind of information that stakeholders might use to define safe minimum standards at a landscape scale.

Whether focused on explicit ecological functions or on defining safe minimum standards applied to landscape conditions, ecosystem management promises to be complex and difficult in implementation. Difficulties arise not only from the complexity and uncertainty regarding underlying biological properties but, just as significantly, difficulties arise from the need to implement ecological solutions through individuals, private firms, and public agencies operating in complex social, economic, and political systems.

Regulation in general, and the coordination of private land management in particular, are at odds with fundamental philosophies regarding resource allocation in the United States. Markets are generally trusted to allocate resources efficiently. When they fail to provide for all social needs (e.g., environmental quality or ecological services), then some form of market intervention by government may be warranted. However, market failure is only a necessary and not a sufficient condition for government intervention (e.g., Baumol and Oates 1988). Rather, the fundamental tension between the free play of markets and the costs of regulation tends to limit market intervention to cases where the returns to regulation clearly exceed their costs. The plausibility of strategies for ecosystem management will clearly depend on their relative costs, upon site-specific conditions and goals, and upon institutional constraints and inertia.

We examine the interaction of physical and social processes and their resulting implications for landscape condition and begin an exploration of strategies that could be applied to large scale ecosystem problems. This article is exploratory and highlights a set of issues that arise when one begins to consider the human and institutional settings and constraints within which ecosystem management would be implemented. An organizing theme is that building an effective approach to managing ecosystems requires insights from both the natural and social sciences (Lubchenco et al. 1991, Ludwig et al. 1993).

Study Area

Our study focused on a study site within the Southern Appalachian Man and the Biosphere (SAMAB) region. The region extends approximately from Chattanooga, Tennessee, northeast to Roanoke, Virginia, crossing four states, with ≈57% of the land held in small private ownerships, and 20% of the land held in U.S. Forest Service (USFS) ownership. Forested lands in the SAMAB region have been experiencing increasing demands for nonmarket services and associated pressures to decrease timber harvests. The Great Smoky Mountains National Park is the most-visited national park in the U.S. because of the tremendous human population within a one-day drive, and this recreation demand also affects adjacent national forests and private lands. The relatively small holdings of the national forests in the southern Appalachians are interspersed among many land owners and are managed in the context of a regional mixed-ownership landscape.

Within the SAMAB region, we selected the Little Tennessee River Basin (LTRB) for intensive study. The 116 090-ha LTRB is located primarily in western North

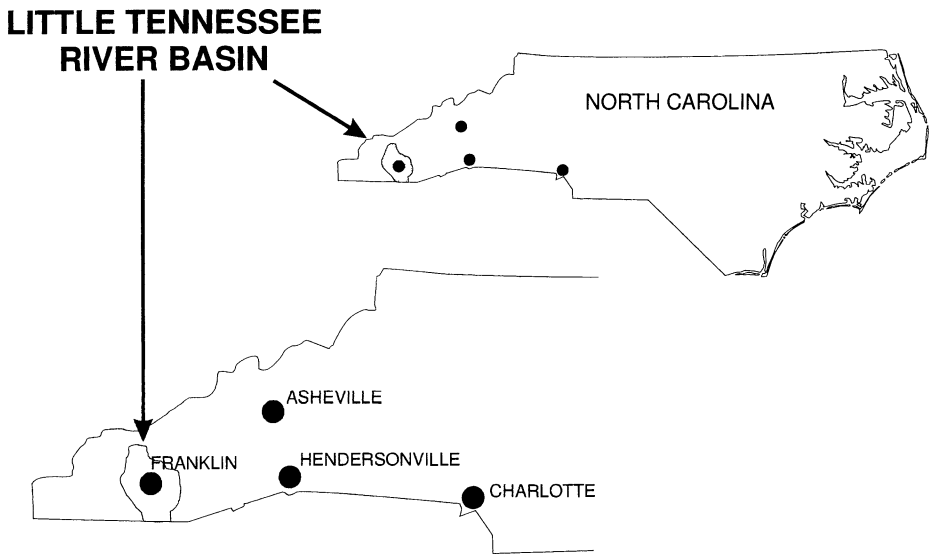

FIG. 1. Map of the Little Tennessee River Basin in North Carolina.

Carolina, extending approximately from the Georgia—North Carolina border to Fontana Dam, just south of the Great Smoky Mountains National Park (Fig. 1). Although ≈10% of the LTRB is located in north Georgia, we considered only the 103 635-ha located within North Carolina because of limited availability of digital spatial data for the Georgia area. The LTRB is characterized by rugged topography and species-rich eastern deciduous forest. Franklin, North Carolina, the major developed area in the LTRB, was experiencing an influx of new residents. Tourism in Franklin was a $50 million per year business and growing. Forest products remained an important industry in the LTRB, and the U.S. Forest Service was a major landholder, owning 35% of the watershed, primarily at the higher elevations. The rotation period of forest cutting on the national forest lands ranged from 80 to 120 yr; harvest was primarily of cove and upland hardwoods for saw timber. The U.S. Forest Service Coweeta Hydrological Laboratory, a Long-term Ecological Research (LTER) site, also was located within the LTRB.

METHODS

We used a set of landscape simulation experiments to examine questions regarding ecosystem management. These experiments were conducted by applying alternative models of land cover change to the land cover existing in the LTRB in 1991. The 1991 condition was defined by a land-cover map developed from Landsat Multispectral Scanner (MSS) imagery, and land cover change was modeled using methods described in Turner et al. (1996) and in Berry et al. (1996). Resulting land cover maps were then evaluated using various landscape metrics.

Model overview

Land use decisions reflected in land cover changes are influenced by social and economic driving forces as well as ecological constraints and existing land cover patterns (Lee et al. 1992). We developed a spatially explicit simulation model in which the probability of a parcel of land being converted from one land cover type to another was conditional upon a variety of factors. Socioeconomic and ecological variables were represented spatially as gridded landscape maps stored in the GRASS geographic information system (GIS) (USACERL 1991). We used the following data layers: land cover (forest, grassy/brushy, and unvegetated), ownership, elevation, slope, aspect, distance to the nearest road, distance along roads to the nearest market center, and population density. Sources of data are described in Turner et al. (1996) and model integration is described in Berry et al. (1996).

Landscape change is driven by conditional transition probabilities. Transition probability equations were estimated empirically as a function of the set of independent variables (i.e., the data layers listed above) by comparing land cover in each of three time intervals (1975–1980, 1980–1986, and 1986–1991) and using multinomial logit models (Wear and Flamm 1993, Turner et al. 1996). Models were estimated separately for lands under different categories of ownership (e.g., USFS and private).

The simulation began with an initial (1991) map of land cover for the LTRB. For each grid cell in the landscape, the value of each data layer described above was used in the multinomial logit equations to generate a set of transition probabilities. For example, a given forested grid cell had associated with it an ownership class, elevation, slope, aspect, distance to road, dis-

tance to market, and population density forming the attribute vector **X**. The value of each of these attributes was used in a set of multinomial logit equations to generate the probabilities of transition to other cover classes:

$$\Pr(Y_i^k = j) = \frac{e^{\mathbf{X}_i\boldsymbol{\beta}_j}}{\sum_s e^{\mathbf{X}_i\boldsymbol{\beta}_s}} \quad \text{for all } j \qquad (1)$$

where $\Pr(Y_i^k = j)$ is the probability of land cover at grid cell i with cover class k (grassy, unvegetated, or forest) at time t having the same cover class at time $t+1$ ($j=0$) or changing to one of the two other cover classes (j = 1 or 2). Each $\boldsymbol{\beta}_j$ is a vector of estimated coefficients from Turner et al. (1996), and separate equations were estimated for National Forest and for private ownerships.

Transition equations were initially estimated for the two ownership groups for all three time periods (1975–1980, 1980–1986, and 1986–1991). After weighting for difference in the length of the periods, we found no significant difference in transition models for 1975–1980 and 1980–1986 but found significant differences between these two periods and 1986–1991. Changes on private lands indicated a reduction in forest cutting and a shift towards residential development in the watershed. These changes had the effect of reducing total transitions but spreading transitions across a larger share of the landscape. There were also significant differences between public and private transition models. Private transitions in general, were significantly influenced by locational variables, such as slope and distance to roads, that define costs of access and development. These variables had little influence on public lands.

The three equations were implemented for each grid cell by drawing a random number from a uniform distribution between zero and one. If the random number fell within the line segment associated with a transition probability, the grid cell was changed; otherwise, the grid cell remained in its current state. This process was repeated for each grid cell in the landscape to generate a new map of land cover. The spatial pattern of land cover was analyzed at the end of each time step, and the simulation was continued for a specified duration of time.

The model described here operated at a spatial resolution of 90 × 90 m grid cells, comparable to the resolution of Landsat Multispectral Scanner (MSS) imagery used to estimate the transition models, and the LTRB contained a total of 127 949 grid cells (103 639 ha). The simulations were conducted for 100 yr (1991 to 2091) with a temporal resolution of 5 yr (20 time steps). Because the model was stochastic, $n = 10$ replicate simulations (for results reported here) were conducted for each selected scenario.

Landscape pattern analysis

Land cover was analyzed at each time step by using a set of landscape metrics. We calculated both the total area and proportion, p, of the landscape area occupied by each cover type. Edges between habitats in the landscape are sensitive to habitat fragmentation and were tabulated in several ways. The length of edge between each pair of land-cover classes was computed (e.g., forest–grassy, forest–unvegetated, grassy–unvegetated) and summed to yield total edge in the landscape. Then, an edge-to-area ratio was computed for each cover type by dividing the total number of edges by the spatial extent of that cover type.

The remaining metrics were computed separately for each land-cover category. For each cover type, every patch in the landscape map was identified and its area and perimeter recorded. A patch was defined as contiguous, adjacent (horizontally or vertically) cells of the same land-cover type; diagonal cells were not considered to be contiguous. The total number of patches, arithmetic mean patch size, standard deviation of mean patch size, size of the largest patch, and mean patch shape (Baker and Cai 1992) were computed for each cover type. The arithmetic mean patch size was calculated by simple division of the summation of the patch sizes by the number of patches. Finally, a cumulative frequency distribution of the number of patches by patch size was generated for each cover type. The set of landscape pattern analyses were computed for each replicate at each time step, and the measures were stored in an output file. We then used ANOVA to determine whether the different scenarios explained the variability observed in simulated landscape patterns.

TABLE 1. Sixteen landscape simulations scenarios defined by applying four different land-cover treatments to public and private lands. Each scenario is labeled with a two-character code defining the treatments applied to private (first character) and public (second character) lands. The four land-use treatments are labeled "7" for 1975–1980 historical patterns of land-cover transitions, "8" for 1986–1991 transitions, "S" for no cutting along streams, and "N" for no cutting at all.

	Treatment for public lands			
Treatments for private lands	1975–1990 historical	1986–1991 historical	No change from forest cover near streams	No change from forest cover
1975–1980 historical	77	78	7S	7N
1986–1991 historical	87	88	8S	8N
No change from forest cover near streams	S7	S8	SS	SN
No change from forest cover	N7	N8	NS	NN

Simulation experiments

We conducted a factorial simulation experiment in which transition probabilities were applied independently on public and private lands in the LTRB to simulate alternative landscape conditions in the future.

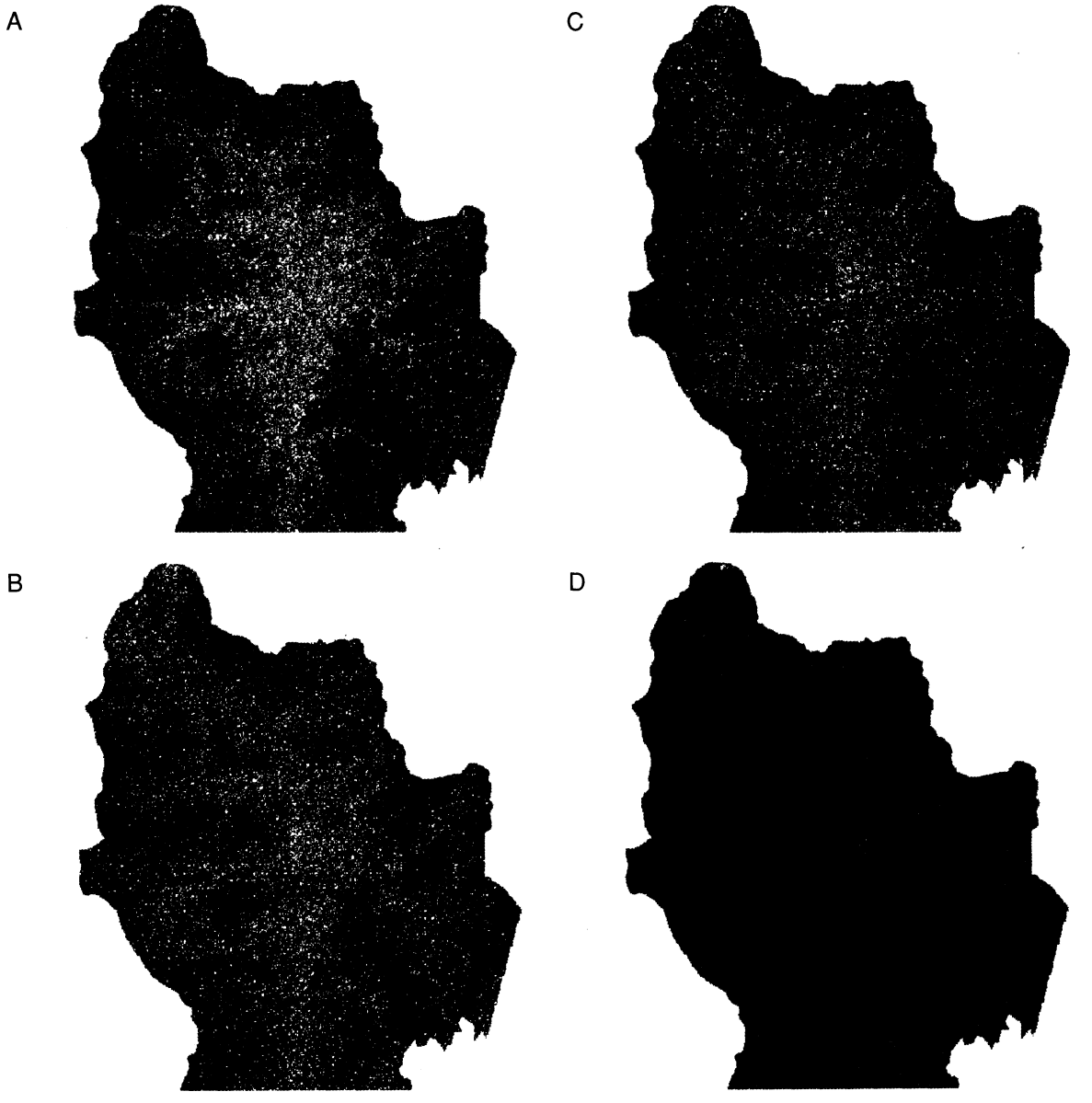

FIG. 2. Land-cover maps in the year 2091 for four landscape simulation scenarios. Colors represent different land-cover categories: green is forest; yellow is grassy; red is unvegetated; and blue is water. (A) Scenario 77 = 1975–1980 treatments (1975–1980 historical pattern of land-cover changes) applied to both private and U.S. Forest Service (USFS) lands. (B) Scenario 88 = 1986–1991 treatments (1986–1991 historical pattern of land-cover changes) applied to both private and USFS lands. (C) Scenario SS = no cutting allowed near streams on both USFS and private lands. (D) Scenario NN = no cutting allowed on either private or public lands.

Simulation of the watershed required selecting one treatment for the public lands and one treatment for the private lands, giving a 4 × 4 factorial design with 16 different scenarios (Table 1). The treatments used were: (1) the 1975–1980 empirically derived transition probabilities for the appropriate owner, (2) the 1986–1991 empirically derived transition probabilities for the appropriate owner, (3) forest cutting eliminated from lands within 90 m of a stream, and (4) all forest cutting eliminated. Although treatment names were the same between owners, actual transition probabilities differed (e.g., a given transition probability for 1975–1980 was different for comparable private and public lands). Each scenario was run for 20 time steps (100 yr) and replicated 10 times. Landscape pattern was analyzed for the whole LTRB at the end of each time step for each replicate.

For discussion of the results, each scenario is labeled with a two-character code identifying the treatments applied to private (first character) and public (second

character) lands. The four treatments were labeled: "7" for 1975–1980 transitions, "8" for 1986–1991 transitions, "S" for no cutting along streams, and "N" for no cutting at all. According to this scheme, Scenario 77 applied 1975–1980 transitions to both public and private lands, Scenario 7N applied 1975–1980 transitions on private lands and allowed no harvesting on public lands, and so on . . . (see Table 1). Treatments "S" and "N" were implemented by restricting 1986–1991 transitions from forest cover only. That is, for an affected grid cell, if the land cover state was forest then its probabilities of transition to other cover types were set to zero. The 1986–1991 transition equations were applied to the unaffected grid cells for these treatments (e.g., for grassy or unvegetated cover or for forest cover not adjacent to a stream in treatment "S"). One-way ANOVA was used to test for differences in landscape pattern due to the scenarios, and Tukey's studentized range test was used on the means to identify significant differences among scenarios. To determine whether the final landscape (i.e., after time step 20) was influenced by the treatments on public lands or private lands, and/or by the interaction between public and private land management, a two-way ANOVA was conducted on the landscape metrics. Differences among means by public or private land management treatment were evaluated by using Tukey's studentized range test. All statistical analyses were conducted by using SAS (SAS Institute 1992).

The scenarios defined by historical transitions (upper left quadrant of Table 1) allowed us to play out the long-run implications of observed land cover dynamics and to examine the potential effects of changes observed in recent years. Simulations based on historical events served further as the benchmark for comparing the results of other scenarios that emphasized regulatory instruments for ecosystem management. Our study area was dominated by forest cover and forestry practices were critical factors in the evolution of landscapes. Scenarios developed here therefore focused on rules governing forest disturbance primarily through timber harvesting. The 4 × 4 design also allowed us to isolate the range of effects resulting from transitions applied to public or private lands.

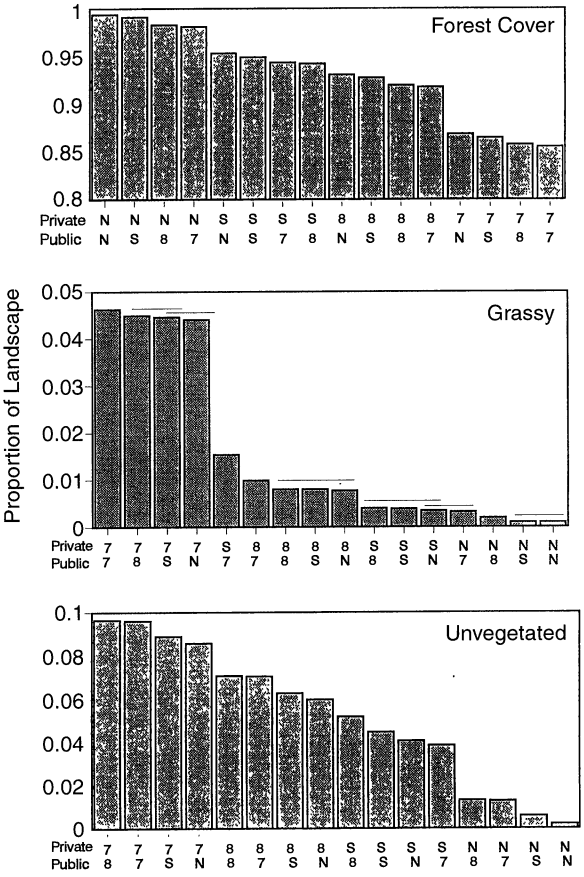

FIG. 3. The mean proportion of the Little Tennessee River Basin occupied by forest, grassy, and unvegetated cover under two land-ownership types at the end of a 100-yr simulation of 16 different land-cover-change scenarios. Data are shown for years 10 and 100 of the simulations. Shared horizontal lines above bars indicate no significant difference between treatments ($P > 0.05$).

RESULTS

Differences in the final landscape pattern

We subsequently examine the relative effects of these various land cover treatments on private and public lands and the effects of historical changes in isolation. Unless stated otherwise, statistical comparisons are based on Tukey's studentized range test.

The sixteen scenarios defined in Table 1 led to substantially different landscape patterns at the end of the 100-yr simulation. Fig. 2 depicts a single representation of the simulated landscape for selected scenarios in the year 2091. The landscape remained dominated by forest in all scenarios, but the proportion of the landscape covered by forest in 2091 varied between 0.86 and 0.99 (Fig. 3, top). Forest cover was least abundant with Scenario 77, which extrapolated into the future the observed rates of change for 1975–1980 on both USFS and private lands. Not surprisingly, forest cover was most abundant with Scenario NN, in which forest cutting was not permitted in either ownership class. Forest cover increased as the transition module on private lands was shifted from 1975–1980 to 1986–1991 and from S to N. Forest cover was secondarily influenced by the treatment on public lands; within each treatment on private lands, forest cover increased according to the same pattern (with one exception in comparing S7 and S8).

The proportion of the landscape in grassy cover (Fig. 3, middle) was greatest with Scenario 77 ($P = 0.05$) and lowest with Scenario NN ($P = 0.001$). Here two levels of scenarios were evident. One is defined by Scenarios 77 through 7N. The remaining scenarios have at most one-third the grassy cover defined under

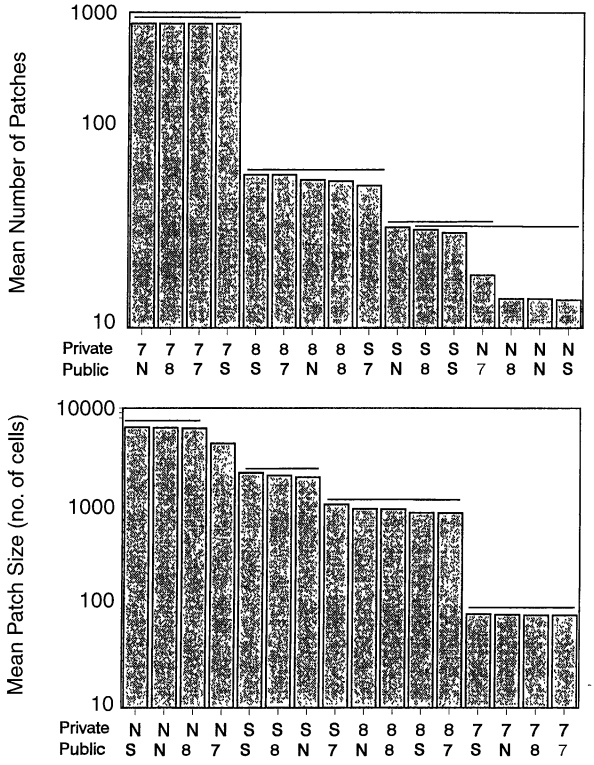

FIG. 4. The distribution of forest cover in the Little Tennessee River Basin at the end of a 100-yr simulation of 16 different land-cover-change scenarios. Study conditions and data presentation are as in Fig. 3.

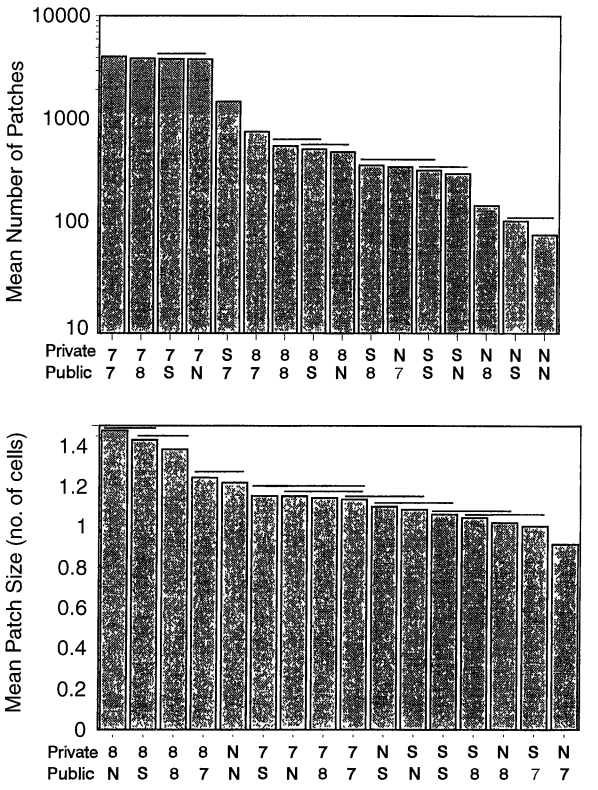

FIG. 5. The distribution of grassy cover in the Little Tennessee River Basin at the end of a 100-yr simulation of 16 different land-cover-change scenarios. Study conditions and data presentation are as in Figs. 3 and 4.

Scenario 7N, again highlighting the important influence of historical changes in land cover transitions (i.e., the shift from 1975–1980 transitions to 1986–1991 transitions). The proportion of the landscape that was unvegetated (Fig. 3, bottom) was greatest with Scenario 78 (P = 0.096), which extrapolated the 1975–1980 transition probabilities on private lands and the 1986–1991 transition probabilities on public lands, and lowest with Scenario NN (P = 0.002). Here there was a strong pattern relative to the treatment of private lands (7 > 8 > S > N) and a different pattern for public lands (8 > 7 > S > N). However, the actual area of unvegetated cover was very small on public lands in the study area.

The number of forest patches, which reflects forest fragmentation, was greatest with Scenario 7N (1012 patches) and least (by nearly two orders of magnitude) with Scenarios NN and NS (15 patches). The ordering of scenarios (Fig. 4, top) shows that the number of forest patches was highest when 1975–1980 treatments were applied to private lands and little affected by treatment of public lands (there is no significant difference in forest patches resulting from Scenarios 7N, 78, 77, and 7S). Average patch size of forests generally followed a trend opposite to that of number of patches (Fig. 4, bottom), ranging from 6509 ha in Scenario NS to 85 ha in Scenario 7N.

Grassy cover was most abundant and had the greatest number of patches with Scenario 77 and least abundant and had the fewest patches with Scenario NN (Figs. 3, middle and 5, top). Six scenarios that applied the 1975–1980 transitions to public and/or private lands (Scenarios 77, 78, 7S, 7N, S7, 87) had the largest number of grassy patches. The ranking of the subsequent scenarios, as with findings for forest patches, was generally dominated by the treatment of private lands. Patch numbers generally declined as public or private treatment shifted from 7 to 8 and from S to N. Average patch size was generally small but showed a different rank ordering, with patch size decreasing from Scenario 8N (1.48 ha) to Scenarios N7 (0.92 ha). Patch shape varied over a narrow range (1.14 to 1.18) with considerable overlap among the scenarios, and the low values indicate relatively simple shapes.

Unvegetated cover was most abundant (P = 0.074–0.084) with Scenarios 78, 77, 7S, and 7N (Fig. 3, bottom), all of which used the 1975–1980 transition probabilities on the private lands, and least abundant with Scenarios NN, NS, N7 and N8 (P = 0.002–0.012), in which no forest cutting was permitted on the private lands. Numbers of patches of unvegetated cover (Fig. 6, top) were greatest among the scenarios that used the actual transition probabilities for both time intervals

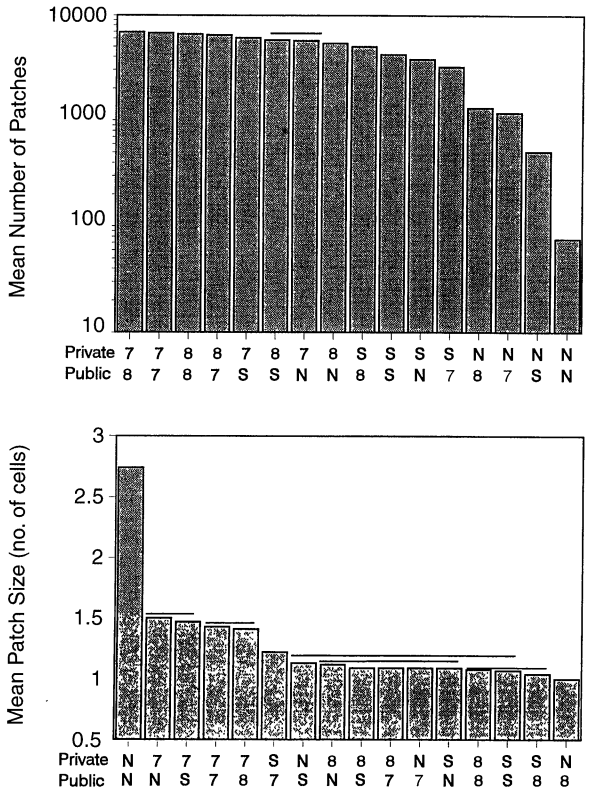

FIG. 6. The distribution of unvegetated cover in the Little Tennessee River Basin at the end of a 100-yr simulation of 16 different land-cover-change scenarios. Study conditions and data presentation as in Figs. 3–5.

on both public and private lands (ranging from 6478 to 6875 patches in Scenarios 87, 88, 77, and 78) and two orders of magnitude lower when no cutting was permitted on private or public lands (76 patches in Scenario NN). Interestingly, mean patch size of unvegetated cover was greatest for Scenario NN but generally low across all other scenarios (Fig. 6, bottom). Average patch shape of unvegetated cover indicated simple shapes (range of 1.14 to 1.24 across the scenarios), with the more complex shape occurring with Scenario NN.

Trajectories through time

The temporal dynamics of the landscape were also informative in discerning the implications of the scenarios (Fig. 7). To contrast selected scenarios, measures of the pattern of forest cover were plotted through time for the scenarios in which the same treatment was applied on both public and private lands (Scenario 77 = 1975–1986; Scenario 88 = 1986–1991; Scenario SS = No cutting along streams; Scenario NN = No forest cutting). Compared to the initial 1991 landscape, the number of forest patches increased only with Scenario 77; the others all showed a decline in patch number (Fig. 7a). Similarly, average size of forest patches declined with Scenario 77 but increased through time (to different levels) with the Scenarios 88, SS, and NN (Fig. 7b). The sizes of the largest contiguous patch of forest followed the same rank order as average patch size. Finally, the shape index showed fluctuation through time in Scenarios SS and 88; these scenarios also result in more complex patch shapes (Fig. 7d). Values of patch shape for Scenarios 77 and NN converge near time step 5 (25 yr) at lower values.

Relative effects of land cover treatments on public and private land

Two-way ANOVA of measures of final landscape pattern revealed significant effects (all $P < 0.0001$) of both public and private land treatments, generally with significant interaction terms. As a rule, more of the variation in final pattern was explained by private land treatments than by public land treatments. For example, when cover on public land was held constant, on the private lands the proportions of the LTRB landscape occupied by forest and unvegetated cover varied over a broad range among treatments applied (Fig. 8). These results also indicate that, among the four alternative land treatments simulated here, treatments on the private land were responsible for more land-cover change within the watershed than treatments on the public lands. This pattern of private land treatment explaining more variance among scenarios than public land treatment was generally true for most measures of landscape pattern (e.g., number of patches, average patch size, average patch shape).

Tukey's studentized range test identified significant differences between treatments on the individual ownerships with land cover on the other ownership held constant (Table 2). Significant rankings were found on both ownerships for nearly all landscape variables. For the proportion of cover in each of the three cover types, there was no overlap between treatments (i.e., each was significantly different from all other treatments), and the ranking of treatments was nearly identical for both ownerships (the exception is the ordering for the proportion of unvegetated cover, where 1975–1980 and 1986–1991 were reversed between the ownership classes). There was also strong similarity between the ranking of treatments on public and private lands for the number of patches, though number of forest patches was not significantly different for 8, S, and N on the public lands. In general, the 1975–1980 treatment produced the most patches and the no-harvest treatment produced the least. For both proportion of cover and patch numbers, the eventual ranking of treatments after 100 yr was borne out after only 10 yr of the simulation (Table 2).

However, treatments influenced average patch size, the shape index, and edge : area ratios differently on the two ownerships. For example, the average size of grassy patches was greatest with the 1986–1991 treatment and least with the "S" and "N" treatments on private lands, but was greatest for the no-harvest treat-

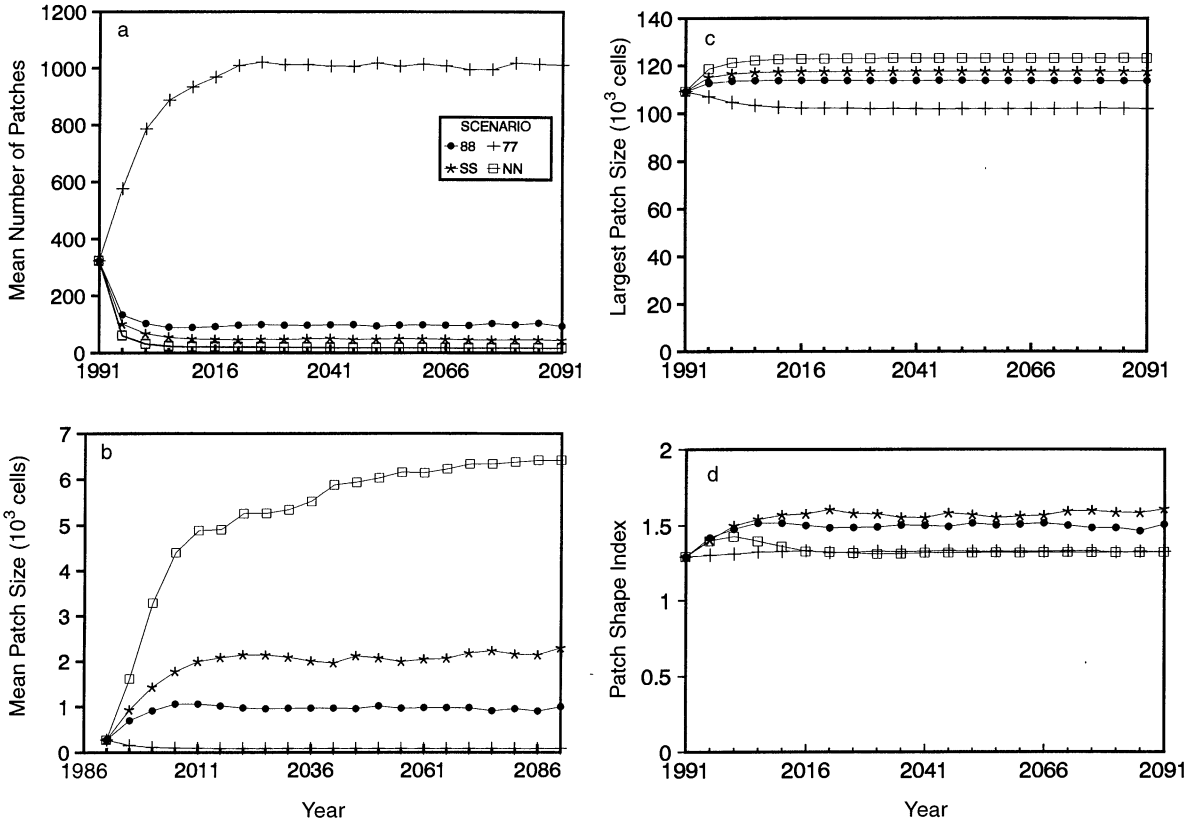

FIG. 7. Changes through time in measures of the spatial pattern of forest cover in four scenarios of land-cover change (Scenario 77 = 1975–1986; Scenario 88 = 1986–1991; Scenario SS = no cutting along streams; Scenario NN = no forest cutting). (a) number of forest patches, (b) mean patch size, (c) size of the largest patch of forest, (d) mean patch shape.

ment and least for the 1975–1980 treatment on public lands. Similarly, the edge : area ratio for forest patches was greatest with the 1975–1980 treatment on private lands but when this treatment was applied to public lands it produced the least edge : area ratio.

We could also compare the relative effects of treatments on public and private lands by examining how different treatments influenced the landscape as a whole when treatments on one ownership were varied while the other changed according to its most-recent history. This, in effect introduced an interaction with the other ownership to the comparison of treatments (Tables 3 and 4).

Table 3 shows the effects of treatments on private lands in order of progressively less change in forest cover, Scenarios from 7 to 8 to S to N. In general, the most substantial difference in landscape measures was found between the two historical treatments: 1975–1980 and 1986–1991. For example, the proportion of forest fell to 86.7% with the 1975–1980 treatment but was 5.1% greater (91.9%) with the 1986–1991 treatment. Between the 1986–1991 treatment and the S treatment, forest cover increased 2.3%; between S and N it rose another 4.1%. Similarly, the eventual patchiness of the landscape was dramatically influenced by the permanent shift to 1986–1991 treatments. The number of forest patches fell by nearly 11 times, from 1011 patches after 100 yr with the 1975–1980 treatment to 92.6 patches with the 1986–1991 module. The S and N treatments resulted in less dramatic reductions to 44 and 16 forest patches, respectively. The same pattern, with historical change having substantially more impact than the externally imposed rules, was found for all landscape metrics.

Table 4 shows the effects of these same treatments applied to public lands, while applying the 1986–1991 transition module to private lands. A similar pattern of results arose, though the magnitude of effects is less than on private lands, consistent with the smaller portion of the landscape controlled by public ownership. Forest cover increased by 0.2%, from 91.7% of the landscape with the 1975–1980 transitions to 91.9% with 1986–1991 transitions. Shifting to S would increase the proportion of forest cover by 0.7%; shifting to N would increase forest cover by another 0.4%. Where shifting from 1975–1980 to 1986–1991 treatments on private lands reduced the number of forest patches by nearly eight times, on public lands this change resulted in only a slight reduction and there were no significant differences in number of forest patches among the four scenarios (see Fig. 4).

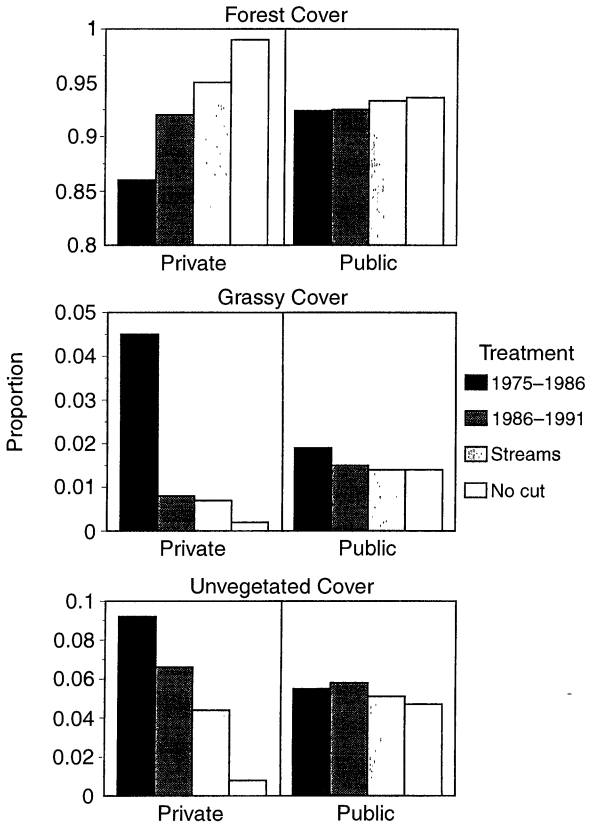

FIG. 8. Differences among mean proportion of the landscape in different land-cover classes as a function of treatment applied to private lands when public-land treatment was held constant (left panels) and as a function of treatment applied to public lands when private-land treatment was held constant (right panels).

Historical scenarios only

The four scenarios defined by the simulation of historical transition modules led to substantially different landscape patterns at the end of the 100-yr period. Our analysis of historical land cover transitions (Turner et al., *in press*) indicated significant differences in transition models between the periods 1975–1980 and 1986–1991, and between the two ownerships, which were borne out further in these simulations. Analysis of variance for the landscape pattern measures revealed significant differences ($P < 0.0001$) between the scenarios for area in each cover type; edge-to-area ratios; and the number, average size, and average shape of patches of each cover type.

The landscape remained dominated by forest in all "historical" scenarios, but the proportion of the landscape covered by forest in 2091 varied between 0.86 and 0.92 (Table 5). Consider first the scenarios on the diagonal in the historical quadrant of Table 1. Forest cover was most abundant with Scenario 88, which extrapolated into the future the observed rates of change that existed in 1986–1991 on both USFS and private lands. Forest cover was least abundant with Scenario 77, which extrapolated into the future the observed rates of change between 1975 and 1980 on both USFS and private lands. Simulation results suggested that if recent changes in land use decisions were permanent, they could result in substantially more forest cover across the landscape.

In addition, the shift from 1975–1980 to 1986–1991 treatments implies a substantial effect on the "patchiness" of the eventual landscape. With the 1975–1980 treatments, the number of forest patches climbed from 324 patches in 1991 to 1011 patches in 2091 (Table 5). In contrast, using 1986–1991 treatments resulted in a reduction from 324 forest patches in 1991 to 102 patches in 2091. Concomitant changes in the number of grassy patches also resulted. The 1975–1980 treatments led to an increase from 687 patches in 1991 to 4078 patches in 2091, while 1986–1991 treatments resulted in only 806 patches in 2091. However, unvegetated patches showed similar patterns of increase for both scenarios. Reduction in the overall patchiness of the landscape and greater patch size (Table 5) imply that changes in patterns of land-use observed between 1975–1980 and 1986–1991 could lead to a less fragmented landscape.

The off-diagonal scenarios in the historical quadrant of Table 1 provide further insights into the potential effects of historical changes on private and public lands. If we started with scenario 77 as a base for comparison, then applying 1986–1991 transitions to private lands (Scenario 87) resulted in an eventual increase in forest cover of 6.2% (from 85.5 to 91.7%, Table 5). In contrast, applying the 1986–1991 transitions to public lands with 1975–1980 transitions applied to private lands (Scenario 78) yielded only a 0.2% increase in forest cover (from 85.5 to 85.7%). While changes on both ownerships may result in more forest cover, the net effect (simulated to 2086) resulting from changes on private lands was much greater than that resulting from changes on public lands. The magnitude of these changes is in fact much more than proportional to the share of the land held by each ownership. (The Forest Service held 35% of the land in the study area.)

Historical changes on public and private lands also implied differential effects on landscape patchiness. Both scenarios 77 and 78 result in 1011 forest patches, indicating that changes on public lands alone had no effect on patchiness. Changes on private lands, however (Scenario 87), showed a great decline to 102 forest patches in 2091. The net effect of changes in private land use on forest patchiness and fragmentation was therefore substantial. Very small effects of changes on public lands on grassy and unvegetated patches seemed consistent with Forest Service lands being dominated by forest cover.

Changes in landscape measures over time provided additional insights into the potential effects of historical changes in land-cover transitions (Fig. 9). In the first 10 yr of the simulated period, Scenarios 88 and

TABLE 2. Differences among treatments on public or private lands while holding land cover constant on the other ownership (Tukey's studentized range test). Differences marked with a ">" are significant at the $P = 0.001$ level. Items separated by a comma are not significantly different. Treatments are labeled "7" for 1975–1980 historical pattern of land-cover transitions, "8" for 1986–1991 transitions, "S" for no cutting along streams, and "N" for no cutting at all.

Landscape measure	Year	Land ownership type: Private land	Land ownership type: Public land
Proportion of cover			
Forest	10	N > S > 8 > 7	N > S > 7, 8
	100	N > S > 8 > 7	N > S > 8 > 7
Grassy	10	7 > S > 8 > N	7 > 8, S, N (8 > N)
	100	7 > 8 > S > N	7 > 8 > S > N
Unvegetated	10	7 > 8 > S > N	8 > 7 > S > N
	100	7 > 8 > S > N	8 > 7 > S > N
Number of patches			
Forest	10	7 > 8 > S > N	7 > 8, S, N
	100	7 > 8 > S > N	7 > N, 8, S
Grassy	10	7 > S > 8 > N	7 > 8 > S > N
	100	7 > S > 8 > N	7 > 8 > S > N
Unvegetated	10	7 > 8 > S > N	8 > 7 > S > N
	100	7 > 8 > S > N	8 > 7 > S > N
Average patch size			
Forest	10	N > S > 8 > 7	N, 8, S > 7
	100	N > S > 8 > 7	S, N, 8 > 7
Grassy	10	N > 8 > S > 7	N > S > 8 > 7
	100	8 > 7 > N, S	N > S > 8 > 7
Unvegetated	10	7 > 8, S > N	N > 7, S > 8
	100	N > 7 > S, 8	N > 7 > S > 8
Patch shape index			
Forest	10	N > S, 8 > 7	8 > S, N, 7 (S > 7)
	100	S > 8, N > 7	8 > S > 7, N
Grassy	10	8, N > S, 7	N > S > 8 > 7
	100	8 > 7 > N > S	N > S > 8 > 7
Unvegetated	10	7 > 8 > S > N	N > 7, S > 8
	100	7 > N > S, 8	N > 7 > S > 8
Patch edge: area			
Forest	10	7 > 8 > S > N	S, 8, N > 7
	100	7 > 8 > S > N	8, S, N > 7
Grassy	10	N > 8, S, 7 (8 > 7)	7 > 8 > S, N
	100	N > 8, S, 7	7 > 8, S, N (8 > N)
Unvegetated	10	N > 8, S > 7	7, 8 > S, N
	100	N > S, 8 > 7	7, N > 8, S

TABLE 3. The effects of simulations of different treatments for private lands with 1986–1991 treatment applied to public lands, on four landscape measures for three cover types (forest, grassy, and unvegetated). Results are reported for years 10 and 100 of the simulations. Treatments are labeled "7" for 1975–1980 historical pattern of land-cover transitions, "8" for 1986–1991 transitions, "S" for no cutting along streams, and "N" for no cutting at all.

Treatments			Proportion of cover (%)			Number of patches			Patch size			Edge : area ratio		
Private	Public	Years	Forest	Grassy	Unvegetated	Forest	Grassy	Unvegetated	Forest	Grassy	Unvegetated	Forest	Grassy	Unvegetated
7	8	10	86.7	3.9	9.1	782.4	3559.5	6753.1	111.5	1.1	1.4	10.6	1.2	2.0
		100	85.7	4.5	9.6	1011.4	3916.6	6875.1	85.2	1.1	1.4	10.7	1.1	1.6
8	8	10	91.6	0.8	7.4	101.8	607.1	6729.3	909.4	1.2	1.1	10.0	1.7	3.6
		100	91.9	0.8	7.1	92.6	588.9	6580.1	998.8	1.4	1.1	9.9	2.1	3.8
S	8	10	93.4	0.6	5.8	66.9	514.1	5432.0	1435.2	1.2	1.1	9.8	2.5	3.9
		100	94.2	0.4	5.2	44.3	388.3	4995.4	2162.3	1.0	1.0	9.7	3.3	4.4
N	8	10	96.7	0.5	2.5	32.0	424.7	2548.8	3065.9	1.3	1.0	9.6	2.5	5.1
		100	98.3	0.2	1.3	15.6	162.0	1313.0	6339.5	1.0	1.0	9.5	8.6	7.2
Values in 1991			89	1.2	9.6	324	687	4336	275.6	1.7	2.2	10.19	1.56	3.35

TABLE 4. The effects of simulations of different treatments for public lands with 1986–1991 treatment applied to private lands, on four landscape measures for three cover types (forest, grassy, and unvegetated). Results are reported for years 10 and 100 of the simulations. Treatments are labeled "7" for 1975–1980 historical pattern of land-cover transitions, "8" for 1986–1991 transitions, "S" for no cutting along streams, and "N" for no cutting at all.

Treatments			Proportion of cover (%)			Number of patches			Patch size			Edge : area ratio		
Private	Public	Years	Forest	Grassy	Unvegetated	Forest	Grassy	Unvegetated	Forest	Grassy	Unvegetated	Forest	Grassy	Unvegetated
1	7	10	91.6	0.9	7.3	104.1	811.8	6541.4	893.4	1.1	1.1	9.9	8.7	4.2
		100	91.7	1.0	7.1	101.7	805.6	6477.5	908.1	1.2	1.1	9.8	9.1	4.1
8	8	10	91.6	0.8	7.4	101.8	607.1	6729.3	909.4	1.2	1.1	10.0	1.7	3.6
		100	91.9	0.8	7.1	92.6	588.9	6580.1	998.8	1.4	1.1	9.9	2.1	3.8
8	S	10	92.4	0.7	6.7	102.3	581.4	5952.4	920.7	1.3	1.1	10.0	0.2	3.1
		100	92.6	0.8	6.3	102.0	551.8	5777.9	914.8	1.4	1.1	9.9	1.6	3.2
8	N	10	92.8	0.7	6.3	101.1	541.2	5531.3	927.9	1.3	1.1	9.9	0.1	3.2
		100	93.0	0.8	6.0	94.1	517.9	5383.2	1007.5	1.5	1.1	9.9	0.2	2.9
Values in 1991			89	1.2	9.6	324	687	4336	275.6	1.7	2.2	10.19	1.56	3.35

87 (which applied 1986–1991 land-use transitions to private lands) resulted in a sharp increase in forest cover as grassy cover became reforested. In addition, the scenarios that applied the 1975–1980 transitions to private lands resulted in reductions in forest cover in the short run, again indicating that landscape dynamics were in a state of disequilibrium.

DISCUSSION

The simulation of historical scenarios allowed us to develop some insights into the long-run implications of recent changes in land-cover dynamics. Our analysis of land cover transitions in the LTRB (Turner et al. 1996) showed that the spatial expression of land cover changes had shifted between the periods 1975–1980 and 1986–1991 for both private and USFS lands. Concurrent timber-harvest reductions and population growth in the region suggested a shift in land use pressures from forest management to residential development. As a result the locations of cover-type transitions changed significantly.

The implications of these changes are not necessarily obvious, and the simulations discussed here allow shifts that may be subtle in the short run to be played out over a long time horizon. These results both illustrate the variability of responses observed over a relatively short history, and demonstrate how models of historical behavior might be used to identify potential problems at a landscape scale. For example, Table 5 shows that extrapolating private land use behavior exhibited in 1975–1980 would lead to highly fragmented forest cover. Used in this way, historical simulations can define the expected trajectory of landscape conditions thereby identifying potential ecosystem-level problems. This would be the first step in formulating an ecosystem management plan.

These projections should not, however, be viewed as forecasts. The historical simulations demonstrated considerable variability over a 15-yr period that is not explained by a single transition model. Clearly, we would not anticipate structural stability in land-cover dynamics over the next 100 yr, nor expect explanatory variables such as population density and road locations to remain constant over this period. In this context, it is best to view landscape simulations as indicative of the expected direction of changes. Long-term simulations also allow insights into whether or not long-term

TABLE 5. The effects of simulations of historical treatments for public and private lands on four landscape measures for three cover types (forest, grassy, and unvegetated). Results are reported for years 10 and 100 of the simulations. Treatments are labeled "7" for 1975–1980 historical pattern of land-cover transitions and "8" for 1986–1991 transitions.

Treatments			Proportion of cover (%)			Number of patches			Patch size			Edge : area ratio		
Private	Public	Years	Forest	Grassy	Unvegetated	Forest	Grassy	Unvegetated	Forest	Grassy	Unvegetated	Forest	Grassy	Unvegetated
7	7	10	86.6	4.1	9.0	786.4	3771.7	6570.0	110.8	1.1	1.4	10.5	2.9	2.0
		100	85.5	4.6	9.6	1010.9	4077.6	6742.0	85.0	1.1	1.4	10.5	3.1	2.5
8	7	10	91.6	0.9	7.3	104.1	811.8	6541.4	893.4	1.1	1.1	9.9	8.7	4.2
		100	91.7	1.0	7.1	101.7	805.6	6477.5	908.1	1.2	1.1	9.8	9.1	4.1
7	8	10	86.7	3.9	9.1	782.4	3559.5	6753.1	111.5	1.1	1.4	10.6	1.2	2.0
		100	85.7	4.5	9.6	1011.4	3916.6	6875.1	85.2	1.1	1.4	10.7	1.1	1.6
8	8	10	91.6	0.8	7.4	101.8	607.1	6729.3	909.4	1.2	1.1	10.0	1.7	3.6
		100	91.9	0.8	7.1	92.6	588.9	6580.1	998.8	1.4	1.1	9.9	2.1	3.8
Values in 1991			89	1.2	9.6	324	687	4336	1.292	1.184	1.239	10.19	1.56	3.35

instability in landscape structure is implied by current activities.

The impact of historical shifts in dynamics of land cover change is nicely illustrated by the differences between Scenarios 88 and 77. The greatest change in the LTRB landscape was observed when the 1975–1980 transition probabilities were applied to both private and USFS lands (Scenario 77). Forest cover exhibited the greatest decline and fragmentation under Scenario 77 (e.g., Figs. 7 and 9). The least change in the LTRB landscape was observed when the 1986–1991 rates of transition were applied across lands under both ownership types (Scenario 88). In this scenario, landscape patterns remained relatively stable through time, as indicated by the proportion of forest and the number of forest patches (Fig. 7a). Recent shifts in historical transitions therefore suggested an increase in the resulting forest coverage of the area and a reduction in forest fragmentation.

In addition, these results suggested important differences between land-ownership classes. Our previous analysis indicated structural dissimilarities for land cover dynamics on public and private lands (Turner et al. 1996) and differences in landscape structure between landowners have been observed in other areas. In the Pacific Northwest, both Spies et al. (1994) and Turner et al. (1996) observed substantial differences in the extent and spatial arrangement of forest cover between public and private landowners. Dale et al. (1994) quantified the influence of attributes of landowners on land management and subsequent landscape pattern in Rondonia, Brazil. Simulations of land-cover change show the long-run implications of these differences. Scenarios 88 and 87 had more forest cover throughout the simulation period than did Scenarios 78 and 77 (Fig. 9). Scenarios 88 and 87 applied 1986–1991 treatments to private lands. This suggested that recent changes in land cover dynamics on private land could have a substantial effect on total forest cover, while changes on USFS lands would have little influence on this measure.

It appears then that the cover dynamics of private land could have the most substantial impact on total forest cover in the LTRB. These effects were borne out in the short run (Fig. 9 demonstrates substantial differences in cover after the first time step). This likely reflects the strong concentration of transitions on land of certain locational characteristics (e.g., on gentle slopes closer to town). These factors quickly became limiting, and transitions on private lands then moderated substantially. In the short run then, the landscape was most sensitive to private land use decisions, which were influenced by site factors that quickly become limiting in the landscape. In contrast, cover changed less on USFS land but changes were more diffuse spatially, so spatial characteristics didn't have the same dampening influence on cover changes. As a consequence, management activities on the USFS land, while much less intensive than on private lands in this area, could have more substantial long-run influence on landscape structure.

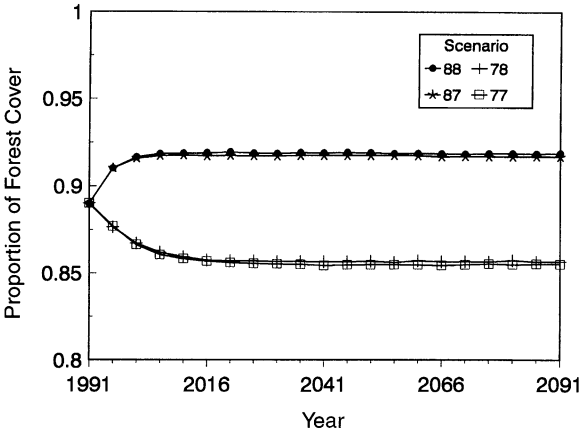

FIG. 9. The mean proportion (n = 5) of the Little Tennessee River Basin occupied by forest cover at 5-yr time steps for the 100-yr simulation of four historical land-cover-change scenarios (see *Methods*).

Historical simulations such as these can provide critical benchmarks for the definition of ecosystem- or landscape-level management issues. They can define what and where problems may arise at the landscape level if historical trends persist. They can also define—and this is illustrated especially well in our case study—the range of landscape implications arising from the variability of observed landowner behaviors. Extrapolating 1975–1980 behavior led to a substantial increase in forest fragmentation and reduction of forest cover. Extrapolating 1986–1991 behavior led to increased connectivity and an increase in forest cover.

Our regulatory scenarios, defined by rules that were externally imposed, provide some insights into a broad range of possible future landscape conditions. We chose restrictions on forest harvesting to illustrate the use of landscape-level simulations, but recognize that these were essentially arbitrary and ad hoc as regulatory instruments. Truly feasible policies and regulations for landscape-level management are conditioned on existing institutions and property rights and must involve all stake-holders. While not intended as plausible regulations for the LTRB, these rules do, however, provide useful insights into a wide range of futures, especially when compared to the historical scenarios.

Regulatory scenarios highlight a number of points relevant for ecosystem-level management. The no-harvest scenario imposed, by virtue of the very large share of the study area in forest cover (89% in 1991), a highly invasive rule. When applied to the private lands, significant changes in landscape structure resulted, as expected. Forest cover grew to 99% while forest patch size increased by more than three times. The number of grassy and unvegetated patches declined substantially. However, when regulation was applied only to grid cells near a stream, thereby influencing a

much smaller share of the private land, substantial gains in forest cover and connectivity were also achieved. This finding suggests that spatially targeted regulation could be much more efficient than blanket restrictions on all lands for achieving certain landscape-level goals.

Our analysis of these same scenarios for public lands produced a similar ranking of effects. The no-harvest rule increased forest cover and connectivity. The S treatment achieved similar results but influenced a much smaller share of the landscape. However, when compared with the effects generated by applying these scenarios to private lands, changing the management of public lands had relatively little influence on the landscape as a whole. While the shift from 1975–1980 to 1986–1991 treatments implies some significant change in overall landscape structure, subsequent shifts to the S and N treatments on public lands produced only relatively small shifts in the landscape measures.

Conclusions

Public lands are quite naturally the focus of ecosystem management. This portion of the landscape is where public goals not obtained through markets have traditionally been addressed through a long history of multiple-use management. The focus of public land management has recently shifted however to a much more complex set of goals addressing ecosystem functions and environmental health. It seems reasonable to ask whether public lands have some physical possibility or advantage for addressing these new goals. Our findings raise the possibility that public lands may not always hold comparative advantage for influencing overall landscape structure and therefore ecosystem function. This clearly depends on the spatial arrangement of private and public lands and on market-driven factors that influence land-use choices. Therefore when formulating ecosystem management plans for public lands we should ask whether specific public forests are large enough and configured in a way so to influence ecosystem function in significant ways.

The interactions between public and private lands have been raised as important considerations in the design of effective reserves. Reserves that are in public ownership cannot be the only or even the primary strategy for maintaining biodiversity (Franklin 1993). The unreserved or "semi-natural matrix" portion of the landscape is dominant in most inhabited regions of the world and may contain the majority of biological diversity (Pimentel et al. 1992), and landscape management expands its viewpoint beyond the distribution of public reserves (Franklin 1993, Mladenoff et al. 1993). Our results further emphasize that scientists and policy makers need to address the condition and dynamics of both reserved and non-reserved lands across the landscape when considering ecological sustainability.

Our findings suggest that spatially targeted regulation might have effects on landscape structure that are disproportionate to the area regulated. Accordingly, specific places within a management area that is scaled appropriately may have critical influence on, for example, forest connectivity. Focusing efforts on these critical areas may prove to be the most effective and efficient means of influencing conditions at a landscape scale. Goals may be achieved without highly invasive regulations that influence all or a large share of lands and landowners. These types of critical areas may be identified with tools such as the simulation approach used here.

Critical areas (areas that have comparative advantage for effecting ecosystem management goals) are not necessarily found on public lands. If they are located on private lands, then it would seem reasonable to ask whether society is better served by allowing markets to determine their use, by regulating their use (considering costs of regulation as well as ecosystem benefits), or by making these lands public. Regulation of private lands usurps property rights and value from the land owner, usually without compensation. Outright purchase of these lands or their development rights (as with conservation easements) by public agencies instead compensates the land owner directly for the use of land to accomplish goals for the public at large.

Changing the objectives of public land management to address ecosystem-level goals leads more generally to questions regarding what lands should be public (Wear 1992). Our present configuration of public lands is the artifact of land acquisitions fueled by different goals and historical accidents such as transcontinental railways and depressions (Steen 1976, Shands and Healy 1977). While perhaps appropriate for yesterday's social goals, all public lands may not be especially well configured to influence important ecological functions significantly. Our findings show that in the LTRB extreme measures applied to the public lands would have little additional influence on the landscape as a whole. In other settings, public lands may have more or less of an effect. Where ecosystem values are high, e.g., in the presence of threatened species, it may be more effective to reconfigure the mosaic of public and private lands than to impose another layer of regulation and cost on private landowners.

The analysis conducted here has been instructive in sketching out large issues that arise with ecosystem management in a multi-owner setting. However, work in several areas is needed to make this type of integrative modeling an effective management tool. The broad measures of landscape structure provided only a first-approximation of ecological impacts. The next and critical step in this type of analysis is to develop indices of actual ecological processes that define where thresholds of biologically meaningful change occur. We continue work on applying models of water quality and species persistence linked to landscape structure in the LTRB. These measures of effects will allow for a direct

linkage between land management and physical process and ecological function.

Nonetheless, the methodology used in this case study of the LTRB offers considerable flexibility for future applications. The spatial data and simulation model were linked in an integrative modeling framework (Berry et al. 1996), and additional rule-based management scenarios could be implemented easily to explore policy-relevant alternatives within the watershed. For example, managers of public land could use the model to compare the effects of alternative land management strategies that might actually be implemented. Furthermore, these alternatives could be evaluated within a wide range of potential directional changes on the private lands.

Another critical extension of the work presented here is to explicitly address the effects of land cover change on natural resource supplies and local income and the costs of the regulatory actions that were modeled. Such information would allow a careful examination of the costs of various approaches to providing ecosystem services from a multi-owner landscape. Finally, the definition of our dependent variable, land cover, was not completely satisfactory for several reasons. First, land cover may mask important differences in actual land use. For example, forest cover corresponds with both land used for forest management and some low-density residential uses. These two uses hold very different implications for, for example, the migration of animals, transport of nutrients, and understory vegetation. Second, the categories we used (forest, unvegetated, and grassy/brushy cover) aggregate a considerable amount of ecologically important variability in species composition, habitat structure, and stand age. For example, forest cover includes stands of varying age, over- and understory species composition, density, and vertical structure. Evaluating the importance of land-cover change for biodiversity or ecosystem processes would be enhanced by use of more detailed land-cover and vegetation classes. Finer-resolution remote imagery (e.g., Landsat Thematic Mapper and SPOT data) provide improved resolution for more recent years, but it is difficult to get a long series of comparable data for a large area. All of these areas deserve further investigation.

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