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LANDSCAPE CHANGE AND HABITAT AVAILABILITY IN THE SOUTHERN APPALACHIAN HIGHLANDS AND OLYMPIC PENINSULA

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Abstract. Methods for predicting the ecological impacts of land use change on biodiversity and ecosystem function are needed to guide land planning and resource management decisions. This study explores the consequences of alternative scenarios of land cover change on the abundance and arrangement of potential habitat for a suite of species in the Little Tennessee River Basin (LTRB) in the Southern Appalachian Highlands and the Hoh River Basin (HORB) on the Olympic Peninsula. We addressed two questions: (1) How does land ownership affect the availability of suitable habitat for a variety of species in changing landscapes (and how do restrictions on forest harvest then change habitat availability)? (2) Are species differentially affected by land cover changes that vary among landowners?

Scenarios of land cover change were projected by using a spatially explicit model in which the probability of land being converted from one cover type to another was conditional upon social, economic, and ecological factors. Potential habitat was defined for each species based on resource needs related to land cover and topography and was mapped at each time step. Spatial pattern of potential suitable habitat for each species was analyzed by computing area, number of patches, mean patch size, and area of the largest patch of suitable habitat. Simulations extended for 100 yr with a 5-yr time step.

The different scenarios, based on historical periods and management options regulating forest loss, produced qualitatively different landscapes. Restrictions on forest harvest produced more, better-connected habitat for forest species. However, habitat changes for species were only partially predicted by changes in land cover types. For example, a 5–10% decrease in the amount of grassy or brushy cover in the HORB resulted in a 10–20% reduction in habitat for honeysuckle. When responses of all species were considered collectively, there were effects of both private and public ownerships in the LTRB but no interaction between the two ownership types. In the HORB, variation in the rates of land cover change for public lands had the greatest effect on species habitats. Our results suggest that both landscape-level approaches, which provide a means to quantify and monitor broad-scale changes related to biodiversity and ecosystem processes, and species-level approaches, which provide an appropriate context for interpreting the significance of landscape-level changes, are useful for effective conservation.

Key words: Appalachian Highlands; biodiversity; conservation; ecosystem management; habitat models; land cover change; land use; Olympic Peninsula; spatial modeling.

INTRODUCTION

Land use change is the leading cause of habitat loss and fragmentation (Skole et al. 1994, Turner et al. 1994, Sinclair et al. 1995). Both worldwide and in the United States, land cover is altered principally by direct human use, through agriculture, pasture, forestry, and development (Meyer 1995). Land use patterns affect both terrestrial and aquatic systems (Reiners et al. 1994, Cooper 1995) and influence biodiversity for several reasons (Turner et al. 1998). First, land use activities may alter the relative abundances of natural habitats and result in the establishment of new land cover types. Species richness may be enhanced by the addition of new cover types, but natural habitats are often reduced, leaving less area available for native species (Walker 1992). Exotic species also may also become established and outcompete the native biota. Second, the spatial pattern of habitats may be altered, often resulting in fragmentation of once continuous habitat. Clearly, the conservation of native species and their habitat requires a landscape-level solution (Franklin 1993, 1994, Tracy and Brussard 1994), and projecting patterns of species presence and abundance under future change scenarios remains a key challenge in sustaining biodiversity (Lubchenco et al. 1991, Hansen et al. 1995*a*). Because species do not respect political boundaries, a predictive understanding of land use dynamics in areas that may be owned or managed by both private and public entities is sorely needed. In this paper, we build upon a comparative study of the causes and consequences of land cover change in two forested landscapes—the

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Southern Appalachian Highlands, western North Carolina, and the Olympic Peninsula, Washington (Lee et al. 1992, Berry et al. 1996, Turner et al. 1996, Wear et al. 1996)—to explore the implications of alternative scenarios of land cover change for potential species persistence.

Understanding ecological dynamics in areas of mixed ownership is an important component of ecosystem management (Slocombe 1993, Christensen et al. 1996), yet few studies have examined landscapes large enough to span multiple ownerships. Simulation models of land use change have been instructive for understanding the implications of alternative policies or management practices for landscape structure and for highlighting the importance of social and economic driving forces. In western North Carolina, activities undertaken on private lands had a disproportionate effect on simulated future landscape structure within a forested watershed of mixed ownership (Wear et al. 1996). Land ownership and management policies in the Pacific Northwest also have been shown to affect the rate and pattern of forest change and the resultant landscape structure (Spies et al. 1994, Turner et al. 1996). Timber-harvesting practices can have a significant impact on landscape structure (Franklin and Forman 1987, Li et al. 1993), and patterns imposed by harvesting can persist for a long time (Wallin et al. 1994). In Rondonia, Brazil, Dale et al. (1993) demonstrated that changes in land use and land cover were a function of individual parcel sizes and shapes, attributes of individual landowners, site characteristics such as soils and agricultural suitability, and distance to the road network.

Ecologists are beginning to develop techniques for assessing the complex impacts of landscape changes on biodiversity. Generalizations are difficult to make because habitat changes affect species in different ways (Pearson et al. 1996). Extensive, repeated surveys of species presence and abundance provide valuable data on population demography and habitat use, but such studies are time consuming and expensive, and frequently are conducted for few species or over short time periods. Predictive modeling that identifies suitable habitat for a variety of species is a necessary first step toward anticipating the potential ecological effects of land use changes. Hansen et al. (1993) recommended that habitat suitability and life history attributes be used as surrogates for detailed demographic data for vertebrate species, an approach they consider as intermediate between the "coarse-filter" and "fine-filter" approaches described by Noss (1987) and Hunter (1991). Associating target species with specific habitat configurations and evaluating alternative management prescriptions using simulation models were key steps in their suggested approach for management of terrestrial vertebrate habitat at landscape scales on multiple-use lands. Habitat-based approaches have offered insight into the implications of variation in landscape pattern for a variety of taxa. For example, Tucker et al. (1997) used a rule-based Bayesian model linked with land cover and physiographic data to predict suitability of a landscape in northeast England for three species of birds.

Assessing spatial and temporal changes in biodiversity by monitoring a suite of species with different habitat requirements has emerged as a useful technique. For example, Miller et al. (1997) chose bird and vascular plant guilds to represent the overall biotic community in a comparative evaluation of how well descriptors of land cover patterns related to anthropogenic disturbances and the biotic community structure in two 100-km^2 watersheds of the Ridge and Valley province of central Pennsylvania. Patterns of deforestation in Rondonia, Brazil, were interpreted from the perspective of species with different area requirements and dispersal capabilities (Dale et al. 1994). In low- to mid-elevation forests in the Pacific Northwest, risk to bird species under four different management scenarios was evaluated by quantifying suitable habitat for each species by using habitat maps, species–habitat associations, and other life history requirements (Hansen et al. 1995*b*). Avian diversity has been used as an indicator of the vertical and horizontal structural complexity of vegetation over a broad region (Flather et al. 1992). Butterflies, both alone (Kremen 1992, 1994) and in combination with birds (Debinski and Brussard 1994), have been used as indicators of biodiversity. Potential effects of landscape pattern on Neotropical migrant bird abundance were explored by merging the North American Breeding Bird Survey data with U.S. Geological Survey land cover data (Flather and Sauer 1996). Recently, White et al. (1997) used habitat and area requirements for a large sample of vertebrate species in Monroe County, Pennsylvania, to assess risks to biodiversity associated with land development. Six possible alternative versions of Monroe County that differed in the extent and spatial distribution of human impact were developed for the year 2020 based on projected current rates of population growth. Their results demonstrated little variation in species richness among the six alternatives (i.e., few species were predicted to become extinct), although loss of habitat might be substantial. Collectively, these studies suggest that analyzing species habitat requirements and changes in habitat availability through time may serve as a suitable starting point for relating land use change to biodiversity.

The present study estimates ecological effects of land cover change by projecting changes in the abundance and spatial distribution of habitats for a suite of species inhabiting two forested watersheds. Scenarios of land cover change were projected by using a spatially explicit model, LUCAS (Berry et al. 1996, Wear et al. 1996), and by extrapolating historical rates of land cover change for a century into the future. Because land ownership is included explicitly in the model, simulated changes in landscape structure and species habitat

can be related to changes on lands under different ownerships. Wear et al. (1996) found that land cover transitions on private lands had a disproportionate effect on landscape structure within an entire watershed, and we explore whether this is also true for effects on species habitat. We address two questions: (1) How does land ownership affect the availability of suitable habitat for a variety of species in changing landscapes, and how do restrictions on forest harvest change habitat availability? and (2) Are species differentially affected by land cover changes that vary among landowners?

Study Areas

We compared landscapes within two forested biosphere reserves (U.S. Man and the Biosphere Program): the Olympic Biosphere Reserve and the Southern Appalachian Man and Biosphere (SAMAB) region. Both occur in mountainous temperate forest and their local economies depend, in part, on forest resources. These areas were selected because they reflect different land ownership patterns and regional economies and may serve as microcosms for many land cover changes observed in forested regions of temperate North America.

Southern Appalachian Highlands

The Southern Appalachian Highlands extend approximately from Chattanooga, Tennessee, northeast to Roanoke, Virginia, crossing four states. Most of the region is held in small private ownerships, but the U.S. Forest Service (USFS) is a major landowner, accounting for ≥25% of land ownership in some counties. Forested lands have experienced 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 United States because of the tremendous human population within a day's drive, and this recreation demand also affects adjacent national forests and private lands. Holdings of the national forests in the Southern Appalachians are interspersed among many landowners and must be managed accordingly.

Within this region, we selected the Little Tennessee River Basin (LTRB) for intensive study. The 116 090-ha LTRB is located primarily in western North Carolina, extending approximately from the Georgia–North Carolina border to Fontana Dam, just south of the Great Smoky Mountains National Park. Although approximately 10% of the LTRB is located in north Georgia, we considered only the 103 635-ha portion 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, is experiencing an influx of new residents. Tourism in Franklin is now a $50 million per year business and growing. Forest products remain an important industry in the LTRB, and the USFS is a major landholder, owning 35% of the watershed, primarily at the higher elevations. The rest of the watershed is dominated by primarily small private holdings (Fig. 1). The rotation of forest cutting on the national forest lands ranges from 80 to 120 yr; harvest is primarily cove and upland hardwoods for saw timber. The USFS Coweeta Hydrological Laboratory, a Long-term Ecological Research (LTER) site, also is located within the LTRB.

The abundance and connectivity of forest cover in the LTRB has increased since 1975 (Turner et al. 1996). However, the period between 1975 and 1986 was characterized by higher rates of forest clearing on private lands (primarily small private owners) at lower elevations and on steeper slopes, resulting in a net loss of 8% of forest on private lands. Forests were cleared for timber harvest, residential development (primarily vacation homes), and industrial development. In contrast, the period 1986–1991 was characterized by an increase in forest cover on private lands. On USFS lands, the pattern of forest cover has remained relatively stable since 1975 (Turner et al. 1996).

Olympic Peninsula

The Olympic Peninsula, Washington, encompasses $\sim 1.6 \times 10^6$ hectares, with the Olympic National Forest and Olympic National Park comprising nearly a third of the land area. The pattern of land ownership on the Olympic Peninsula is quite different from that in the SAMAB region. Both public and private lands are generally held in large blocks, and most of the nonfederal lands are managed for timber production by Washington State's Department of Natural Resources (DNR) and by large private corporations. Small private ownerships comprise only ~21% of the Olympic Peninsula, compared to ~57% in the Southern Appalachians. The controversy over the harvest of old-growth timber and conservation efforts focused on the Northern Spotted Owl (*Strix occidentalis*) in the Pacific Northwest have underscored the importance of understanding landscape dynamics on the Olympic Peninsula.

We selected the Hoh River Basin (HORB) on the Olympic Peninsula for this study. The basin originates in the high elevations of the Olympic National Park, centrally located on the Peninsula. The 78 007-ha basin extends west from the park to the Pacific Ocean. Major landholders in the HORB include the National Park Service, the DNR, and large commercial private owners (Fig. 1).

Both DNR lands and private lands (primarily large commercial owners) in the HORB have shown low to moderate levels of fluctuation in landscape pattern since 1975 (Turner et al. 1996). Coniferous forest lands generally occupied ~50% of the DNR lands but only 22–40% of the private lands. The DNR and private commercial lands in the HORB are both managed for timber production, and rates of land cover change are strongly influenced by timber prices; timber markets were especially strong between 1975 and 1980, with

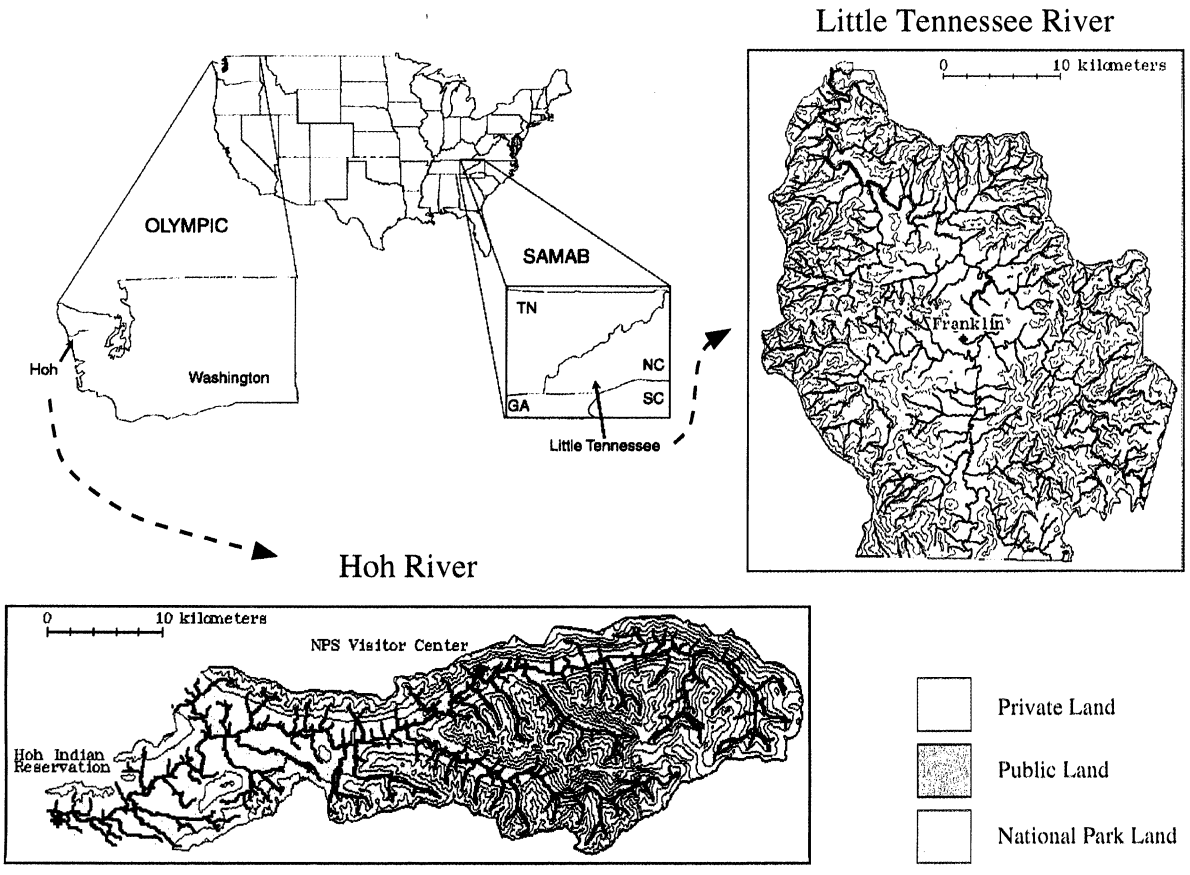

Fig. 1. Spatial arrangement of major categories of land ownership in the Little Tennessee River Basin, North Carolina, and the Hoh River Basin, Washington. Blue lines are streams, and black lines are 200-m contours.

timber prices for West Coast species increasing at unprecedented rates. Thus, rates of land cover change in the HORB may be very sensitive to temporal change in the relative prices of wood products, optimal depletion schedules, and forestry policies (Turner et al. 1996).

Methods

Land-cover change model

A spatially explicit simulation model, LUCAS (Berry et al. 1996, Wear et al. 1996), was used to project various future land cover scenarios. The probability of land being converted from one cover type to another was conditional upon a variety of social, economic, and ecological factors. Socioeconomic and ecological variables were represented spatially on gridded landscape maps stored in the GRASS geographic information system (GIS) (USA CERL 1991). We used the following data layers: land cover (forest, grassy/brushy, and unvegetated), derived from Landsat Multispectral Scanner (MSS) data; land ownership class (National Forest, State Forest, or private); elevation; slope; aspect; distance to the nearest road; distance to the nearest market center (e.g., Franklin, North Carolina); and human population density. Sources of data are described in Turner et al. (1996). The model operates at a spatial resolution of 90 × 90 m grid cells, comparable to the resolution of the MSS data. The LTRB contained a total of 127 949 grid cells (103 638 ha), and the HORB a total of 96 296 grid cells (78 000 ha).

Landscape change was simulated by using conditional transition probabilities (Wear et al. 1996). Transition probabilities 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 by using a multinomial logit model (Wear and Flamm 1993, Turner et al. 1996). Models were estimated separately for National Forest and privately owned lands in the LTRB and for DNR and private lands in the HORB. Change was not simulated in National Park lands (Great Smoky Mountains National Park and Olympic National Park). Transition probabilities were estimated and implemented separately for each watershed. The equations derived from the multinomial logit model were used in the landscape simulator as follows. The simulation begins with an

TABLE 1. Species used in this study and the mapping rules used to define potential habitat in two temperature forest watersheds. Map cells were 90 × 90 m.

Species	Habitat description
A) Little Tennessee River Basin	
Showy orchis (*Orchis spectabilis*)	Cells with forest at elevations <1210 on north-facing slopes
Catawba rhododendron (*Rhododendron catawbiense*)	Cells with elevations >900 m (unvegetated or grassy/brushy cover, or forested cells adjacent to these nonforest covers)
Princess tree (*Paulownia tomentosa*)	Exotic species found in open areas or forest edges at elevations <762 m
Mountain dusky salamander (*Desmognathus ochrophaeus*)	Forested cells with northerly aspects; restricted to cells containing streams or adjacent to cells with streams at elevations <950 m; found throughout north-facing forests at elevations ≥950 m
Southeastern shrew (*Sorex longirostris*)	Cells with unvegetated or grassy/brushy cover areas at elevations <760 m
Northern flying squirrel (*Glaucomys sabrinus*)	Forested cells at elevations above 1210 m
European Starling (*Sturnus vulgaris*)	Exotic species found in cells with unvegetated or grassy/brush cover throughout the watershed
Wood Thrush (*Hylocichla mustelina*)	Forest-interior habitat (forest cells >180 m from forest edge) at elevations <1370 m
B) Hoh River Basin	
Horsetail (*Equisetum telmateia*)	Cells of grassy/brushy and unvegetated habitats containing streams or adjacent to cells with streams in the western hemlock zone
Cascade Oregon grape (*Berberis nervosa*)	Cells of conifer forest in montane forest zone
Mountain alder (*Alnus sinuata*)	Cells of grassy/brushy and unvegetated habitats in the montane forest zone
Mountain huckleberry (*Vaccinium membranaceum*)	Cells of deciduous forest in the montane forest zone
Licorice fern (*Polypodium glycyrhiza*)	Cells of deciduous forest containing streams or cells adjacent to streams in the western hemlock zone
Twinflower (*Linnaea borealis*)	Cells with conifer forest in western hemlock zone
Honeysuckle (*Lonicera ciliosa*)	Cells with grassy/brushy areas with slopes ≥4° in the western hemlock zone
Heather vole (*Phenacomys intermedius*)	Cells with grassy habitats in the montane forest zone
Red squirrel (*Tamiasciurus hudsonicus*)	Cells with conifer forest in the western hemlock zone

initial map of land cover. In the simulations reported here, we began with the 1991 land cover maps. For each grid cell, the value of each data layer described above was used in the logit equation to generate a transition probability. We then drew a random number between zero and one. If the random number was less than or equal to the transition probability, the grid cell was changed; otherwise, the grid cell remained in its present state. This process was repeated for each 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.

Species responses to land cover change

Species may respond very differently to the same changes in a landscape. Therefore, it is difficult to relate "biodiversity" to landscape change; a given change may result in increased habitat for some species and decreased habitat for others. To examine a range of potential responses to land cover changes in each watershed, we selected species with diverse habitat requirements across a range of taxa (Table 1). The limitations of the landscape change model influenced our choice of species. The number of species was limited to eight for each watershed because of the complexity in discerning the consequences of landscape changes for even a small number of species. Our primary purpose in this study was to explore the implications of landscape change driven by dynamics of different kinds of landowners. A small suite of species with diverse habitat requirements was adequate to fulfill this purpose.

The selected species included those that require both late and early successional habitats (e.g., orchis vs. rhododendron, Oregon grape vs. alder), both natives and exotics (e.g., thrush vs. starling), and both generalists and specialists (e.g., red squirrel vs. horsetail). Moreover, potential habitat for these species must be predictable using the coarse land cover classes available from the landscape change model. Species that require specific seral stages or microhabitat conditions (e.g., levels of coarse woody debris, specific plant hosts) could not be mapped using our land cover data. Thus, species requiring sophisticated, data-intensive habitat suitability models could not be used. The spa-

tially explicit data necessary for these sophisticated habitat models are often unavailable for extensive areas and multiple time periods, and are difficult to simulate through time with confidence using landscape change models. Simple habitat models, nevertheless, provide a means for quantifying the consequences of landscape change for various species.

A variety of methods can be employed for identifying suitable habitat (Hansen et al. 1993), ranging from associations with seral stage or stand structure (Hansen et al. 1995*a*), habitat suitability models (Boroski et al. 1996), logistic regression (Mladenoff et al. 1995), Bayesian rules (Miller et al. 1997), and multivariate statistical methods. In this study, we chose to employ simple rules that could be easily obtained from natural history information and that would be compatible with relatively coarse data describing land cover, topography, and simple geographic relationships (such as patch size or proximity to edge). We recognize that more sophisticated relationships can be developed with more extensive empirical data. In addition, we also recognize the need to link models of land use change to models that incorporate the dynamics of populations. Demographic data to implement dynamic models remain limited for many species, however, and we suggest that the habitat-based approach remains viable for identifying species that may be at particular risk.

Potential habitat for each species in the model was defined based on the species' resource needs that could be mapped using the land cover and topographic data available in the model. Landscape changes could then be interpreted from an organism-based rather than an anthropocentric perspective (Wiens 1976, 1989). Habitat descriptions for the species in the LTRB were developed from Radford et al. (1968) for plants, Martof et al. (1980) for amphibians, Webster et al. (1985) and French (1980) for mammals, and Simpson (1992) and Potter et al. (1980) for birds. Habitat descriptions for the Hoh River watershed were developed from studies by Kruckeberg (1991), Defarrari (1994), and Whitney (1989). Grassy/brushy and unvegetated land covers were considered open, nonforest habitats. Forest edge habitats included forest cells adjacent to cells with nonforest land covers. Likewise, the Wood Thrush, a forest-interior species, was excluded from forest cells within 180 m of a cell of nonforest land cover. This was equivalent to two 90-m cells. Streamside habitats (i.e., salamander, horsetail) were cells of the appropriate land cover crossed by streams or directly adjacent to cells having streams. The grassy/brushy land cover was considered suitable for species requiring either grassy or shrubby habitats (e.g., honeysuckle, vole).

Habitat for species in the LTRB could be mapped using a combination of land cover, elevation, and aspect. Species in the HORB also respond to differences in topography, and the wider range of elevations in this watershed allows biogeographers to identify distinct life zones that relate to broad-scale differences in habitat and species distributions. To facilitate mapping of species habitat in the HORB, a map of life zones was used to show elevation and topographic information. This life-zone map was produced by reclassifying vegetation classes on the Olympic National Park vegetation map (produced from a September 1991 Thematic Mapper image into four zones and provided by R. Hoffman, *unpublished data*) into four life-zone classes (Table 2, based on Kruckeberg 1991). The reclassified map was subjected to a nine-cell (3 × 3 cell) majority-rule filter to smooth the edges between life zones and to fill in gaps left by water, rock, meadow, and shrub covers in the original vegetation map. The park vegetation map was not used as a data source for the model's land cover maps. A large block of unclassified land between the mountains in the national park and the seashore within the Hoh watershed was classified as Western Hemlock Zone based on elevation. The map was then resampled to 90-m cell resolution to match the other data layers used by the land cover change model.

TABLE 2. Reclassification of the Olympic National Park vegetation map to the Hoh River Basin life-zone map used in defining species habitat.

Life-zone cover types	Vegetation cover types from Olympic National Park map
Western hemlock zone	Douglas-fir, western hemlock, sitka spruce, western red cedar, big leaf maple, red alder
Pacific silver fir zone	Pacific silver fir
Montane forest zone	Mountain hemlock, subalpine fir, Alaska yellow cedar, lodgepole pine
Alpine zone	Rock, snow, and meadow covers located at high altitudes

Based on the habitat "rules" for each species (Table 1), the land cover maps for the LTRB and HORB were converted to a maps of potential habitat for each species at each time step during a simulation. The spatial pattern of potential suitable habitat was analyzed by computing a set of spatial metrics: area, number of patches, mean patch size, and area of the largest patch of suitable habitat. Both adjacent and diagonal grid cells (i.e., an eight-neighbor rule) were used to demarcate patches. These metrics provide information on the abundance and connectivity of the habitat. Differences in these metrics were compared among land cover scenarios at the end of the simulation (e.g., year 2086).

Simulation experiments

Two sets of simulations were conducted to compare effects of alternative scenarios on suitable habitat for a variety of species. The first set of simulations (Question 1) compared four scenarios that varied in their rates of forest loss and were based on historical transitions or management alternatives with forest loss restrictions. The scenarios were: (1) observed land cover changes during 1975–1986; (2) observed land cover

changes during 1986–1991; (3) the 1986–1991 observed rates, but with a constraint that prohibited any loss of forest within 90 m of a stream and on slopes greater than 20%; and (4) the 1986–1991 rates, except that all forest loss was prohibited. Hereafter, scenario 3 will be referred to as the stream/slope restriction, and scenario 4 will be referred to as the no-forest-loss scenario.

The second set of simulations (Question 2) explicitly explored the influence of land ownership. These simulations also compared four scenarios, but the historical transition probabilities for the two distinct time periods were applied on the public and private lands separately in a 2 × 2 factorial design, and no management restrictions were included. The scenarios involved the following transition probabilities: (1) 1975–1986 on public and private lands; (2) 1975–1986 on public lands, and 1986–1991 on private lands; (3) 1986–1991 on public lands and 1975–1986 on private lands; and (4) 1986–1991 on public and private lands. A factorial design was used because prior analysis (Turner et al. 1996) demonstrated that transition probabilities between land cover classes were not stationary between time periods. In addition, transition rates may change independently between time periods on different land ownerships. For example, public lands may respond to regulatory changes that increase or decrease transition rates, whereas private lands may respond to a suite of market drivers. All simulations began with the 1991 land cover maps and extended for a century with a 5-yr time step. Because the model is stochastic, replicate simulations ($n = 5$) were conducted for each scenario. Transition probabilities for public and private lands were estimated separately for public and private ownerships in each watershed. In the HORB, transition probabilities for public lands were based on an analysis of state DNR lands. Land covers were not allowed to change in Olympic National Park.

Variation in the habitat metrics at the end of the simulations for each species were analyzed by using SAS (SAS Institute 1992) to test for significant differences in habitat metrics due to alternative scenarios of landscape change. ANOVA and Tukey's Studentized range test were used to test for significant differences in each metric among scenarios for Question 1. To examine the influence of land ownership on the species habitat (Question 2), a two-factor MANOVA was used; the two factors were public vs. private ownership. Each ownership factor had two levels of forest disturbance: high (1975–1986) versus low (1986–1991) rates of transition from forest to other land cover classes.

Results

Question 1: historical and forest-cutting restriction scenarios

Land cover change in the LTRB.—The LTRB was dominated initially by forest cover and remained so under all scenarios (Fig. 2). Forest cover declined by nearly 4% and became more fragmented when the 1975–1986 historical transitions were extrapolated into the future, but increased and became better connected when the 1986–1991 rates were simulated (Table 3). As expected, restrictions on forest loss resulted in increased forest cover in the landscape, by ~7% when the stream/slope scenario was simulated and by ~12% when no forest losses were permitted. Unvegetated cover, which was low initially, tripled under the 1975–1986 historical scenario but declined with all other scenarios. Grassy/brushy cover decreased with the 1986–1991 historical scenarios and with both management scenarios.

Land cover change in the HORB.—Conifer forest cover in the HORB increased by 3.5–5% across all scenarios with only slight changes in the number and mean size of patches (Fig. 3, Table 4). Grassy/brushy cover and unvegetated cover declined in area and became more fragmented, although size of the largest patch for each did not change. Deciduous/mixed forest varied most among the scenarios (Table 4). Under the historical scenarios, deciduous/mixed forest declined in area and became more fragmented. With the two management scenarios, however, deciduous/mixed forest increased from 12% to 19%, and the number of patches increased.

Species response in the LTRB.—Potential habitat for two species (showy orchis and Wood Thrush) increased in abundance as forest cover increased (Table 5). For the showy orchis, potential habitat was reduced and fragmented under the 1975–1986 scenario, but habitat increased and became more connected with the other three scenarios. With the no-forest-loss scenario, changes in the spatial patttern of habitat were greater than might be suggested by the changes in habitat abundance. Although habitat for showy orchis increased by only 11%, mean patch size increased by 62%, and the size of the largest patch increased by >400%. For the Wood Thrush, both historical scenarios led to habitat reduction and fragmentation, whereas both management scenarios led to increased potential habitat (Fig. 4). Interestingly, the stream/slope restrictions resulted in additional but fragmented habitat, indicated by increased number of patches and decreased mean patch size. When no forest losses were permitted, potential habitat for the Wood Thrush increased by >120% and was well connected with fewer larger patches.

Potential habitat for four species (Catawba rhododendron, southeastern shrew, European Starling, and princess tree) increased when forest loss was high, then declined substantially as the rate of forest loss diminished (Table 5). These species are characteristic of open or forest edge habitats. For Catawba rhododendron and princess tree, potential habitat increased with both the 1975–1986 and 1986–1991 historical transitions; in contrast, habitat for southeastern shrew and European Starling increased with the 1975–1986 transitions but

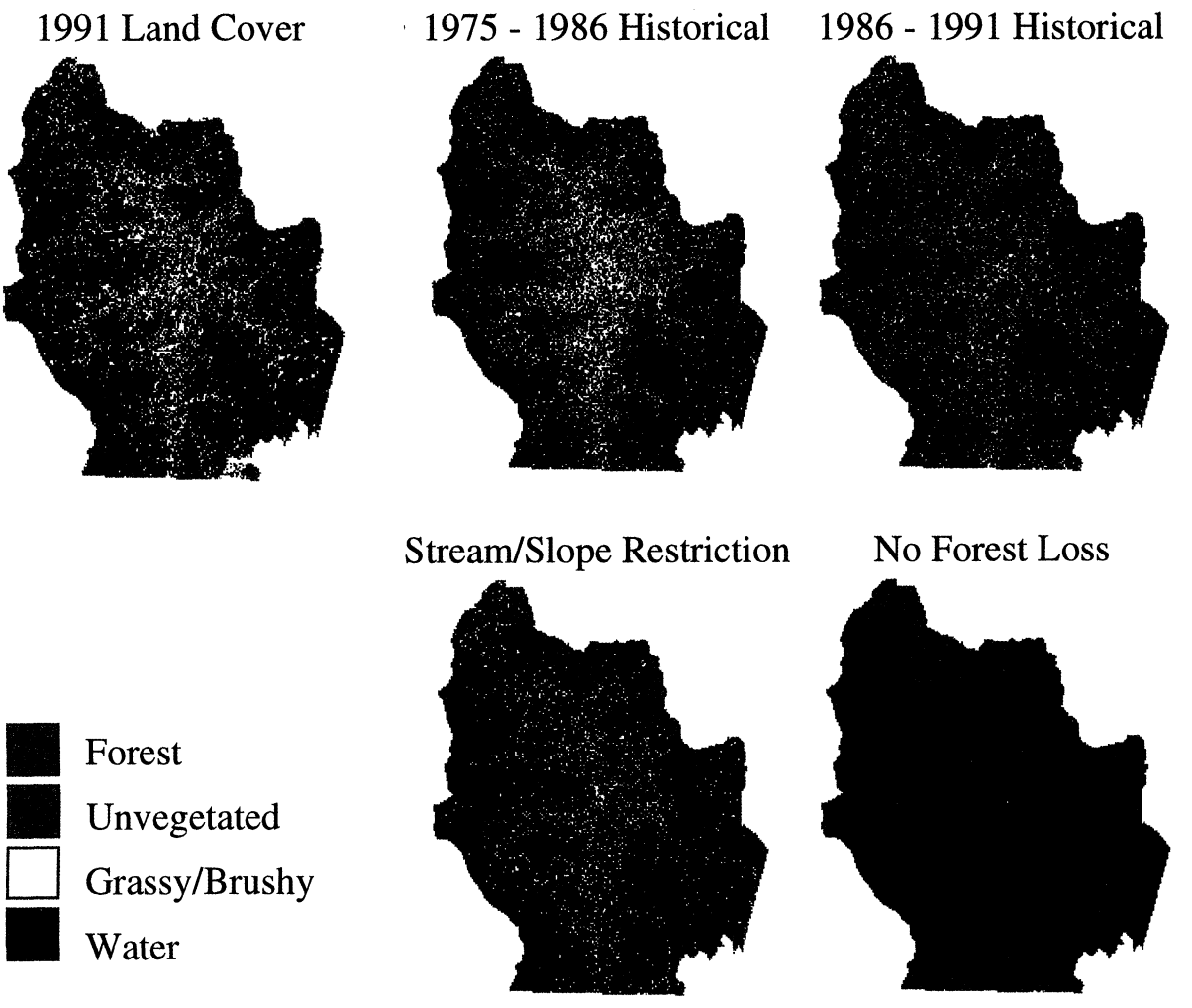

Fig. 2. Land cover maps for the Little Tennessee River Basin. The 1991 land cover map shows the initial conditions for the simulations. The remaining maps show simulated land cover at the end of a 100-yr simulation for four scenarios: the 1975–1986 historical transitions, the 1986–1991 historical transitions, the stream/slope restriction, and the scenario that permitted no forest loss.

TABLE 3. Mean percentage change in the area and spatial pattern of land covers in the Little Tennessee River Basin across six scenarios at the end of a 100-yr simulation. For initial conditions, all area and patch size data are in hectares.

			Management scenarios		Historical scenarios			
Cover type	Metric	Initial conditions	No forest loss	Stream–slope restrictions	Public 1986–1991; Private 1986–1991	Public 1975–1986; Private 1975–1986	Public 1986–1991; Private 1975–1986	Public 1975–1986; Private 1986–1991
Forest	Total area	89 286	11.8	6.7	3.3	−3.9	−3.7	3.1
	Number of patches	324	−95.0	−86.8	−68.8	208.1	212.8	−69.2
	Mean patch size	275.6	2140.6	734.7	235.9	−68.8	−69.2	236.6
	Largest patch size	88 355	12.9	7.8	4.2	−6.6	−6.4	4.0
Unvegetated	Total area	1156	−90.7	−67.5	−28.3	304.0	289.5	−14.1
	Number of patches	687	−87.0	−48.7	−12.3	499.3	472.9	16.7
	Mean patch size	1.7	−28.4	−36.6	−18.2	−32.6	−32.0	−26.3
	Largest patch size	101	−94.9	−91.7	−62.9	−11.2	−25.3	−66.1
Grassy/brushy	Total area	9683	−97.9	−53.9	−27.0	−0.2	−0.3	−26.9
	Number of patches	4336	−98.3	−3.3	52.1	55.8	57.9	49.8
	Mean patch size	2.2	23.9	−52.3	−52.0	−36.0	−36.8	−51.2
	Largest patch size	228	−78.0	−77.7	−77.7	−77.6	−77.9	−77.9

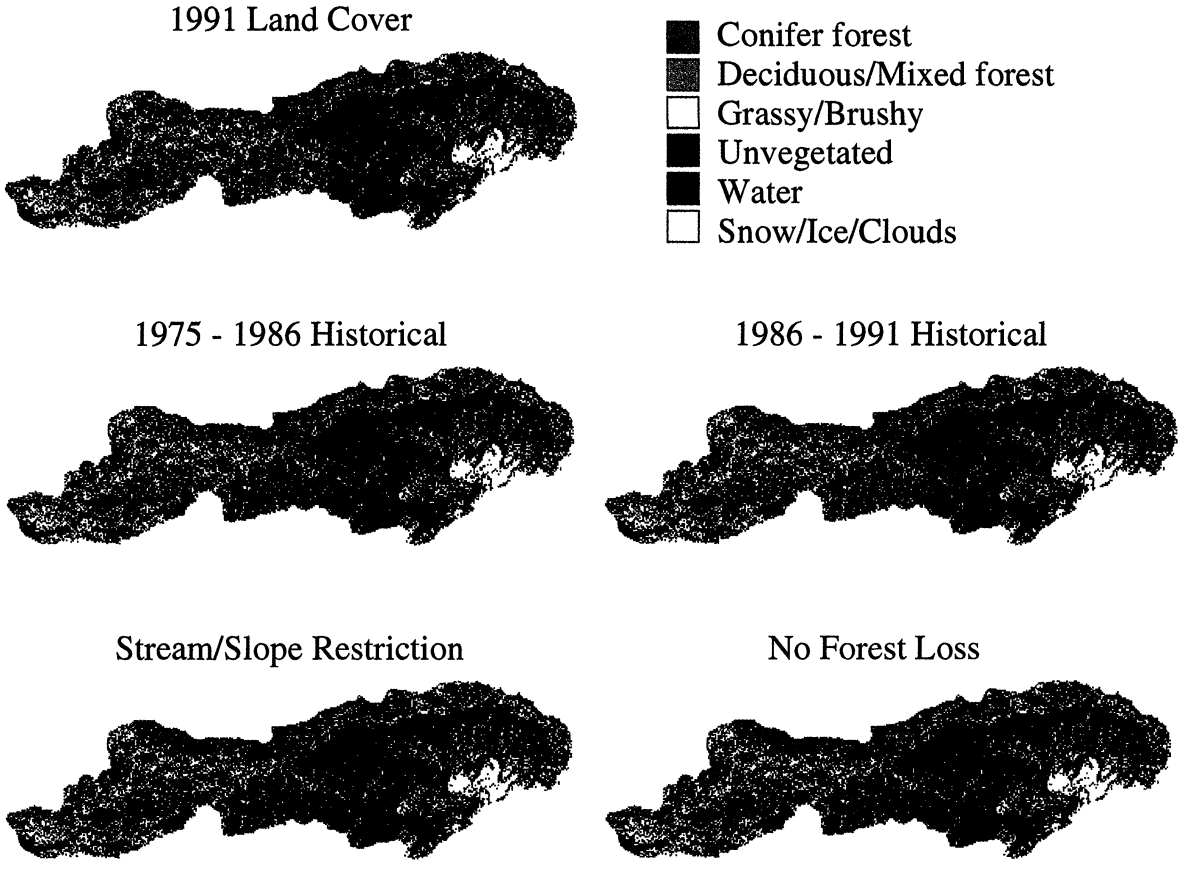

Fig. 3. Land cover maps for the Hoh River Basin. The 1991 land cover map shows the initial conditions for the simulations. The remaining maps show simulated land cover at the end of a 100-yr simulation for four scenarios, as in Fig. 2.

TABLE 4. Mean percentage change in the area and spatial pattern of land covers in the Hoh River Basin across six scenarios at the end of a 100-yr simulation. For initial conditions, all area and patch size data are in hectares.

			Management scenarios		Historical scenarios			
Cover type	Metric	Initial conditions	No forest loss	Stream–slope restrictions	Public 1986–1991; Private 1986–1991	Public 1975–1986; Private 1975–1986	Public 1986–1991; Private 1975–1986	Public 1975–1986; Private 1986–1991
Coniferous forest	Total area	46 185	3.7	3.6	3.5	5.0	3.5	5.1
	Number of patches	1542	5.1	6.4	3.6	−0.4	2.8	−0.4
	Mean patch size	29.9	−1.3	−2.6	−0.1	5.5	0.7	5.5
	Largest patch size	34 280	6.7	6.6	8.5	11.0	7.5	11.0
Deciduous forest	Total area	5964	19.5	12.6	−10.1	−14.1	−10.3	−14.0
	Number of patches	2297	19.9	20.6	13.2	3.4	13.1	3.5
	Mean patch size	2.6	−0.3	−6.6	−20.6	−16.8	−20.7	−16.9
	Largest patch size	287	4.5	−16.7	−37.6	−37.7	−37.9	−37.1
Grassy/brushy	Total area	9359	−11.6	−10.4	−5.7	−5.0	−5.2	−5.7
	Number of patches	4420	−11.1	−8.7	0.8	0	1.1	−0.8
	Mean patch size	2.1	−0.5	−1.8	−6.5	−5.0	−6.3	−5.0
	Largest patch size	154	0	0	0	0	0	0
Unvegetated	Total area	13 165	−13.5	−11.1	−3.6	−7.6	−3.9	−7.4
	Number of patches	1990	−2.3	9.9	44.9	27.3	42.8	28.7
	Mean patch size	6.2	−11.5	−19.1	−33.4	−27.4	−32.7	−28.1
	Largest patch size	1137	0	0	0	0	0	0

TABLE 5. Mean percentage change in the area and spatial pattern of habitat for each species in the Little Tennessee River Basin across six scenarios at the end of a 100-yr simulation. For initial conditions, all area and patch size data are in hectares.

			Management scenarios		Historical scenarios			
Species	Metric	Initial conditions	No forest loss	Stream–slope restrictions	Public 1986–1991; Private 1986–1991	Public 1975–1986; Private 1975–1986	Public 1986–1991; Private 1975–1986	Public 1975–1986; Private 1986–1991
Showy orchis	Total area	41 558	11.3[a]	6.5[b]	2.6[c]	−4.6[d]	−4.6[d]	2.5[c]
	Number of patches	2451	−31.5[d]	−17.7[c]	−6.2[b]	19.3[a]	19.1[a]	−5.0[b]
	Mean patch size	17.0	62.4[a]	29.5[b]	9.4[c]	−20.0[d]	−19.9[d]	7.9[c]
	Largest patch size	2615	444.6[a]	214.6[b]	71.3[c]	3.0[d]	0.7[d]	79.4[c]
Catawba rhododendron	Total area	6371	−92.8[d]	−38.3[c]	29.9[b]	37.5[a]	29.4[b]	36.4[a]
	Number of patches	424	−89.6[d]	−7.0[c]	74.5[a]	68.5[ab]	75.9[a]	59.4[b]
	Mean patch size	15.0	−31.1[cd]	−33.6[d]	−25.5[b]	−18.3[a]	−26.4[bc]	−14.4[a]
	Largest patch size	802	−90.1[c]	−73.4[bc]	−58.7[ab]	−44.2[a]	−81.3[c]	−40.2[a]
Mountain dusky salamander	Total area	15 910	5.2[a]	4.1[b]	1.6[c]	0.1[f]	0.5[e]	1.3[d]
	Number of patches	1738	5.6[a]	7.2[a]	1.1[b]	−7.5[c]	−7.7[c]	1.4[b]
	Mean patch size	9.2	−0.3[b]	−2.8[c]	0.4[b]	8.3[a]	8.8[a]	−0.1[b]
	Largest patch size	1285	40.8[a]	37.2[a]	20.8[a]	25.2[a]	21.3[a]	31.2[a]
Southeastern shrew	Total area	7413	−97.6[d]	−52.5[c]	−31.1[b]	7.5[a]	6.5[a]	−29.7[b]
	Number of patches	3222	−98.0[d]	−1.9[c]	38.3[b]	53.2[a]	52.5[a]	39.7[b]
	Mean patch size	2.2	18.3[a]	−51.7[c]	−50.2[c]	−29.6[b]	−30.1[b]	−49.6[c]
	Largest patch size	62	−36.8[a]	−36.8[a]	−36.8[a]	−32.1[a]	−31.3[a]	−36.8[a]
Northern flying squirrel	Total area	6342	3.4[a]	2.8[b]	1.8[c]	0.4[d]	1.8[c]	0.4[d]
	Number of patches	67	−16.4[c]	−12.2[bc]	−9.0[ab]	−3.3[a]	−9.6[b]	−3.6[a]
	Mean patch size	94.7	23.8[a]	17.2[ab]	12.0[b]	4.0[c]	12.6[b]	4.2[c]
	Largest patch size	933	7.1[a]	5.3[a]	4.4[a]	4.9[a]	4.5[a]	5.4[a]
European Starling	Total area	10 848	−97.1[f]	−55.3[e]	−27.2[d]	32.1[a]	30.6[b]	−25.6[c]
	Number of patches	3949	−96.4[e]	9.8[d]	70.6[c]	76.2[a]	74.8[ab]	72.4[bc]
	Mean patch size	2.7	−20.4[a]	−59.3[c]	−57.3[c]	−25.1[b]	−25.3[b]	−56.8[c]
	Largest patch size	383	−86.3[b]	−86.0[b]	−83.5[b]	331.7[a]	333.2[a]	−82.7[b]
Wood Thrush	Total area	42 866	121.3[a]	11.2[b]	−30.2[c]	−38.2[d]	−38.6[d]	−29.4[c]
	Number of patches	223	−96.7[c]	62.2[b]	125.2[a]	74.2[b]	77.0[b]	115.5[a]
	Mean patch size	192	6753.4[a]	−31.4[b]	−69.0[b]	−64.5[b]	−65.2[b]	−67.0[b]
	Largest patch size	15 351	517.6[a]	58.0[b]	−53.1[cd]	−52.3[cd]	−70.2[d]	−47.6[c]
Princess tree	Total area	26 952	−96.0[e]	−20.9[d]	5.1[c]	29.2[a]	28.8[a]	6.4[b]
	Number of patches	219	−74.7[d]	138.6[a]	51.8[b]	−5.0[c]	3.9[c]	43.3[b]
	Mean patch size	123.1	−84.1[e]	−66.9[d]	−30.5[c]	36.3[a]	24.1[b]	−25.7[c]
	Largest patch size	22 142	−99.1[d]	−73.1[c]	3.5[b]	41.2[a]	43.3[a]	5.1[b]

Note: Superscripts that are the same across a row indicate no significant difference in the value of that metric between scenarios; different letters indicate significant difference (Tukey's Studentized Range Test, $P < 0.05$).

declined by nearly a third with the 1986–1991 transitions. For both historical scenarios, habitat generally became more fragmented, as indicated by the increase in the number of patches and the decrease in mean patch size. Two exceptions to this were observed. Under the 1975–1986 transitions where forest cover declined most, the size of the largest patch of suitable habitat for European Starlings increased by >330%. For princess tree, both mean patch size and the size of the largest patch increased (by 36 and 41%, respectively). Thus, habitat was best connected for these species with the 1975–1986 historical scenario.

Potential habitat for these four open or edge species declined under the two management scenarios in which rates of forest loss were reduced (Table 5). With the stream/slope restrictions, potential habitat declined by 20–55%. With all forest losses precluded, 93–97% of the potential habitat for the species was lost (Fig. 4). In general, habitat reduction was accompanied by declines in number of patches, mean patch size, and size of the largest patch. However, fragmentation of potential habitat occasionally increased as habitat was being reduced, as seen for the European Starling and princess tree. For both species, the number of patches increased with the stream/slope restriction scenario as potential habitat declined.

Potential habitat for two species typically found at higher elevations (northern flying squirrel and mountain dusky salamander) showed little response to any of the scenarios (Table 5). Habitat area increased as forest loss decreased, but the increase was generally <5%. Habitat for the northern flying squirrel became better connected in all four scenarios, as indicated by the decrease in number of patches and increase in mean patch size. For the mountain dusky salamander, the size of the largest habitat patch increased by 20–40% across the four scenarios.

Species response in the HORB.—Potential habitat

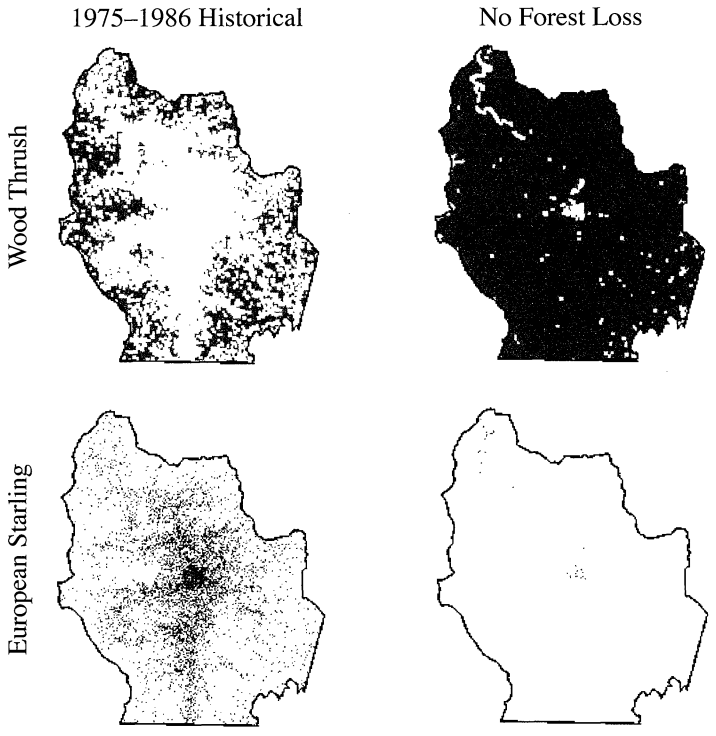

FIG. 4. Maps of potential habitat (black) for two bird species (Wood Thrush and European Starling) in the Little Tennessee River Basin in 1991 and at the end of a 100-yr simulation using the 1975–1986 historical transition scenario and the no-forest-loss scenario.

for two open-habitat species (honeysuckle and horsetail) declined under all scenarios (Table 6). Habitat for these species also became increasingly fragmented, characterized by a greater number of smaller patches and a reduction in size of the largest patch. Maximum habitat loss of 19–21% for honeysuckle and 8–9% for horsetail occurred with the mangement scenarios in which forest losses were restricted.

Potential habitat for red squirrel and twinflower increased slightly (~3–5%) under all scenarios (Table 6). In addition, there was a consistent increase in habitat connectivity under all four scenarios (Fig. 5). The greatest increase in habitat occurred with the 1975–1986 historical transitions.

Potential habitat for licorice fern changed in different directions among the scenarios (Fig. 5). With the 1975–1986 historical scenario, potential habitat declined in abundance and became slightly more fragmented (Table 6). With the 1986–1991 scenario, habitat increased only slightly, but still became more fragmented. The management scenarios that restricted loss of forest resulted in a 15–17% increase in potential habitat. The number of patches increased but mean patch size declined, indicating that habitat was added in small dispersed patches.

Species occurring in the montane forest life zone (mountain alder, mountain huckleberry, heather vole, and Cascade Oregon grape) were unaffected by the scenarios because their habitat was contained within the Olympic National Park.

Question 2: effects of land ownership

LTRB.—When the responses of all species were considered collectively, there were effects of both private and public ownerships in the LTRB, but no interaction between the two ownership types was evident (Table 7). Changes on private lands had the greatest effects on species habitat within this watershed, as revealed by the magnitude of the F values in Table 7. Forest land cover increased and became less fragmented in scenarios involving the private 1986–1991 treatment, whereas forest cover declined in the private 1975–1986 treatment (Table 3). Unvegetated cover changed in the opposite manner. Grassy/brushy cover declined and became more fragmented for all scenarios, but its total area declined most in treatments involving the private 1986–1991 rates.

Except for the northern flying squirrel, habitats for all species in the LTRB were influenced by variation in rates of change for private lands (Tables 5, 8). The northern flying squirrel is restricted to high elevations, which are dominated by public ownership. The total areas of salamander, shrew, and starling habitats were affected by both public and private treatments, but the other spatial pattern metrics were affected by the private factor only. The salamander habitat changed very little (<2%) in total area, and the largest patch size was not affected. The habitat became less fragmented in the treatments using the private 1975–1986 rates of change. Although rates of forest loss were higher during 1975–1986, forest loss was concentrated at lower

TABLE 6. Mean percentage change in the area and spatial pattern of habitat for species in the Hoh River Basin across six scenarios at the end of a 100-yr simulation. For initial conditions, all area and patch size data are in hectares.

			Management scenarios		Historical scenarios			
Species	Metric	Initial conditions	No forest loss	Stream–slope restrictions	Public 1986–1991; Private 1986–1991	Public 1975–1986; Private 1975–1986	Public 1986–1991; Private 1975–1986	Public 1975–1986; Private 1986–1991
Licorice fern	Total area	1785	17.3[a]	14.9[b]	1.2[c]	−3.2[d]	0.6[c]	−3.1[d]
	Number of patches	1077	19.1[a]	17.0[b]	8.3[c]	0.9[d]	8.0[c]	1.2[d]
	Mean patch size	1.7	−1.5[a]	−1.8[a]	−6.6[c]	−4.0[b]	−6.8[c]	−4.2[b]
	Largest patch size	24	5.3[a]	3.3[a]	−1.3[b]	−3.3[b]	−3.3[b]	−3.3[b]
Twinflower	Total area	44 272	3.8[b]	3.8[b]	3.6[c]	5.2[a]	3.7[c]	5.3[a]
	Number of patches	1286	6.1[a,b]	7.7[a]	4.3[b,c]	−0.5[d]	3.3[c]	−0.5[d]
	Mean patch size	34.4	−2.1[c,d]	−3.6[d]	−0.6[b,c]	5.8[a]	0.3[b]	5.9[a]
	Largest patch size	32 927	7.0[b]	6.9[b]	8.9[b]	11.4[a]	7.8[b]	11.4[a]
Honeysuckle	Total area	5083	−21.4[d]	−19.1[c]	−10.5[b]	−9.3[a]	−9.6[a]	−10.5[b]
	Number of patches	3122	−15.9	−12.5[d]	1.1[a,b]	0.2[b]	1.6[a]	−0.9[c]
	Mean patch size	1.6	−6.5[a]	−7.5[b]	−11.6[d]	−9.4[c]	−11.1[d]	−9.8[c]
	Largest patch size	63	−2.6[a]	−2.6[a]	−2.6[a]	−2.1[a]	−2.6[a]	−2.6
Red squirrel	Total area	44 272	3.8[b]	3.8[b]	3.6[c]	5.2[a]	3.7[c]	5.3[a]
	Number of patches	1286	6.1[a,b]	7.7[a]	4.3[b,c]	−0.5[d]	3.3[c]	−0.5[d]
	Mean patch size	34.4	−2.1[c,d]	−3.6[d]	−0.6[b,c]	5.8[a]	0.3[b]	5.9[a]
	Largest patch size	32 927	7.0[b]	6.9[b]	8.9[b]	11.4[a]	7.8[b]	11.4[a]
Horsetail	Total area	3364	−9.2[d]	−8.4[c]	−4.5[b]	−3.5[a]	−4.1[b]	−4.1[a,b]
	Number of patches	1989	−8.8[b]	−7.6[b]	−1.1[a]	−0.8[a]	−0.3[a]	−1.5[a]
	Mean patch size	1.7	−0.4[a]	−0.9[a]	−3.5[c]	−2.7[b]	−3.8[c]	−2.6[b]
	Largest patch size	26	0.0[a]	0.0[a]	0.0[a]	0.0[a]	0.6[a]	0.6[a]

Note: Superscripts that are the same across a row indicate no significant difference in the value of that metric between scenarios; different letters indicate significant difference (Tukey's Studentized Range Test, $P < 0.05$). Four species (mountain alder, mountain huckleberry, Cascade oregon grape, and heather vole) did not change and are not included.

elevations (Table 3; see also Turner et al. 1996). Salamander habitat (i.e., forest) is concentrated at higher elevations. Habitat for the rhododendron, a high-elevation species, increased for all scenarios, especially for the public 1986–1991 treatments, which had greater rates of forest loss at high elevations (Turner et al. 1996). The shrew and starling require nonforest habitats. These habitats increased in the private 1975–1986 treatments and declined in the private 1986–1991 rates. The nonforest land covers became more fragmented in all scenarios (Table 3).

Effects on habitat used by Wood Thrush and princess tree were more complex. The Wood Thrush's habitat declined and the number of patches increased for all treatments—most dramatically for the treatments using the private 1975–1986 rates (Table 5). Mean patch size did not change, but the largest patch declined most for the private 1975–1986/public 1986–1991 treatment

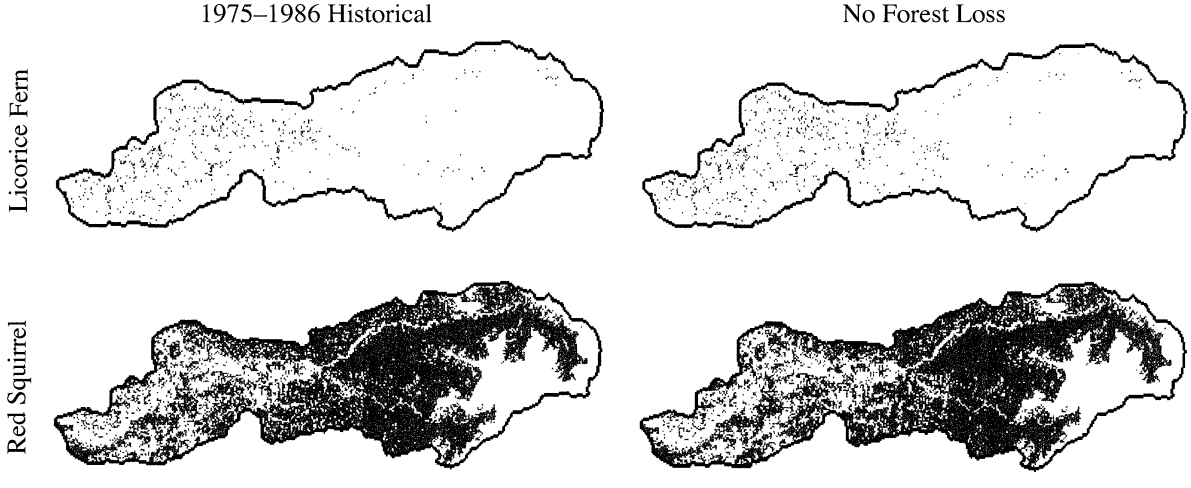

FIG. 5. Maps of potential habitat (black) for two species (licorice fern and red squirrel) in the Hoh River Basin in 1991 and at the end of a 100-yr simulation using the 1975–1986 historical transition scenario and the no-forest-loss scenario.

TABLE 7. Results of MANOVA comparing effects of public (U) and private (R) ownership factors on the suite of species in two watersheds using the four historical scenarios.

Test statistic	Factor	Test statistic for each habitat metric: Area (ha)	Size of largest patch (ha)	Mean patch size (ha)	Number of patches
A) Little Tennessee River Basin					
Wilks' lambda	U	0.006	0.164	0.042	0.152
	R	<0.001	0.005	<0.001	0.003
	U × R	0.655	0.425	0.713	0.742
$F_{8,9}$	U	195.7	5.8	25.5	6.3
	R	6872.5	220.6	7255.3	353.2
	U × R	0.6	1.5	0.4	0.4
P	U	<0.001	0.008	<0.001	0.006
	R	<0.001	<0.001	<0.001	<0.001
	U × R	0.714	0.272	0.453	0.900
B) Hoh River Basin					
Wilks' lambda	U	0.006	0.193	0.059	0.035
	R	0.283	0.699	0.472	0.550
	U × R	0.847	0.684	0.757	0.853
$F_{7,10}$	U	562.2	13.6	51.6	89.8
	R	8.2	1.4	3.6	2.7
P	U × R	0.6	1.5	1.0	0.6
	U	<0.001	<0.001	<0.001	<0.001
	R	0.002	0.287	0.034	0.080
	U × R	0.680	0.259	0.423	0.700

Notes: Each ownership factor had two levels of forest disturbance: high (1975–1986) and low (1986–1991) (see *Methods*). Analyses were conducted separately for each of four metrics used to quantify spatial pattern of potential habitat.

combination, resulting in a private × public interaction (Tables 5, 8). The princess tree's habitat increased and became less fragmented in scenarios using private 1975–1986 rates.

HORB.—When all species were considered together in the HORB, variation in the rates for public lands had the greatest effect on species habitats (Table 7). Land cover changes for these four scenarios were consistent with those described for the historical treatments reported for Question 1 (Table 4). In general, conifer forest habitat increased for all scenarios; the other three land covers declined. There were few differences among the scenarios for grassy/brushy cover. Both deciduous/mixed forests and unvegetated covers declined more for the public 1975–1986 treatment.

Rates of change on public lands affected most species in the HORB (Table 8). The private ownership factor influenced habitats for only two species: horsetail and honeysuckle. No interactions between the private and public factors were observed (Table 8). For

TABLE 8. Results of ANOVA evaluating the effects of land ownership on species habitat in the two watersheds studied.

Species	Significant factors for each habitat metric: Area	Size of largest patch	Mean patch size	Number of patches
A) Little Tennessee River Basin				
Showy orchis	R	R	R	R
Catawba rhododendron	U	U, R	U	U
Mountain dusky salamander	U, R		R	R
Southeastern shrew	U, R		R	R
Northern flying squirrel	U		U	U
European Starling	U, R	R	R	R
Wood Thrush	R	U, R, U × R	R	R
Princess tree	R	R	R	U, R
B) Hoh River Basin				
Licorice fern	U		U	U
Twinflower	U	U	U	U
Honeysuckle	R		U, R	U, R
Horsetail	U, R		U	
Red squirrel	U	U	U	U

Notes: The four historical scenarios (see *Methods*) were used for the simulations analyzed. For each habitat metric, the table lists the land ownership factors that had significant effects ($P < 0.05$): public (U) and private (R) lands, as well as their interaction (U × R). Each ownership factor had two levels of forest disturbance: high (1975–1986) vs. low (1986–1991). Analyses were conducted separately for each of four metrics used to quantify potential habitat.

the twinflower and red squirrel, habitats increased in area for all scenarios. Number of patches increased for the private 1986–1991/public 1986–1991 combination (Table 6). Habitats for honeysuckle and horsetail declined in area in all simulations. For honeysuckle, habitat became more fragmented for the public 1986–1991 treatment, but the size of the largest patch was not affected. For the horsetail, differences between the treatment combinations were minor, although both public and private factors were statistically significant. Habitat declines were most pronounced using the 1986–1991 rates. Habitat for the licorice fern increased in abundance for the public 1986–1991 rates and declined for the public 1975–1986 rates. There were no significant effects of the private factor for this species (Table 8). For each scenario, the habitat became more fragmented for all treatments, as shown by increases in the number of patches and decreases in mean patch size and largest patch size (Table 6).

Discussion

The simulations revealed several points important for ecosystem management: (1) habitat changes for species were only partially predicted by changes in land cover types (i.e., forest, grassy/brushy, unvegetated); (2) simple changes in land cover patterns can produce complex changes in species habitats; and (3) patterns of land ownership, by affecting rates and patterns of land cover change, influence the policy options for conserving regional biodiversity.

This study demonstrated that changes in land cover alone may only approximate the changes in habitat experienced by a given species. For example, a 5–10% decrease in the amount of grassy/brushy cover in the HORB resulted in a 10–20% reduction in habitat for honeysuckle. A 12% increase in the size of the largest forested patch in the LTRB produced a >400% increase in the size of the largest patch of showy orchis habitat. Potential habitat was sometimes more patchy in distribution than the land cover class that included the habitat. For example, ~2400 patches of habitat were identified for the showy orchis in the LTRB in the initial map, whereas only 325 patches of forest cover were observed. In the initial map of the HORB, the number of patches of suitable habitat for licorice fern, a deciduous forest species, was considerably less than the number of patches of deciduous forest. This fern requires deciduous forest adjacent to streams in the western hemlock life zone, so many forest patches in the land cover map were not suitable for this species.

The potential for inconsistencies between maps of land cover types and potential habitat for species has important implications for broad-scale monitoring. Remotely sensed images provide one of the best means of monitoring land cover change over large areas, but inferring changes in potential habitat for different species may require augmentation with additional data. For example, the abundance and spatial arrangement of forest cover may be derived from a satellite image, but habitat for a species sensitive to forest age would not be accurately mapped with cover data alone. Likewise, habitat for species that depend upon finer scale features of a landscape could not be accurately mapped with the 30 × 30 m resolution of the Landsat Thematic Mapper. For example, in a study of wintering birds in early successional habitats, the presence and abundance of parids was related to the abundance of deciduous forest at the scale of 1 ha, but White-throated Sparrows responded to habitat features at the scale of 10 m (Pearson 1993). Thus, a satellite-derived map of land cover might be used to predict the abundance of parids in a landscape, but would be of little use for mapping sparrow habitat. Relevant spatial information, such as topography or hydrology, can be used to refine land cover maps if the species of interest respond to these variables. In the LTRB, the distribution of forest tree communities was predicted reasonably well when topographic data were used to augment the land cover map (Rutledge 1995). Likewise, some riparian habitats may be too small in area to be mapped by a 90 × 90 m cell, but combining maps of land cover and hydrology permits a more accurate prediction of the presence of habitat for riparian species.

Our study also revealed how simple changes in land cover could produce complex changes in the spatial pattern of species habitats. Consider the changes in area and mean patch size of potential habitat for mountain dusky salamander in the LTRB. In the management scenarios, forest cover and salamander habitat both increased in area; mean patch size increased for forest but decreased for the salamander habitat. Mean patch size of the salamander habitat declined because the addition of forest at low elevations created additional small, isolated patches of habitat. At low elevations, this species is restricted to streamside forests. Thus, changes in forest cover, per se, were only approximate indicators of changes in the spatial pattern of habitat because of the specific requirements of this species.

These results indicate that changes in habitat abundance and the spatial pattern of habitat (fragmentation) should be considered separately. Fragmentation, as measured by increased number of patches or decreased mean patch size, may be caused either by breaking existing large patches into smaller units or by adding many small patches without changing existing patches. The salamander would presumably do better on landscape produced by the no-forest-loss scenario, which leaves more habitat on the landscape, than on that produced by the 1975–1986 historical scenario. The additional habitat in the no-forest-loss scenario was produced by adding small patches, which skewed the frequency distribution of patch sizes toward a smaller mean. Similarly, mean patch size could be changed by adding or removing area to existing patches without altering the number of patches. Thus, a suite of landscape metrics that measure different aspects of the pat-

tern will provide the most complete record of changes in potential habitat. Relying on one or two metrics may lead to incorrect conclusions about the effects of landscape change on a species.

Land use decisions affect the abundance and spatial pattern of habitats in any developed area. The importance of the social and economic factors that influence these decisions must be considered in developing policies designed to promote the sustainable use of natural resources (e.g., Ojima et al. 1994, Skole et al. 1994). Land ownership is a social factor that affects the rate and spatial pattern of land cover change (Spies et al. 1994, Turner et al. 1996, Wear et al. 1996). Measures of landscape pattern varied more across scenarios in the LTRB than in the HORB. This result is due, in part, to at least two factors related to land ownership. First, a large portion of the HORB is contained within the Olympic National Park, and land cover in the park was not changed in our simulations. Therefore, these constant land cover patterns would dampen the variation in landscape pattern at the scale of the whole watershed. In contrast, land cover changes could occur throughout the entire watershed in the LTRB. Second, the state and private lands in the HORB are both managed for timber harvesting (Wear et al. 1996), and therefore both ownerships exert similar influences on land cover. In the LTRB, however, the reduced forest harvesting on federal lands and increased forest disturbance on private lands leads to a greater divergence in landscape pattern among the scenarios.

This study demonstrated that these ownership-based differences in rates of land cover change between watersheds and among time periods can influence habitat for both native and exotic species. Habitats for the species in the LTRB were strongly affected by rates of change on private lands, but the dynamics on public lands were more important for species habitats in the HORB. These differences should influence management decisions related to protecting biological diversity at the watershed scale. In the LTRB, private lands had a greater effect on landscape pattern than did public lands (Wear et al. 1996), and this influence carried over to effects on potential habitat. Except for the high-elevation species (Catawba rhododendron and northern flying squirrel), all species were principally affected by dynamics on the private lands. Exotic species, such as the European Starling and princess tree, benefitted from the increased rates of forest loss characteristic of the 1975–1986 period on private lands. These results imply that policies designed to protect biodiversity in the LTRB must incorporate means to influence land use decisions by private landowners. The relative importance of a given ownership on potential habitat will depend on the magnitude of the difference in rates of change between ownerships and on the proportion of the study area controlled by the respective owners.

Public lands tend to be clustered in large blocks in both watersheds (Fig. 1). This spatial pattern of ownership reflects opportunistic purchases or arbitrary decisions made decades ago, but it creates large regions with distinct patterns of land cover change. Such an arrangement might allow for policies on public lands to mitigate changes in landscape pattern and species habitat on private lands. For example, high rates of disturbance on private lands might be balanced by lower rates of disturbance on public lands. The segregation of ownership types into large blocks would maintain large areas experiencing similar dynamics. Alternatively, ownership blocks could be broken up by increasing the number of parcels and the interspersion of ownerships. If land cover changes were correlated with ownership type but differed among owners, a dispersed ownership pattern could produce more habitat fragmentation compared to keeping similar owners in aggregated blocks.

Methods for predicting the ecological impacts of land use change on biodiversity and ecosystem function are needed to guide land-planning and resource management decisions. Many areas of the United States continue to experience substantial rates of land use change, and fragmentation of once-continuous habitat is likely to continue. Effects of habitat fragmentation on biodiversity are numerous (Saunders et al. 1991, Noss and Csuti 1994). Linking land cover change models with habitat models should be useful for demonstrating the possible outcomes of different land management decisions for species of interest. Although management for "biodiversity" is often desired, it is impossible to manage simultaneously for all species present at a site. However, species with varying requirements and characteristics may serve as indicator species for biodiversity, and an analysis of potential habitat can be used to begin to model risks to biodiversity at landscape scales (White et al. 1997). In addition, the methodology provides a reasonable approach for examining the ecological implications of future scenarios of land use change that could be employed in other landscapes.

Interpreting habitat maps requires an understanding of the natural history of the organism and its responses to landscape-scale patterns. Species–habitat associations are complicated by numerous factors, including natural disturbances, competition and predation, and differences in habitat quality and configuration. For example, the suitability of landscapes for the Delmarva fox squirrel (*Sciurus niger cinereus*) depended on both the abundance and spatial arrangement of forest and open habitats (Dueser et al. 1988). These complementary habitats (sensu Dunning et al. 1992) provide distinct foraging and nesting habitats. Thus, two landscapes having the same area of these habitats but differing in spatial arrangement could differ substantially in their suitability for this species.

This research sought to better understand landscape change by linking simulations of land cover change to simple habitat models. Our approach was straightfor-

ward, but it did have significant limitations. Habitat models were limited by the temporal and spatial resolution of the land cover change model and by the number of land cover classes and their relevance to species' habitat needs. These simple habitat models predicted only *potential* habitat that may be unoccupied in nature for various reasons. The models did not incorporate population dynamics or area requirements for the focal species and could not predict which patches were occupied or estimate the total population size based on a given land cover map. Nevertheless, such an approach is a useful step toward understanding the implications of landscape change for biodiversity. For example, GAP analysis (Scott et al. 1987, 1993) has demonstrated an ability to identify areas with high biological diversity over broad, state-level scales using maps of land cover and rough relationships between cover types and species diversity. However, it remains challenging to identify the species for which habitat area alone is a good indicator of vulnerability to extinction. By tracking changes in the abundance and spatial pattern of habitats, land managers and conservation biologists can identify species that are most affected during landscape change by loss or fragmentation of habitat.

Our results suggest that both landscape-level (i.e., top-down) and species-level (i.e., bottom-up) approaches are useful for conservation. Indeed, to abandon either of these perspectives would be a mistake (see Franklin 1993, 1994, Tracy and Brussard 1994). Landscape-level study provides a means to quantify and monitor broad-scale changes related to biodiversity and ecosystem processes. Species- or population-level approaches are useful for properly interpreting the significance of landscape-level changes. Species-level analyses can contribute a more mechanistic understanding of the impacts of landscape change, while broader scale investigations provide information on broad-scale patterns that can enhance or constrain the conservation of native biological diversity.

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