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Research article

A multi-scale assessment of human and environmental constraints on forest land cover change on the Oregon (USA) coast range

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Abstract

Human modification of forest habitats is a major component of global environmental change. Even areas that remain predominantly forested may be changed considerably by human alteration of historical disturbance regimes. To better understand human influences on the abundance and pattern of forest habitats, we studied forest land cover change from 1936 to 1996 in a 25 000 km^2 landscape in the Oregon (USA) Coast Range. We integrated historical forest survey data and maps from 1936 with satellite imagery and GIS data from 1996 to quantify changes in major forest cover types. Change in the total area of closed-canopy forests was relatively minor, decreasing from 68% of the landscape in 1936 to 65% in 1996. In contrast, large-conifer forests decreased from 42% in 1936 to 17% in 1996, whereas small-conifer forests increased from 21% of the landscape in 1936 to 39% in 1996. Linear regression models were used to predict changes in the proportion of large conifer forest as a function of socioeconomic and environmental variables at scales of subbasins (mean size = 1964 km^2, $n = 13$), watersheds (mean size = 302 km^2, $n = 83$), and subwatersheds (mean size = 18 km^2, $n = 1325$). The proportion of land in private ownership was the strongest predictor at all three spatial scales (partial R^2 values 0.57–0.76). The amounts of variation explained by other independent variables were comparatively minor. Results corroborate the hypothesis that differing management regimes on private and public ownerships have led to different pathways of landscape change. Furthermore, these distinctive trajectories are consistent over a broad domain of spatial scales.

Introduction

Continual alteration of the earth's vegetation cover is perhaps the most ecologically significant human impact on the global environment, with particularly serious implications for habitat loss and the maintenance of biodiversity (Vitousek 1994). Empirical studies have consistently demonstrated that changes in the abundance and spatial configuration of forest habitats can impact communities of birds (McGarigal and McComb 1995; Drapeau et al. 2000), mammals (Hargis et al. 1999; Lomolino and Perault 2000), and plants (Matlack 1994; Halpern and Spies 1995). Some species exhibit nonlinear responses to habitat loss, with relatively small decreases in habitat near a critical threshold resulting in rapid population declines (With and Crist 1995). Community-level responses to habitat fragmentation may also result in an extinction debt, in which there is a temporal lag between habitat alteration and an irrevocable loss of species (Tilman et al. 1994; Loehle and Li 1996). Because of this potential delayed response, the ultimate impacts of land cover change on biodiversity may not be realized for decades or longer.

Given these ecological concerns, it is essential that we expand our knowledge of how land use decisions, environmental constraints, and ecological processes interact to influence the spatial pattern of forest land cover. This information can be utilized to identify areas where the risk of habitat loss is particularly high; to develop models to assess future pathways of land cover change; and ultimately to devise more effective strategies for habitat conservation. Our understanding of landscape change is complicated, however, by the fact that the critical processes and driving variables influencing land cover patterns can vary with spatial scale (Verburg and Chen 2000). Furthermore, ecological responses to shifts in land cover pattern may vary with scale depending on the unique life-history traits of individual species (Addicott et al. 1987) and the spatial domains of different ecosystem processes (Wiens 1989). Thus, there is a need for research that examines the influences of multiple factors on patterns of forest landscape change across a range of spatial scales.

Landscape change has been studied extensively in many forested regions. Satellite remote sensing has been used to characterize forest dynamics over large areas in northeastern Minnesota (Hall et al. 1991), the Pacific Northwest (Spies et al. 1994; Cohen et al. 2002), southern New England (Vogelmann 1995), the southern Appalachians (Turner et al. 1996; Wear et al. 1996), the coastal plain of South Carolina and Georgia (Pinder et al. 1999), and the pine barrens of northwest Wisconsin (Radeloff et al. 2000). Historical aerial photographs have been used to assess landscape change in Georgia (Turner and Ruscher 1988), central Japan (Nagaike and Kamitani 1999), and the interior Columbia River basin (Black et al. 2003). Other researchers have capitalized on a variety of historical datasets. Government Land Office (GLO) surveys have been used to study forest dynamics in northern Wisconsin (White and Mladenoff 1994; Radeloff et al. 1999), and historical timber inventories have been used to quantify landscape change in western Oregon (Ripple et al. 2000) and Sweden (Axelsson et al. 2002). Land ownership, particularly the distinction between privately- and publicly-owned lands, has been shown to be a primary correlate of land cover change in many of these studies (Spies et al. 1994; Turner et al. 1996; Nagaike and Kamitani 1999; Pinder et al. 1999; Radeloff et al. 2000; Radeloff et al. 2001; Black et al. 2003). Other spatial variables such as topography (Turner et al. 1996), soils (Radeloff et al. 2000), population density (Vogelmann 1995; Black et al. 2003), and distance from roads and urban centers (Turner et al. 1996; Wear and Bolstad 1998), also constrain the rates and pathways of land cover change, although the nature and magnitude of these relationships can vary greatly in different landscapes.

Despite this large body of research, our ability to generalize these results is constrained by the inherent limitations of land cover change studies. The temporal extent of satellite-based studies is restricted by the oldest available satellite data, typically from the early 1970s. Rates of landscape change and the relative influences of environmental and socioeconomic constraints can fluctuate considerably over relatively short (less than a decade) time intervals (Turner et al. 1996), raising the question of whether short-term observations can be generalized to longer-term trends. Furthermore, sensor limitations often restrict the number of cover classes for which change can be tracked using satellite imagery. Many landscape-scale studies of forest dynamics have therefore emphasized shifts between forested versus non-forested land or open- versus closed-canopy forests, even though important scientific and management questions may be more closely linked to particular seral stages or specific tree species and habitat structures that are not as easily mapped (Spies et al. 1994). Assessments of various human and environmental impacts on landscape change are often confounded by the correlations among these variables. For example, public lands may be found at higher elevations (Spies et al. 1994; Ohmann and Spies 1998) or on different soil types (Radeloff et al. 2000) than private lands. Although a strong argument can be made that variation in forest landscape change across ownerships arises primarily from human land use, a question often remains as to how much of this variation could be explained by patterns in forest community composition, tree regeneration and growth, or natural disturbance regimes that covary with ownership.

As recognized by Turner et al. (1996), land cover change research is typically conducted at a fixed and often arbitrary spatial scale. The spatial extent selected for study may be based on physical landscape features such as watersheds; human-imposed political borders such as state, county, or ownership boundaries; or the coverage of available historical data. Similarly, the spatial grain of landscape change analyses is often determined by the minimum mapping unit of a particular data source rather than a consideration of the most appropriate scale for mapping and modeling land cover change. It is typically not known whether results can be extrapolated to smaller or larger scales. If local topography constrains rates of forest conversion at the site level, will physiographic variability among watersheds influence larger-scale patterns of land cover change? If ownership is the primary correlate of aggregate landscape change across an entire region, will it also be an effective predictor of landscape dynamics within individual watersheds?

The overarching goal of this research was to examine the relationships between forest land cover change and major human and environmental constraints over a range of spatial scales. The study was carried out for the Oregon Coast Range, a 25 000 km^2 forest landscape located in the Pacific Northwest Region of the United States, and encompassed the period from 1936 to 1996. Specific objectives were: (1) to quantify shifts in the distribution of major forest stand types in the Oregon Coast Range from 1936 to 1996; (2) to compare the relative influences of human and environmental constraints on land cover change; and (3) to determine whether the relative importance of these spatial constraints varies with spatial scale. Our work expands on the body of existing landscape change research by examining changes over a relatively long time period (60 years), addressing shifts between early and late-successional stand types within a predominantly forested region, and contrasting the human and environmental drivers of these changes within a hierarchical set of nested hydrologic units. Results emphasize that major changes in landscape structure can occur even in areas that remain predominantly forested, and indicate that land ownership is the primary driver of landscape change over a broad domain of scale ranging from subwatersheds (1000s of ha) to subbasins (100 000s of ha).

Methods

Study Area

The Oregon Coast Range encompasses more than 25 000 km^2 of land in western Oregon USA, bounded by the Pacific Ocean to the west, the Klamath Mountains to the south, the Willamette Valley to the east, and the Columbia River to the north (Figure 1). Elevations range from sea level to over 1000 m at the highest peaks. Physiography is characterized by highly dissected terrain with steep slopes and high stream densities. Soils are predominantly well-drained Andisols and Inceptisols derived from a variety of parent materials, including marine sandstones, shales, and basaltic volcanics. The climate is generally wet and mild, with most precipitation falling between October and March. Precipitation is highest and summer temperatures are lowest along the coast, resulting in low growing-season moisture stress and high forest productivity. Decreasing precipitation and increasing temperature create a gradient of increasing growing-season moisture stress with distance from the coast. Major conifer species include Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), with Sitka spruce (*Picea sitchensis*) prevalent near the coast. Hardwoods, including red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*), often dominate recently disturbed sites and riparian areas (Franklin and Dyrness 1973).

Forestry is the predominant land use in the Oregon Coast Range. Cities are concentrated near the coast and along the Willamette Valley margin. Agriculture is mostly limited to the Willamette Valley and other large river valleys. Major forest landowners in the Coast Range include private industry, private nonindustrial owners, the state of Oregon, and the federal government (Spies et al. 2002). Private industrial ownerships comprise 38% of the total land area, concentrated into several large blocks in the northern, central, and southern portions of the study area (Figure 1c). Private non-industrial ownerships cover 26% of the study area, primarily along the Willamette Valley margin and in the large river valleys. Federal lands managed by the Forest Service and the Bureau of Land Management also occupy a substantial area in the Coast Range (11% and 13% of the study area, respectively). A significant portion of the land controlled by the Bureau of Land Management is interspersed with private industrial land in a checkerboard pattern. State forestlands occupy 11% of the study area, consisting primarily of the Tillamook and Clatsop State Forests in the northern Coast Range and the Elliot State Forest in the southern Coast Range.

Data sources

The 1936 forest vegetation map (hereafter referred to as the 1936 map) was developed by the Pacific Northwest Research Station as part of a nation wide effort to survey forestlands and inventory timber resources. This survey was carried out from 1933 to 1936 in the Douglas fir region, which encompasses the forested lands of the states of Oregon and Washington located west of the crest of the Cascade Mountains. Timber cruises and existing inventory records were used to classify land into forest types based on tree sizes and species composition. Forest types were mapped using a combination of ground reconnaissance and aerial photography. The minimum mapping unit was about 40 acres (16 ha) for most forest types, although mapping units as small as 20 acres (8 ha) were sometimes used to delineate narrow hardwood patches along riparian corridors. Details of the methods used in the survey are provided in Andrews and Cowlin (1940). Copies of the original paper maps were digitized and converted to a vector GIS data format by the US Forest Service.

The 1996 forest vegetation map (hereafter referred to as the 1996 map) was created using the Gradient Nearest Neighbor (GNN) method (Ohmann and Gregory 2002). This process consisted of four main steps. First, stepwise canonical correspondence analysis (CCA) was used to develop a multivariate model quantifying the relationship between multiple vegetation attributes from georeferenced forest inventory plots and predictor variables from a raster GIS database. Predictor variables included Landsat TM imagery, climate, topography, geology, and ownership. Each inventory plot was thereby assigned a set of axis scores identifying its location in an abstract, multidimensional, spectral and environmental space. Second, the coefficients from the CCA model were applied to the entire GIS database to project each cell into the same multidimensional space as the inventory plots. Third, for each cell, the closest plot in the multidimensional gradient space was identified. This step effectively matched each cell with the ground plot that had the most similar suite of spectral and environmental characteristics. Fourth, all inventory measurements from this nearest-neighbor plot were imputed to the cell. The end product was a landscape grid with a 25 m grain in which each cell was associated with a detailed tree list that included tree species, sizes, and expansion factors. Additional details on the production and accuracy assessment of the 1996 map are provided by Ohmann and Gregory (2002). Non-forested land (including urban areas and agriculture) were distinguished from forest openings (such as clearcuts and natural disturbances) in a separate GIS analysis. Non-forested areas were identified with a rule-based classification based on current and historical vegetation layers derived from Landsat imagery, land ownership, urban area boundaries, and topography (K.N. Johnson, unpublished data).

The 1996 map contained more detailed information about forest structure and composition and had a finer spatial resolution than the 1936 map. To make the maps comparable, the 1996 map was reclassified and rescaled to match the 1936 map. Forest types in the 1936 map were generally defined based on the proportion of volume in various species classes, and by the sizes of trees that contained the majority of that volume (Andrews and Cowlin 1940). Tree list information from the 1996 map was used to compute cubic-foot volume for each tree, based on species-specific volume equations. Individual-tree volumes were aggregated into species- and size classes, and these classes were used to assign each cell from the 1996 map to one of the 1936 forest types (Table 1). The 1936 map was converted from its native vector format into a 400 m raster layer (16 ha cell size), corresponding to the largest minimum mapping unit used in the 1936 Forest Survey (Figure 1a). To match the minimum mapping unit of the 1936 map, the 1996 map was rescaled from a 25 m to a 400 m cell size by assigning each 400 m cell the forest type belonging to the majority of the 25 m cells within its boundaries (Figure 1b).

Landscape change analysis

Prior to analysis, forest types from the 1936 and 1996 maps were aggregated into two sets of land cover classes (Table 1). The first set of land cover classes was based on dominant tree species as well as tree sizes. The second set of classes collapsed the forest types into broader forest structure categories based primarily on tree size. Preliminary sensitivity analysis indicated that changes in the relative areas of these land cover classes were relatively insensitive to assumptions made in the reclassification of the 1996 map and the spatial grain of the landscape change analysis. Shifts in relative area were similar whether they were examined at a 200 m, 400 m, or 600 m spatial grain. However, the magnitude and even the direction of change of many spatial indices such as patch density, mean patch size, patch shape, and mean nearest-neighbor distance varied with the reclassification and rescaling parameters used. Because of these uncertainties, and because the ecological significance of many of these spatial indices is not well understood, we quantified only changes in the total area of each cover type.

Potential independent variables were identified based on hypothesized relationships with land cover change and the availability of mapped data (Table 2). The spatial pattern of all the selected variables was assumed to have remained relatively stable over the 60-year period of the study. Private ownership (PRIVATE)

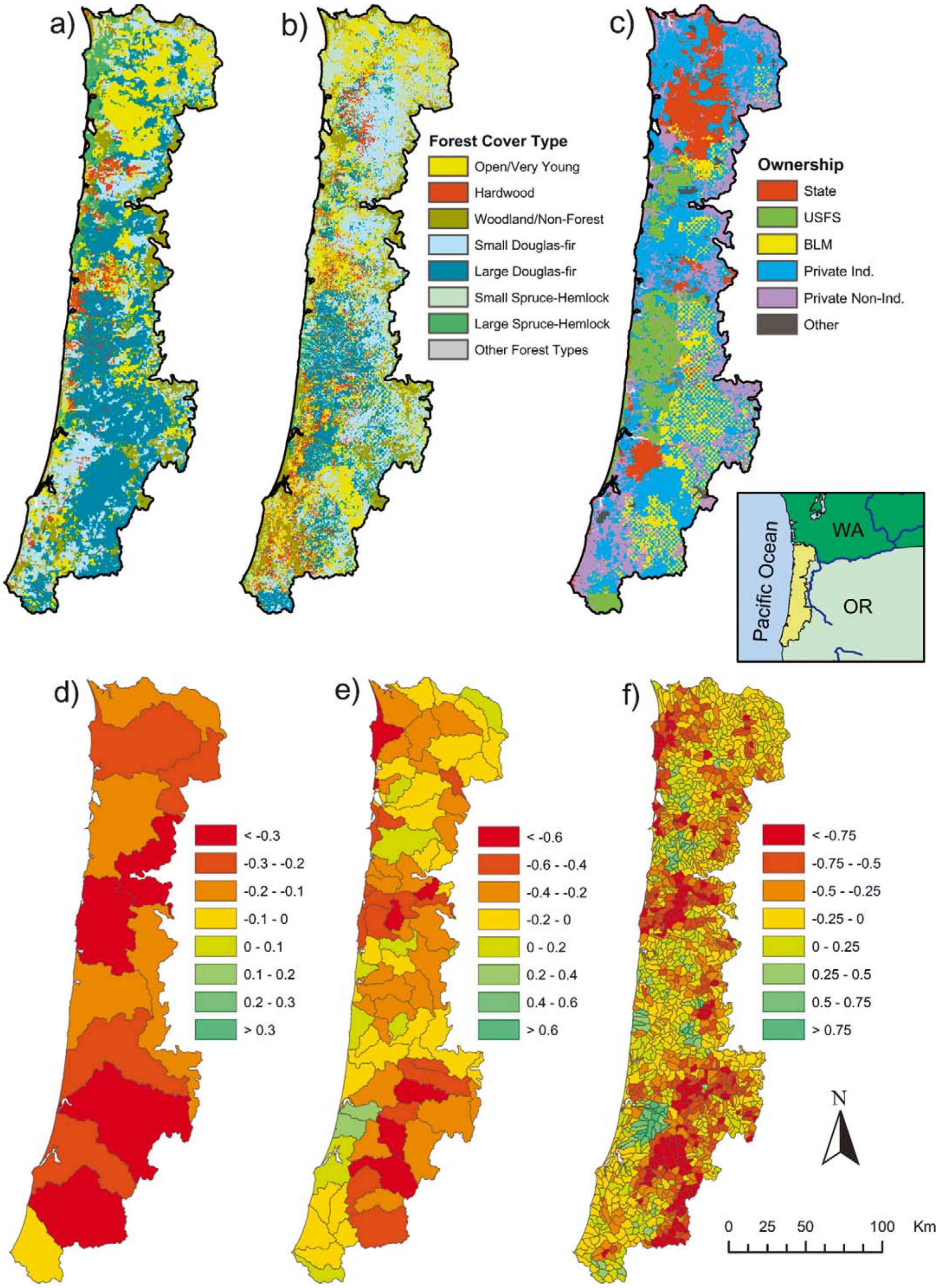

Figure 1. Changes in the pattern of forest cover types in the Oregon Coast Range from 1936 to 1996. (a) 1936 pattern of forest cover types; (b) 1996 pattern of forest cover types; (c) major land ownership classes; (d) LCCHNG summarized by subbasin; (e) LCCHNG summarized by watershed; (f) LCCHNG summarized by subwatershed.

Table 1. Criteria used to reclassify the 1996 map into 1936 map classes, and to aggregate map classes into forest cover types.

1936 Map class	Classification criteria for 1996 map	Cover type 1	Cover type 2
Nonforest / agriculture / noncommercial	Nonforest mask[1]	Nonforest	Nonforest
Hardwood/oak-madrone	> 60% oak or madrone[1]	Nonforest	Nonforest
Recent cutover/ non-restocked cutover/ deforested burn	Age < 16 and total volume < 5000 ft^3/acre, or total basal area < 8.5 ft^2 acre	Open	Early successional
Hardwood, alder-ash-maple	> 50% hardwoods	Hardwood	Early successional
Douglas fir small second-growth	> 60% Douglas-fir/6–22 in dbh	Small Douglas- fir	Small conifer
Douglas fir seedling-sapling-pole	> 60% Douglas-fir/< 5 in dbh	Small Douglas-fir	Small conifer
Spruce/hemlock/ cedar small	> 50% Sitka spruce/< 24 in dbh or > 50% western hemlock/> 20 in dbh or > 40% western redcedar/ < 24 in dbh or > 40% Port Orford cedar/ < 30 in dbh	Small spruce/ hemlock/cedar	Small conifer
Douglas fir old growth/large second-growth	> 60% Douglas-fir/> 22 in dbh	Large Douglas-fir	Large conifer
Spruce/hemlock large	> 50% Sitka spruce/> 24 in dbh or > 50% western hemlock/> 20 in dbh	Large spruce/ hemlock/ cedar	Large conifer
Cedar/redwood large	> 40% western redcedar/ > 24 in dbh or > 20% Port Orford cedar/ > 30 in dbh or >80% redwood	Large spruce/ hemlock/cedar	Large conifer
Fir/hemlock/upper slope types large	Most dominant trees > 16 in dbh	Other	Other
Ponderosa pine small	> 50% ponderosa pine/ 6-22 in dbh	Other	Other
Fir/hemlock/upper slope types small	Most dominant trees < 16 in dbh	Other	Other
Lodgepole pine	> 50% lodgepole pine	Other	Other

[1]Nonforest areas in the 1996 map were identified using a rule-based classification that incorporated Landsat imagery, land ownership, urban area boundaries, and topography

was hypothesized to influence both forest management goals and regulatory constraints, thereby affecting rates of harvest and types of forest management applied (Spies et al. 1994; Spies et al. 2002) (Figure 1c). Distance to the nearest highway (HWYDIST) was computed as an index of accessibility and transportation costs (Turner et al. 1996) (Figure 2a). Distance from the nearest city (CTYDIST) was computed as an indicator of proximity to markets and the potential effects of urban sprawl on land use and forest management (Wear et al. 1999; Kline et al. 2001) (Figure 2b). Topographic relief (RELIEF) reflected the steepness and ruggedness of terrain, which may influence soil characteristics, forest community composition, and the potential for agricultural use or development (Turner et al. 1996; Wear and Bolstad 1998) (Figure 2c). The dominant regional climate gradient, summarized by the SMRTP index, has a strong effect on patterns of forest community composition and may also influence rates of tree growth and the risk of wildfires (Impara 1997, Ohmann and Spies 1998; Wimberly 2002) (Figure 2d). Exposure to solar radiation (SOLARAD) is a driver of vegetation growth, evapotranspiration, and other ecosystem processes (Figure 2e).

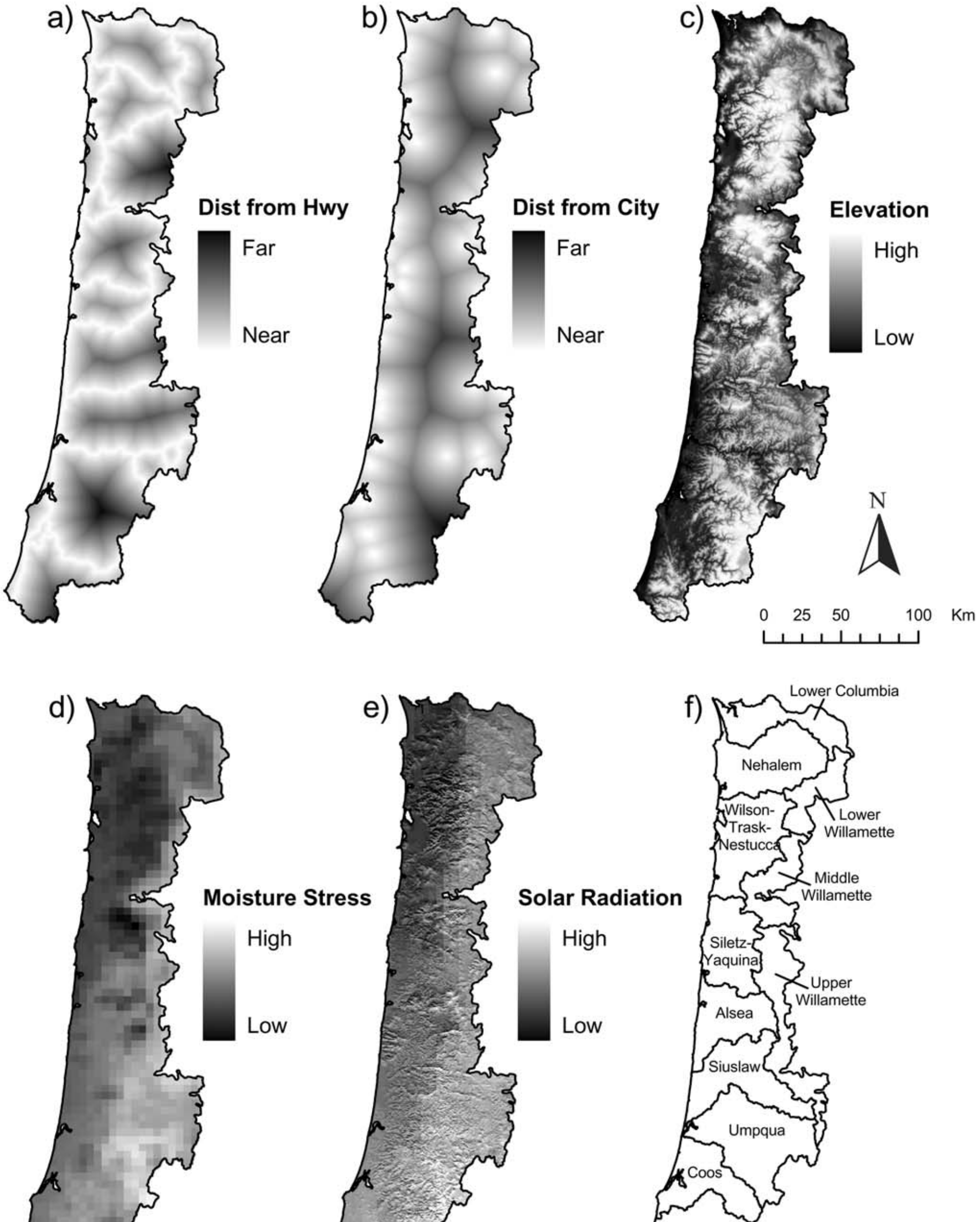

Figure 2. Independent variables used to model forest land cover change in the Oregon Coast Range. (a) Distance from the nearest highway; (b) Distance from the nearest city; (c) Elevation (used to compute topographic relief); (d) Moisture stress index; (e) Solar radiation (see Table 2 for additional details); (f) names and locations of the 13 subbasins used to summarize land cover change in Table 4.

Table 2. Dependent and independent variables used in the regression model of forest land cover change.

Variable	Description
LC36	Percentage of a hydrological unit occupied by large conifer forest in 1936; Based on a GIS layer derived from maps of the 1933-1936 forest survey of the Douglas-fir region[1]
LC96	Percentage of a hydrological unit occupied by large conifer forest in 1996; Based on reclassification and rescaling of a 1996 vegetation map created from Landsat TM imagery and GIS data layers using the Gradient Nearest-Neighbor (GNN) method (Ohmann and Gregory 2002)[2]
LCCHNG	Change in the percent of a hydrological unit occupied by large conifer forest from 1936–1996; Computed as LC96–LC36
PRIVATE	The proportion of land within a hydrological unit that is privately-owned (includes private industrial and private non-industrial) as opposed to publicly owned (US Forest Service, US Bureau of Land Management, and Oregon State Department of Forestry); Derived from a GIS layer of forest ownership in Western Oregon available from the Oregon Geospatial Data Clearinghouse (OGDC)[3]
HWYDIST	Distance from each 100 m grid cell to the nearest highway (km), averaged across all cells within a hydrologic unit; USGS highway layer available from the OGDC[3]
CTYDIST	Distance from each 100 m grid cell to the nearest city (km), averaged across all cells within a hydrologic unit; Oregon Department of Transportation map of city limits available from the OGDC[3]
RELIEF	Difference between the lowest and highest elevations (m) within a hydrologic unit, computed from a 100-m digital elevation model (DEM)
SMRTP	Growing season moisture stress index averaged across each hydrological unit; Computed as SMRTMP/SMRPRE, where SMRTMP is the mean temperature (C) in May-September and SMRPRE is the natural logarithm of annual precipitation from May–Sept. (mm); Based on mean monthly precipitation and temperature surfaces generated by the precipitation-elevation regression on independent slopes model (PRISM) (Daly et al. 1994)[4]
SOLARRAD	Solar radiation (cal/cm^2) computed from the 100-m DEM using the SolarImg program developed by Mark Harmon and Barbara Marks[5]

[1]http://www.icbemp.gov/
[2]http://www.fsl.orst.edu/clams/
[3]http://www.gis.state.or.us/
[4]http://www.ocs.orst.edu/prism/
[5]http://www.fsl.orst.edu/lter/

Change in the percent area of large conifer forest (LCCHNG) was computed as the difference between the percent area of large conifer forest in 1996 (LC96) and 1936 (LC36). We focused on large conifer forest as the response variable based on previous research which showed that a decline in older forests was the dominant trend over the time period of our study (Ripple et al. 2000), and because a large number of wildlife species are associated with this habitat type (Olson et al. 2001). Landscape change and the spatial predictor variables were summarized at three spatial scales, derived from the USGS hierarchy of hydrologic units (Table 3). Subbasins (4th-field hydrologic units) were the largest spatial units, ranging from 990 to 3260 km^2 (Figures 1d, 2f). Several of the smaller subbasins, along with subbasin fragments that overlapped the study area boundary, were merged with adjacent hydrologic units to increase the minimum subbasin size. Watersheds (5th-field hydrologic units) were nested within subbasins and ranged from 43 to 789 km^2 (Figure 1e). Subwatersheds (6th-field hydrologic units), the smallest spatial units, were nested within watersheds and ranged from 6 to 56 km^2 (Figure 1f). Hydrologic units were used in this analysis because the spatial datasets were readily available and provided a convenient method of stratification. In addition, the use of hydrologic units provides a means for linking land cover data with stream processes and aquatic habitats, making our analyses relevant for watershed analysis and restoration efforts. Changes in

Table 3. Dependent and independent variables used to model change in the area of large conifer forest. Mean (μ) standard deviations (s), and sample size (n) summarized at three spatial scales.

	Subbasin (n = 13)		Watershed (n = 83)		Subwatershed (n = 1325)	
	μ	s	μ	s	μ	s
Area (km^2)	1964	640	302	177	18	8
LC36	0.40	0.16	0.43	0.24	0.44	0.34
LC96	0.18	0.14	0.19	0.18	0.20	0.25
LCCHNG	−0.23	0.095	−0.24	0.22	−0.24	0.38
PRIVATE	0.66	0.18	0.62	0.24	0.61	0.32
HWYDIST	7.3	2.2	7.0	4.2	7.5	5.7
CITYDIST	12.7	2.7	12.3	5.9	13.4	7.3
RELIEF	1049	114	742	212	428	180
SMRTP	2.7	0.25	2.7	0.30	2.7	0.34
SOLARAD	319	15.7	316	17.9	318	19.9

the relative area of forest cover types were computed for the entire Coast Range, and separately for each of the subbasins. Linear regression models were used to predict changes in the area of the large conifer forest class (LCCHNG) as a function of environmental and socioeconomic variables at each of the three spatial scales.

Relationships between these six predictor variables and LCCHNG were examined at each scale using partial correlation analysis, with LC36 included as a covariate to account for the effects of initial landscape condition on land cover change. Stepwise linear regression (forward and backward) was then used to develop a multiple regression models of LCCHNG. Because each dataset represents all of the hydrologic units in the Coast Range at a given scale, and because most variables are spatially autocorrelated with neighboring hydrologic units, standard parametric methods of significance testing based on the assumption of a random sample of independent data have questionable relevance and are potentially biased (Manly 1991; Legendre 1993). Permutation testing offers an alternative, non-parametric method of hypothesis testing that does not requires the assumptions of random sampling and independent error terms. In additional to the parametric statistical tests, we used a randomization test based on permutations under the reduced model to test the contribution of each variable to the final regression models while taking into account the presence of covariates (Anderson and Legendre 1999). Each significance test was based on 999 random permutations, and only variables with $p < 0.05$ were retained in the final models. Because of concerns about the potential influences of heteroskedasticity, we also carried out standard significance tests on the final models using weighted regression. Appropriate weights for each model were derived by examining the relationship of the residuals with the independent and dependent variables (Neter et al. 1989). All regression modeling and permutation tests were carried out using Splus (Insightful 2001).

Results

The total area of closed canopy forests (hardwood, small Douglas fir, large Douglas fir, small spruce-hemlock, large spruce-hemlock, and miscellaneous forest cover types) remained fairly stable, decreasing from 17 382 km^2 in 1936 to 16 609 km^2 in 1996. However, major shifts occurred in the distribution of these forested cover classes. The most significant trend was an overall change from a large-conifer dominated landscape to a small-conifer dominated landscape. In 1936, extensive patches of large Douglas fir forest connected much of the central and southern Coast Range, whereas patches of large Douglas fir and spruce-hemlock forest were smaller and more dispersed in the northern Coast Range (Figure 1a). In 1996, the main blocks of remaining large conifer forest occurred on federal and state lands in the central Coast Range (Figure 1b). Elsewhere, large conifer forest occurred mainly as scattered fragments on various blocks of public land. Decreases in the areas of the large Douglas fir (5315 km^2) and large spruce-hemlock (891 km^2) cover types combined to produce a 58% drop in the total area of large conifer forest (Table 4). The areas of small Douglas-fir and spruce-hemlock forests increased by 3250 km^2 and 1453 km^2, respectively, resulting in an 87% increase in the total area of small conifer forest.

The areas of hardwood and open forest increased by 984 km^2 (101%) and 940 km^2 (21%) respectively (Table 4). At the subbasin scale, turnover of both of these patch types was extremely high. In the Nehalem, Lower Willamette, and Wilson–Trask–Nestucca subbasins, for example, the area of open forests declined by 732 km^2 as large open areas created by the Tillamook fires and early 20th-century logging succeeded to a mosaic of hardwood and conifer forests. Conversely, the area of early-successional forest in the Umpqua, Coos, and Coquille subbasins increased by 1248 km^2 while the areas of both small and large conifer forest in these subbasins declined. Hardwood forest dynamics also varied across the Coast Range. Hardwoods decreased in the Alsea subbasin as stands that had established after historical fires either succeeded to conifers or were converted to conifer plantations, and increased in the Umpqua, Coos, and Coquille subbasins where logging of conifer forests created a landscape dominated by early successional vegetation. The total area of non-commercial woodlands and other non-forest cover types (predominantly urban and agricultural) was relatively stable, decreasing by only 211 km^2 (equivalent to 6% of the total non-forest area in 1936). To some degree, these changes in non-forest area may reflect differences in the criteria used to map non-forest areas in 1936 and 1996. The comparatively large (80%) decrease in the area of miscellaneous forest cover types may result from uncertainty in the mapping of this rare forest type in both the 1936 and 1996 maps.

The aggregate trend in large conifer forest change was negative at all three spatial scales (Table 3). However, the distribution of changes among hydrologic units varied with scale (Figures 1d–f, 3). All of the subbasins exhibited a decrease in the relative area covered by large conifer forest, ranging from −0.6 to −0.36. Large conifer forest cover decreased in most of the watersheds, but large conifer forest cover increased by up to 0.33 in 14% of the watersheds. At the finest spatial scale, 22% of the subwatersheds exhibited increases in the relative area covered by large conifer forest, up to a maximum increase of 0.95. At the subbasin and watershed scales, only PRIVATE had a statistically significant partial correlation with LCCHNG after including LC36 as a covariate to account for initial landscape conditions (Figure 4). At the subwatershed scale PRIVATE had the strongest partial correlation with LCCHNG, whereas CTYDIST and RELIEF had statistically significant but weaker partial correlations.

The regression models explained substantial proportions of the variability in large conifer forest change at the subbasin (57%), watershed (81%), and subwatershed (77%) scales (Table 5). The negative sign associated with the LC36 coefficient reflected the fact that decreases in late successional forest were constrained by the initial watershed condition, with large decreases occurring only where there was a large initial area of large conifer forest. After accounting for initial conditions by including LC36 as a covariate, the socioeconomic and environmental predictor variables still accounted for considerable portions of the remaining variability in large conifer forest change at the subbasin (45%), watershed (64%), and subwatershed (46%) scales.

PRIVATE was the most important predictor variable at all three spatial scales, explaining 45%, 54%, and 39% of the remaining variability at the subbasin, watershed, and subwatershed scales after including LC36 to account for initial conditions (Table 5). The negative regression coefficient indicated that decreases in large conifer forest were typically greatest (most negative) in hydrological units dominated by privately-owned land. At the watershed and subwatershed scales, changes in the area of large conifer forest were positively associated with SMRTP and negatively associated with RELIEF. At the subwatershed scale, change in the area of large conifer forest was negatively associated with SOLARRAD. However, the amount of additional variability explained by these variables was relatively small compared with PRIVATE. Statistical analyses based on the permutation tests (Table 5) and the weighted regression models (not shown) produced congruent results, with all parameters in the final models significant at the $p < 0.05$ level.

Discussion

Our results agree with previous research documenting declines in the amount of older forests in the Oregon Coast Range over the latter half of the 20th century (Ripple et al. 2000). Our work also corroborate the results of the Coastal Landscape Analysis and Mod-

Table 4. Total area of each cover class (km^2) within each subbasin in 1936 and 1996.

Subbasin	Year	Forest cover type							
		NF	Open	HW	SDF	LDF	SS/H	LS/H	Other
Lower	1936	237	440	34	322	42	244	223	19
Columbia	1996	260	673	56	191	17	341	24	0
Nehalem	1936	127	1144	8	223	559	148	321	17
	1996	119	765	118	845	161	510	29	0
Lower Willamette	1936	193	334	0	271	258	0	0	0
	1996	129	224	39	637	4	15	7	1
Wilson–Trask–Nestucca	1936	247	897	256	346	317	72	300 5	
	1996	205	385	241	880	292	373	66	0
Middle Willamette	1936	415	93	5	350	450	0	13	2
	1996	330	197	32	704	42	23	1	0
Siletz–Yaquina	1936	178	350	251	195	731	29	203	11
	1996	135	602	244	452	203	268	44	0
Upper Willamette	1936	703	291	2	594	535	0	0	0
	1996	544	366	42	1044	119	2	1	7
Alsea	1936	110	148	191	237	958	31	83	18
	1996	93	172	103	473	699	151	86	0
Siuslaw	1936	183	285	70	236	1491	7	45	25
	1996	184	343	194	640	912	44	22	4
Umpqua	1936	471	115	18	641	2003	1	12	0
	1996	483	611	181	1106	839	17	6	17
Coos	1936	169	151	44	673	740	43	15	33
	1996	294	645	194	326	297	100	10	2
Coquille	1936	356	237	35	482	1112	10	1	58
	1996	382	494	314	641	362	69	17	12
Sixes	1936	161	107	13	293	328	10	4	73
	1996	187	105	110	171	252	137	19	10
Total	1936	3556	4599	928	4860	9514	595	1223	262
	1996	3345	5583	1868	8110	4199	2048	332	52

NF = non-forest; HW = hardwood; SDF = Small Douglas fir; LDF = large Douglas fir; SS/H = small spruce/hemlock; LS/H = large spruce/hemlock

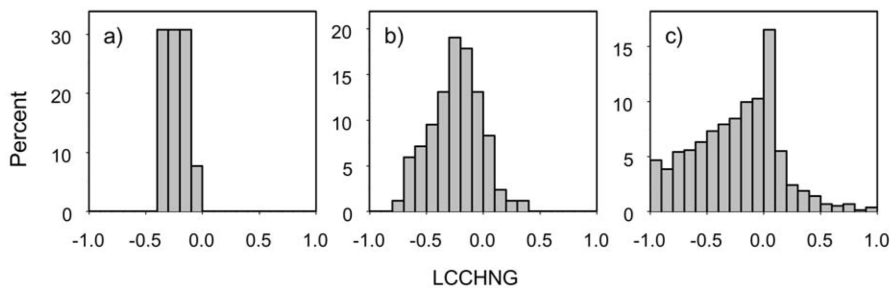

Figure 3. Probability distribution of LCCHNG summarized by (a) Subbasin; (b) Watershed; (c) Subwatershed.

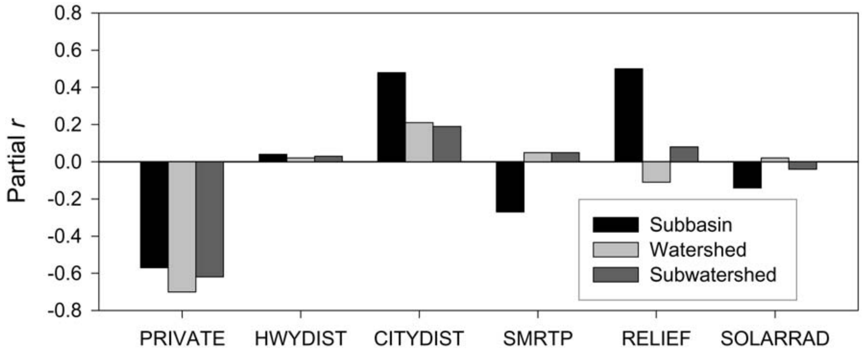

Figure 4. Partial correlation of LCCHNG with independent variables at three spatial scales. LC36 is included as the covariate.

Table 5. Stepwise regression models used to predict change in the area of large conifer forest at three spatial scales.

Model	Variable	Coefficient	F	p-value[1]	Partial R^2	Cumulative R^2
Subbasin	LS36	−0.511	5.07	0.002	0.22	0.22
	PRIVATE	−0.377	8.22	0.015	0.45	0.57
Watershed	LS36	−0.806	203.7	<0.001	0.48	0.48
	PRIVATE	−0.578	118.3	<0.001	0.54	0.76
	RELIEF	−0.000166	15.0	0.004	0.15	0.80
	SMRTP	0.103	7.2	0.009	0.08	0.81
Subwatershed	LS36	−0.896	3367.4	<0.001	0.58	0.58
	PRIVATE	−0.523	951.3	<0.001	0.39	0.74
	SMRTP	0.280	104.9	<0.001	0.07	0.76
	SOLARRAD	−0.00283	52.8	<0.001	0.04	0.77

[1]Derived from a randomization test based on permutations under the reduced model.

eling Study (CLAMS) which projected future land cover changes from 1996 through 2096 based on spatially explicit simulation of land use change, forest landowner behavior, and forest growth and succession (Spies et al. 2002). CLAMS showed that in the future, regional patterns of forest cover classes will be increasingly constrained by ownership, with early-successional forests dominating on private lands and late-successional forests restricted to public lands. Our statistical models of historical landscape dynamics demonstrate that these projected trends are consistent with the spatial pattern of land cover change over the past 60 years.

We estimated that large conifer forests occupied 42% of the study area in 1936, but had declined to only 18% of the study area by 1996. A simulation model of historical variability in forest age classes under the presettlement fire regime estimated that late-successional forests (defined as forests > 80 years after a stand-replacing or partial disturbance) occupied between 52% and 85% of the landscape over the 1000 years prior to Euro-American settlement (Wimberly et al. 2000). If the late-successional age class is assumed to be broadly similar to the large-conifer forest cover type, we can infer that the pattern of these older forests had already been reduced to the lower bounds of its historical range of variability by 1936. These changes likely resulted from a sharp increase in the areas burned by human-ignited fires during the late 19th and early 20th centuries (Impara 1997) as well as the onset of logging, particularly in the areas in the vicinity of Portland in the northern Coast Range and Coos Bay in the southern Coast Range (Robbins 1997). Although most wildfires were successfully suppressed in the latter half of the 20th century, increased rates of timber harvesting led to continuing declines in the area of old forests through 1996.

The significant decline in the area of large-conifer forest and the corresponding increases in the areas of small conifer and early successional forest have probably influenced regional biodiversity in several ways. Most significantly, populations of species associated with early-successional and small-conifer forest habitats have likely increased at the expense of those species associated with late-successional habitats. Coast Range species occurring primarily in older forests dominated by large trees include the northern spotted owl (*Strix occidentalis caurina*), which is positively associated with the density of trees > 75 cm dbh (McComb et al. 2002). McGarigal and McComb (1995) identified 15 additional bird species associated with late-seral forests (defined as having $> 20\%$ of overstory cover composed of trees with a mean dbh > 53.3 cm). Martin and McComb (2002) similarly identified 10 small mammal species that had higher capture rates in late-seral forests than in younger forests. Furthermore, the ecological importance of large pieces of dead wood in Pacific Northwest forests is well established for both terrestrial and aquatic systems (Harmon et al. 1986; Spies et al. 1988). Forests dominated by large conifers are the primary source for large dead wood, and their decline likely foreshadows changes in the amount of dead wood in coastal ecosystems.

Human impacts

Our research corroborates previous work that has demonstrated the importance of ownership as a key socioeconomic variable structuring landscape patterns and dynamics (Mladenoff et al. 1993; Spies et al. 1994; Turner et al. 1996; Crow et al. 1999; Cohen et al. 2002; Stanfield et al. 2002). However, contrary to many of these studies, we found that landscape change had comparatively weak relationships with climate, topography, and distances to cities and highways. Previous research has found that disturbance history has a much stronger influence than environmental heterogeneity on patterns of forest structure in the Coast Range (Wimberly and Spies 2001; Ohmann and Gregory 2002). Although environmental gradients can influence rates of tree establishment, mortality, and growth, the structural changes arising from these individual-tree level processes operate relatively slowly. In contrast, structural changes resulting from disturbance are practically instantaneous. Even though patterns of climate and topography may have strong effects on patterns of forest community composition, their influence on broad-scale patterns of forest structure is expected to be relatively weak (Ohmann and Spies 1998). Furthermore, local influences of physical and socioeconomic constraints on natural disturbances and human land use are likely to be diluted as these variables are aggregated within hydrological units.

Although ownership emerged as the most important predictor of land cover change, it was also used in the development of the 1996 GNN vegetation map (Ohmann and Gregory 2002). However, ownership by itself could account for only a small portion (2.2%) of the total inertia in CCA. In contrast indices derived from Landsat TM imagery could account for a much larger proportion (15.2%) of the total inertia. Other sets of variables accounting for significant portions of the total inertia included latitude and longitude (5.2%), topographic indices (4.5%), and geology (1.8%). Because of the relatively low importance of ownership relative to the other variables in the GNN model, we concluded that the relationships between ownership and land cover change within hydrologic units reflected real differences between public and private lands, and were not just an artifact of the methods used to create the 1996 vegetation map.

One major distinction between this research and many other studies of forest land cover change is that forestry remained the primary land use across the Oregon Coast Range over the time period of the analysis. In contrast to many other landscapes, loss of forest to development has not been a major driver of land cover change in the Coast Range. Although the total decline in closed-canopy forests was relatively modest (773 km^2, equal to 4% of the area of closed canopy forests in 1936), the decline in large conifer forests was considerable (6206 km^2, equal to 58% of the area of large conifer forests in 1996). Landscape change studies that focus on shifts between forest and non-forest cover types, or transitions among broad physiognomic classes such as hardwood and conifer-dominated forests, may fail to capture significant shifts in the size- and age-class distributions of forested landscapes.

Ownership explained a large proportion of the spatial variability in the dynamics of large conifer forests, even when the initial amount of large conifer forest was included in the model as a covariate. This result emphasizes that the different trajectories of change on private and public lands represent a difference in actual change between 1936 and 1996 rather than simply an artifact of different initial landscape conditions in 1936. The predominance of negative LCCHNG values indicates that these changes have primarily resulted from disturbance, rather than forest establishment and growth. Wildfires occurred infrequently over the period of study, with the largest fires during this time period being the Tillamook reburns in 1939 and 1945 which affected 44 km^2 and 63 km^2 of unburned forest, respectively; and the Oxbow fire in 1966, which burned 170 km^2. From 1972 to 1995, only 11 km^2 were disturbed by stand-replacing fire in the Coast Range, whereas 4804 km^2 were disturbed by clearcut timber harvests (Cohen et al. 2002). Harvest rates are much higher on private land (1.7% per year) than on public land (0.6% per year), supporting the contention that spatial variation in timber harvesting, rather than natural disturbance, is the dominant process shaping forest landscape patterns in the modern landscape (Spies et al. 1994).

Effects of scale

Although the aggregate change in land cover was a shift from a large-conifer to a small-conifer-dominated landscape, pathways of landscape dynamics were spatially variable at the subbasin scale. For example, percentage losses of large conifer forest were particularly high in the Lower Willamette and Middle Willamette subbasins, but were relatively low in the Alsea and Sixes subbasins. There was even more variability at smaller scales, with significant proportion of both watersheds (14%) and subwatersheds (22%) exhibiting increases in the area of large conifer forests. This spatial variability accounts for the differences between our findings of increased hardwood area across the entire Coast Range, and another aerial photograph-based study which reported declines in hardwood area in the central Coast Range (Kennedy and Spies in press). Our data also showed a significant decline in hardwoods in the Alsea subbasin and stable levels of hardwoods in the Siletz subbasin, which together encompass a large portion of the central Coast Range. The overall trend in increasing hardwoods was driven primarily by increases in the Siuslaw, Umpqua, Coos, and Coquille subbasins located in the southern Coast Range.

The statistical models predicting change in the area of large conifer forests were consistent at three spatial scales spanning two orders of magnitude in landscape extent. PRIVATE was always the most important predictor variable after accounting for the area of large conifer forest in 1936. Although the strong effect of ownership on land cover change was not surprising, its dominance in all three models emphasizes that ownership patterns can influence land cover change across a broad domain of scale (Wiens 1989). In contrast, environmental variables were only statistically significant at the watershed and subwatershed scales. The inclusion of environmental variables in the finer-scale models may reflect the fact that these variables are expected to have fairly localized effects on ecological processes and land use decisions. However, these models also had larger sample sizes than the subbasin-scale model, which allowed for inclusion of statistically significant variables that accounted for a relatively small portion of the total variance.

Changes in the area of large conifer forests were most predictable at the watershed scale, as evidenced by the partial correlations of individual predictor variables, the total R^2 of the final model, and the partial R^2 values of the variables included in the final model. Although the total R^2 of the subwatershed-scale model was only slightly lower, partial R^2 values indicated that the amount of variability predicted by the environmental and socioeconomic variables was less than at the watershed scale. Developing effective models of land cover dynamics requires identifying spatial variables that can serve as predictors of change, and also identifying the appropriate spatial and temporal scales for modeling change. Our research suggests that in the Coast Range, the watershed (average size about 300 km^2) is the most appropriate scale for predicting aggregate changes in forest cover over multiple decades as a function of coarse environmental and socioeconomic variables. At finer scales, variability in land cover change on individual ownership parcels or management units is contingent upon the diverse ecological characteristics of individual sites, as well as the social and economic forces operating on individual landowners. Fine-scale patterns of land cover change may also be highly sensitive to short-term fluctuations in climate or the economy, necessitating a narrower temporal analysis window (Turner et al. 1996; Wear and Bolstad 1998).

Conclusions

Inferences about landscape change derived from general classifications of land cover (e.g., open versus closed forest) may fail to reflect larger and potentially more ecologically relevant shifts in the age and size structure of the forest landscape. A major challenge for future landscape change research will be to incorporate more ecologically relevant measurements of forest habitats rather than the limited number of broad classes that can be easily derived from satellite imagery. Similarly, regional summaries of land cover change may mask variability occurring at finer spatial scales. Although the area of large conifer forest decreased within all subbasins within the Coast Range, there was a substantial proportion of subwatersheds (22%) within which large conifer forest increased. Despite these scale-related differences in landscape changes, the area of private land within each hydrologic unit was the most important predictor of landscape change across all three spatial scales, spanning two orders of magnitude in size (1000s–100 000s of ha). Ownership has been consistently shown to be an important predictor of landscape change in many different forested regions, and this influence also extends across a broad domain of scale.

References

Addicott J.F., Aho J.M., Antolin M.F., Padilla D.K., Richardson J.S., and Soluk D.A. 1987. Ecological neighborhoods: Scaling environmental patterns. Oikos 49: 340–346.

Anderson M.J. and Legendre P. 1999. An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. Journal of Statistical Computation and Simulation 61: 271–303.

Andrews H.J. and Cowlin R.W. 1940. Forest resources of the Douglas-fir region. Miscellaneous Publication No. 389, United States Department of Agriculture, Washington, D.C., USA.

Axelsson A.-L., Ostlund L. and Hellberg E. 2002. Changes in mixed deciduous forests of boreal Sweden 1866–1999 based on interpretation of historical records. Landscape Ecology 17: 403–418.

Black A.E., Morgan P. and Hessburg P.F. 2003. Social and biophysical correlates of change in forest landscapes of the interior Columbia Basin, USA. Ecological Applications 13: 51–67.

Cohen W.B., Spies T.A., Alig R.J., Oetter D.R., Maiersperger T.K. and Fiorella M. 2002. Characterizing 23 years (1972–95) of stand replacement disturbance in western Oregon forests with Landsat imagery. Ecosystems 5: 122–137.

Crow T.R., Host G.E. and Mladenoff D.J. 1999. Ownership and ecosystem as sources of spatial heterogeneity in a forested landscape, Wisconsin, USA. Landscape Ecology 14: 449–463.

Daly C., Neilson R.P. and Phillips D.L. 1994. A statistical topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33: 140–158.

Drapeau P., Leduc A., Giroux J.-F., Savard J.-P.L., Bergeron Y. and Vickery W.L. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecological Monographs 70: 423–444.

Franklin J.F. and Dyrness C.T. 1973. Natural vegetation of Oregon and Washington. General Technical Report GTR-PNW-8, USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Hall F.G., Botkin D.B., Strebel D.E., Woods K.D. and Goetz S.J. 1991. Large-scale patterns of forest succession as determined by remote sensing. Ecology 72: 628–640.

Halpern C.B. and Spies T.A. 1995. Plant-species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5: 913–934.

Hargis C.D., Bissonette J.A. and Turner D.L. 1999. The influence of forest fragmentation and landscape pattern on American martens. Journal of Applied Ecology 36: 157–172.

Harmon M.E., Franklin J.F., Swanson F.J., Sollins P., Gregory S.V., Lattin J.D., Anderson N.H., Cline S.P., Aumen N.G., Sedell J.R., Lienkaemper G.W., Cromack K. and Cummins K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

Impara P.C. 1997. Spatial and temporal patterns of fire in the forests of the central Oregon Coast Range. Oregon State University, Corvallis, Oregon, USA.

Insightful. 2001. Splus 6 user's guide. Insightful Corporation, Seattle, Washington, USA.

Kennedy R.S.H. and Spies T.A. in press. Forest cover changes in the Oregon Coast Range from 1939 to 1993. Forest Ecology and Management.

Kline J.D., Moses A. and Alig R.J. 2001. Integrating urbanization into landscape-level ecological assessments. Ecosystems 4: 3–18.

Legendre P. 1993. Spatial autocorrelation – trouble or new paradigm? Ecology 74: 1659–1673.

Loehle C. and Li B.L. 1996. Habitat destruction and the extinction debt revisited. Ecological Applications 6: 784–789.

Lomolino M.V. and Perault D.R. 2000. Assembly and disassembly of mammal communities in a fragmented temperate rain forest. Ecology 81: 1517–1532.

Manly B.F. 1991. Randomization and Monte Carlo methods in biology. Chapman & Hall, London, UK.

Martin K.J. and McComb W.C. 2002. Small mammal habitat associations at patch and landscape scales in Oregon. Forest Science 48: 255–264.

Matlack G.R. 1994. Plant-species migration in a mixed-history forest landscape in eastern North America. Ecology 75: 1491–1502.

McComb W.C., McGrath M.T., Spies T.A. and Vesely D. 2002. Models for mapping potential habitat at landscape scales: An example using northern spotted owls. Forest Science 48: 203–216.

McGarigal K. and McComb W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecological Monographs 65: 235–260.

Mladenoff D.J., White M.A., Pastor J. and Crow T.R. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecological Applications 3: 294–306.

Nagaike T. and Kamitani T. 1999. Factors affecting changes in landscape diversity in rural areas of the Fagus crenata forest region of central Japan. Landscape and Urban Planning 43: 209–216.

Neter J., Wasserman W. and Kutner M.H. 1989. Applied linear regression models. Irwin, Boston, Massachusetts, USA.

Ohmann J.L. and Gregory M.J. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. Canadian Journal of Forest Research 32: 725–741.

Ohmann J.L. and Spies T.A. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecological Monographs 68: 151–182.

Olson D.H., Hagar J.C., Carey A.B., Cissel J.H. and Swanson F.J. 2001. Wildlife of westside and high montane forests. *In* Johnson D.H. and O'Neill T.A. (eds), Wildlife-habitat relationships in Oregon and Washington, pp. 187–212. Oregon State University Press, Corvallis, Oregon, USA.

Pinder J.E., Rea T.E. and Funsch D.E. 1999. Deforestation, reforestation and forest fragmentation on the upper coastal plain of

South Carolina and Georgia. American Midland Naturalist 142: 213–228.

Radeloff V.C., Hammer R.B., Voss P.R., Hagen A.E., Field D.R. and Mladenoff D.J. 2001. Human demographic trends and landscape level forest management in the northwest Wisconsin Pine Barrens. Forest Science 47: 229–241.

Radeloff V.C., Mladenoff D.J. and Boyce M.S. 2000. Effects of interacting disturbances on landscape patterns: Budworm defoliation and salvage logging. Ecological Applications 10: 233–247.

Radeloff V.C., Mladenoff D.J., He H.S. and Boyce M.S. 1999. Forest landscape change in the northwestern Wisconsin Pine Barrens from pre-European settlement to the present. Canadian Journal of Forest Research 29: 1649–1659.

Ripple W.J., Hershey K.T. and Anthony R.G. 2000. Historical forest patterns of Oregon's central Coast Range. Biological Conservation 93: 127–133.

Robbins W.G. 1997. Landscapes of promise: The Oregon story 1800–1940. University of Washington Press, Seattle, Washington, USA.

Spies T.A., Franklin J.F. and Thomas T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69: 1689–1702.

Spies T.A., Reeves G.H., Burnett K.M., McComb W.C., Johnson K.N., Grant G., Ohmann J.L., Garman S.L. and Bettinger P. 2002. Assessing the ecological consequences of forest policies in a multi-ownership province in Oregon. *In* J. Liu and Taylor W.W. (eds). Integrating landscape ecology into natural resource management, pp. 179–207. Cambridge University Press, Cambridge, UK.

Spies T.A., Ripple W.J. and Bradshaw G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4: 555–568.

Stanfield B.J., Bliss J.C. and Spies T.A. 2002. Land ownership and landscape structure: A spatial analysis of sixty-six Oregon (USA) Coast Range watersheds. Landscape Ecology 17: 685–697.

Tilman D., May R.M., Lehman C.L. and Nowak M.A. 1994. Habitat destruction and the extinction debt. Nature 371: 65–66.

Turner M.G. and Ruscher C.L. 1988. Changes in landscape patterns in Georgia, USA. Landscape Ecology 1: 241–251.

Turner M.G., Wear D.N. and Flamm R.O. 1996. Land ownership and land-cover change in the southern Appalachian highlands and the Olympic peninsula. Ecological Applications 6: 1150-1172.

Verburg P.H. and Chen Y.Q. 2000. Multiscale characterization of land-use patterns in China. Ecosystems 3: 369–385.

Vitousek P.M. 1994. Beyond global warming – ecology and global change. Ecology 75: 1861–1876.

Vogelmann J.E. 1995. Assessment of forest fragmentation in southern New England using remote-sensing and geographic information-systems technology. Conservation Biology 9: 439–449.

Wear D.N. and Bolstad P. 1998. Land-use changes in southern Appalachian landscapes: Spatial analysis and forecast evaluation. Ecosystems 1: 575–594.

Wear D.N., Liu R., Foreman J.M. and Sheffield R.M. 1999. The effects of population growth on timber management and inventories in Virginia. Forest Ecology and Management 118: 107–115.

Wear D.N., Turner M.G. and Flamm R.O. 1996. Ecosystem management with multiple owners: Landscape dynamics in a southern Appalachian watershed. Ecological Applications 6: 1173–1188.

White M.A. and Mladenoff D.J. 1994. Old-growth forest landscape transitions from pre-European settlement to present. Landscape Ecology 9: 191–205.

Wiens J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385–397.

Wimberly M.C. 2002. Spatial simulation of historical landscape patterns in coastal forests of the Pacific Northwest. Canadian Journal of Forest Research 32: 1316–1328.

Wimberly M.C. and Spies T.A. 2001. Influences of environment and disturbance on forest patterns in coastal Oregon watersheds. Ecology 82: 1443–1459.

Wimberly M.C., Spies T.A., Long C.J. and Whitlock C. 2000. Simulating historical variability in the amount of old forests in the Oregon Coast Range. Conservation Biology 14: 167–180.

With K.A. and Crist T.O. 1995. Critical thresholds in species responses to landscape structure. Ecology 76: 2446–2459.