



Forest cover changes in the Oregon Coast Range from 1939 to 1993

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Abstract

Understanding the shifts over time in the distribution and amount of forest vegetation types in relation to forest management and environmental conditions is critical for many policy and ecological questions. Our objective was to assess the influences of ownership and environment on changes in forest vegetation from post-settlement historical to recent times in the central Coast Range of Oregon. We evaluated land cover types on 1475 20 m plots, using scanned, geo-referenced historical (1939) and recent (1993) aerial photos. The amount of older conifer cover declined by 63% relative to its former amount, from 36 to 13% of the landscape, during the 54-year period. Dominant ownership of older conifer stands shifted from industrial private to Forest Service lands. Younger conifer stands showed the greatest expansion in cover, increasing more than two-fold, from 21 to 44% of the landscape. Shrub and hardwood cover declined by 16%, from 31 to 25% of the landscape. Shrubs and hardwoods occurred at lower slope positions and closer to streams at the end of the period than at the beginning. Ownership was not an important determinant of the presence of large and very large conifer cover or shrub and hardwood cover in 1939, but was a very important factor affecting the presence of these cover types in 1993. Landscape transitional pathways were distributed among many types and no single transitional pathway was dominant. Even the most stable cover types (hardwood trees and herbs) had low absolute stability, with over 65% of their plots changing to another cover type by 1993. Our research indicates that the importance of ownership as a factor affecting the type of vegetation cover present has increased greatly during this time, whereas the relative influence of environment has lessened considerably. Land owners in the Oregon Coast Range have altered the cover and distribution of vegetation in diverse ways, changing the landscape to one dominated by young conifers, shifting the distribution of younger successional shrubs and hardwoods toward streams, and restricting the location of older coniferous stands to particular ownerships and site types.

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1. Introduction

Understanding the historical dynamics, composition, and environmental distribution of landscapes provides a context for monitoring changes, describing trends, and establishing reference conditions. Landscape vegetation dynamics are constrained by processes of disturbance and succession, which are mediated by physiographic factors, such as topography, soils, and climate, as well as biotic factors, such as seed source availability and herbivory (Crawley, 1986; van der Maarel, 1996). Pathways and rates of succession may also be controlled by stable vegetation types (Hobbs, 1994) which can halt further change. Moreover, in most landscapes, rates of change in vegetation types are directly or indirectly influenced by human activities (Wear et al., 1996), since humans act as disturbance agents and interact with the physical environment and successional processes.

Recent research has demonstrated relationships between shifts in vegetation patterns and human activities, succession, and topography (Turner et al., 1996; Cohen et al., 2002). Human activities have altered the spatial configuration of landscapes (Baker, 1992), including patch size and relative cover of different forest types, such as old growth or open forest types (White and Mladenoff, 1994; Manier and Laven, 2002). Land ownership and topography may play an important role in the spatial distribution and magnitude of change in vegetation patterns (Wear and Flamm, 1993; Spies et al., 1994; Turner et al., 1996; Cohen et al., 2002). While the importance of human activities is widely recognized, the relative influence of human activities and environmental factors is less well understood.

Studies of landscape change over time have been typically limited to relatively coarse spatial grains, relatively broad vegetation classes, and short time periods that do not span the timeframe of forest management cycles or successional change. They are often defined by the time period and spatial resolution of satellite images, i.e., the last 30 years, and have a resolution of 25–80 m or more. Broad-scale changes in vegetation types in relation to forest harvest and land use have been described at fairly coarse spatial grains, using remote sensing techniques (Spies et al., 1994; Motzkin et al., 1996; Cohen et al., 2002; Manier and Laven, 2002) and GIS analysis of histor-

ical vegetation maps (Ripple et al., 2000; Petit and Lambin, 2002; Wimberly and Ohmann, *in press*). Most frequently, studies of change in land cover, land use, or the spatial pattern of vegetation that use satellite imagery or aerial photographs have covered from 5 years to a few decades (Gruell, 1983; Hall et al., 1991; Hester and Sydes, 1992; Hart and Laycock, 1996; Turner et al., 1996; Wirth et al., 1996; Knapp and Soule, 1998; Cohen et al., 2002; Manier and Laven, 2002; Wolter and White, 2002).

The coarse scales typical of historical maps also limit the kinds of changes that can be detected as they are too coarse for one-to-one spatial comparison with current high resolution, satellite imagery-based maps. To address this limitation, some studies have reduced the resolution of recent maps to make them more compatible with historical maps (Wimberly and Ohmann, *in press*). These aggregation approaches are suitable for describing general patterns of vegetation change, but are unable to examine how broad-scale changes are influenced by finer scale landscape elements and processes, such as gap dynamics, individual large conifer trees and small patches of trees that are important to ecosystem processes and biodiversity (Hazell and Gustafsson, 1999; Fischer and Lindenmayer, 2002). For example, small patches of shrubs and hardwoods can inhibit establishment of late successional species, and small patches of late successional species in hardwood patches can be nuclei for the recovery of slow colonization species. These problems can only be investigated with a fine-grained study. Information from historical US public land survey records and other land survey efforts has also been used to evaluate land cover (Manies and Mladenoff, 2000) and land cover change (Burgi and Turner, 2002). These studies have exposed subtleties in terms of land use effects on land cover and the strengths and limitations of using survey records. However, aggregation or spatial interpolation methods are commonly used to evaluate land cover when using survey data, and this may also preclude evaluation of fine-scale patterns of change and related processes.

Some studies that incorporate the use of aerial photographs have covered longer time periods but customarily have used oblique (non-vertical) photographs (Manier and Laven, 2002), generalized cover type classes (Callaway and Davis, 1993; Turner et al.,

1996; Mast et al., 1997), or coarse spatial scales (Frelich and Reich, 1995) in airphoto interpretation. These studies have yielded valuable insights into many processes, such as succession, tree invasion into grasslands at ecotones, and the effects of ownership on land cover change. However, the use of aerial photographs in these studies typically has been fairly restricted in terms of the kinds of land cover change characteristics measured and the subsequent inferences drawn related to spatially heterogeneous landscape features.

The overall objective of this study was to characterize fine-scale patterns of vegetation change in the central Oregon Coast Range for a time period extending from just before the start of intensive timber management to recent times that are characterized by the advent of ecosystem management on public lands. We were interested in determining patterns of change across all cover types, and alterations to two ecologically important cover types in particular: large coniferous forest, and early successional hardwood trees and shrubs. Our goals were to describe changes in forest cover, relate these changes to patterns of ownership and topography and make inferences about relationships between land cover change, succession and disturbance. The three specific objectives of this study were to: (1) characterize overall patterns of land cover change in this managed forest landscape, especially focusing on large conifer trees and shrubs or hardwood trees; (2) relate these changes in cover types to ownership and environment; and (3) describe the major transitional pathways of the cover types for this landscape.

A better understanding of the dynamics of forest vegetation is relevant to forest sustainability questions. The amount of old-growth forest has dwindled relative to its historical extent in many forested landscapes (White and Mladenoff, 1994; Ripple et al., 2000), leading to policies designed to maintain or restore late successional forest habitats (U.S. Department of Agriculture & U.S. Department of Interior, 1993; Oregon Department of Forestry, 2001). Minor cover types, such as hardwoods and shrubs, are important to succession, biogeochemistry, and biodiversity (McComb, 1994; Pabst and Spies, 1999; Compton et al., 2003; Kennedy and Spies, in press), but some forest managers and ecologists are concerned that these early successional vegetation types may be

increasing and outcompeting with economically important conifers (Carlton, 1988; Hibbs and Giordano, 1996; Spies et al., 2003).

In a related study of landscape change in the central Oregon Coast Range (Kennedy and Spies, in press), we characterized the spatio-temporal dynamics of hardwood tree patches in relation to ownership and environment. We found that the spatial structure changed in several ways: hardwood patch number and average size declined; patch shapes became more complex; and within-patch heterogeneity of hardwood patches declined. Hardwoods declined on Forest Service lands, remained fairly stable in amount on industrial private lands, and increased on non-industrial private lands. Hardwood patch locations also became more restricted to near-stream, lower elevation sites. In the present study, we examined multiple forest cover types, characterizing the transitions among them and the relationships of these changes to environment and ownership.

2. Study area

The study area is in the central part of the Coast Range Mountains of Oregon, extending from about 44.2°–45.0°N and 123.7°–124.1°W, and is bounded on the west by the Pacific Ocean. The total area is 280,798 ha. We selected this area for study because of the wide coverage of historical aerial photos of an early photo date (i.e., 1939) and mix of ownerships. The rugged terrain has slope gradients between 0 and 69 degrees, elevations ranging from sea level to 1102 m, and a dense network of intermittent and perennial streams. Winters are mild and wet, and summers are relatively cool and dry. The western part of the study area is in the Sitka spruce (*Picea sitchensis* [Bong.] Carr.) vegetation zone and the balance lies in the western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) zone (Franklin and Dyrness, 1988). Major forest tree species include the coniferous species Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock, western redcedar (*Thuja plicata* Donn), and Sitka spruce, the latter restricted to the areas nearest the coast. Hardwood tree species, primarily red alder (*Alnus rubra* Bong.) and bigleaf maple (*Acer macrophyllum* Pursh), are less common but occur in patches throughout the coniferous matrix.

The vegetation consists primarily of blocks of conifer-dominated forest which are up to 60 years old on private lands and up to 150 years old on public lands. Industrial private forestry companies (IP) own 44% of the land in the study area, the USDA Forest Service (FS) 31%, and non-industrial private owners (NIP) 17%. The remaining 8% is under BLM, State, and miscellaneous ownership. A network of forest reserves was established on federal lands in 1991 to promote and maintain habitat for late-successional and old-growth forest related species (U.S. Department of Agriculture and U.S. Department of Interior, 1993). These reserves hold most of the remnant patches of unmanaged late successional forest in the Coast Range (Ohmann and Gregory, 2002). Stand development of unmanaged forests, which occur mainly on public lands, is primarily in the mature or understory reinitiation stage (Oliver and Larson, 1990; Spies, 1997). Lands under IP and FS ownership are not distinguished strongly by differences in topography, unlike other areas in the Pacific Northwest. NIP lands tend to be located along streams in the larger valleys. Dominant NIP land uses include agriculture, forestry, and low-density residential housing (Azuma et al., 2002). Clearcutting and associated road construction have replaced fire as the most influential disturbance, since the advent of fire suppression in the 1950s. The last catastrophic fires in the area took place in the 1850s and 60s (Crane, 1951; Parry, 1985); pre-suppression, fire had a return interval of 200–300 years (Agee, 1993; Impara, 1997; Long et al., 1998). Other large disturbance events include: large floods in the winters of 1964 (Strome, 1986) and 1996 (Plumley, 1997); storms characterized by heavy rains and high winds during the 1950s and 60s; and the Columbus Day windstorm of 1962 (Ruth and Yoder, 1953; Orr, 1963).

3. Methods

3.1. Preparation of aerial photographs

To evaluate land cover change, we first scanned and geo-referenced two sets of high resolution vertical aerial photographs that encompassed a 54-year time period from the historical period of early logging (1939) to recent times (1993) and covered the same

geographic area. The historical photos had a scale of 1:27,000 and were scanned at a resolution of 400 dots per inch, while the recent photos had a scale of 1:12,000 and were scanned at a resolution of 200 dots per inch; this resulted in similar grain sizes of 1.7 and 1.5 m, respectively, for the two photo sets. One-third of the 1939 aerial photos were selected at random by first subdividing the study area into rough longitudinal thirds, and then selecting one-third of the aerial photos from each area, based on the results of a random number generator and the rule that no adjacent aerial photos could be selected. This insured even coverage of the study area. We systematically sampled, registered, and rectified all photo images, using an affine transformation and existing streams and roads coverages in ARCGIS (Environmental Systems Research Institute, 1998). Accuracy of registration was measured, using the root mean squared error (RMS error) for the image, and the distance between calculated x , y and true x , y coordinates for each link (Environmental Systems Research Institute, 1998). Images were re-registered (links added and dropped iteratively) until the following two criteria were met: any single link on an image could not have an RMS error greater than 30 m, and the mean RMS error for the entire image could not exceed 25 m. We used an average of 27 links per photo to join photo and GIS coverage locations. RMS errors for individual links customarily fell within the 3–20 m range but were typically less than 10 m and mean RMS errors for entire images were 15 m or less, regardless of photo date. It should be noted that geo-referencing aerial photos in areas of great topographic relief, such as the study area, is complicated by the high degree of variable distortion which is present on aerial photographs; this may limit the registration accuracy available even under optimal registration conditions. We selected the total coverage area shared between the two sets of photos (intersection area) for potential interpretation, but interpreted plots that fell only the central regions of the historical photos to avoid geometric fidelity problems common to historical photography.

3.2. Plot selection and aerial photograph interpretation

To evaluate cover types on the scanned, geo-referenced images, using a GIS we digitally superimposed

a square grid over the study area. The grid was comprised of 1.6 million 20 m cells. We selected 1500 cells at random from this population to consider as plots for cover type evaluation. We evaluated the same 1500 plots for both photo dates, omitting plots where imagery was of inferior quality at either date. A single researcher (Kennedy) interpreted cover types on all digital photo images in order to limit interpreter error. The plot size of 20 m was selected because it accommodated the range of crown and patch types found in unmanaged forests in the Pacific Northwest, it was larger than the crown size of the latest successional patch type (very large conifer) and smaller than the smallest patch size we thought we might encounter (hardwood tree). Although we evaluated individual plots, the patches within which plots fell were typically larger than the size of an individual 20 m plot, regardless of cover type. Thus, we expected that any potential locational differences from date to date resulting from registration error would be accommodated by the plot size we used, which was small in relation to the typical patch size. For example, in a related study in which we evaluated patch dynamics of hardwood trees over the same time period (Kennedy and Spies, *in press*), we found that fewer than 1% of hardwood patches in this landscape at either date were comprised by just one plot; in fact, the mean size for what we classified as very small hardwood patches (0.04–0.5 ha) was 0.23 ha, or about six plots, but the mean patch size of all hardwood patches was much greater, at 3.67 ha (92 plots) historically and 2.40 ha (60 plots) at the recent date. In addition to plot size considerations, we were able to use the context around each 20 m plot to assist in cover type determination. Further, because we used digital imagery, we were able to easily display, zoom, and compare photographs of different dates that covered the same land area to compare locations and land cover conditions. Therefore, we concluded that our selected plot size and land cover evaluation method would adequately and accurately characterize landscape change and related transitional pathways.

One of the following 14 possible cover types was assigned to each plot: water, road, bare soil, herb, shrub, hardwood tree, small mixed conifer, medium mixed conifer, large mixed conifer, very large mixed conifer, small conifer, medium conifer, large conifer, and very large conifer. These cover types were utilized

because they were characteristic types in the area and they corresponded roughly with classes used in prior satellite imagery interpretation in the area (Cohen et al., 2002). Mixed cover types contained less than 70% conifer. A conifer crown was considered to be very large, and the cover type designated accordingly, if a single crown filled greater than 25% of the plot (greater than 100 m²; crown diameter >10 m); large if a single crown filled from 6.25 to 25% of the plot (25–100 m²; crown diameter 5–10 m); medium if a single crown filled from 1.56 to 6.25% of the plot (6.25–25 m²; crown diameter 2.5–5 m); and small if a single crown filled less than 1.56% of the plot (<6.25 m²; crown diameter <2.5 m). We ground-truthed a subset of our classified plots on the recent imagery and found our airphoto-based interpretation to be consistent with what was found in the field. This was not surprising given that this was a plot-based approach wherein the contents of the entire plot were manually measured, using high resolution images.

3.3. *Land cover change metrics and land cover change analysis with respect to spatial variables*

Because we were interested in the change over time of groups of cover types having similar ecological functions, for a portion of our analysis we combined the four large and very large mixed and pure conifer types into a single class (LVL), and the shrub and hardwood tree cover types into a single class (SHW). Patterns were similar among mixed and pure conifer plots of each size class, so some general results reported are for combined classes (i.e., small mixed + small pure conifer cover types = small cover).

We created or used existing GIS coverages for a suite of ownership- and environment-related variables including those associated with topography (i.e., elevation, slope position, percent slope, topographic curvature, aspect, annual solar radiation), streams (i.e., distance to nearest stream, riparian or upslope, stream order, valley bottom), roads (i.e., distance to nearest road), ecoregion, and ownership. We used a 1993 ownership coverage as the basis for both historical and present-day ownership information, because, in our study area, changes of land ownership have occurred during this time period primarily within and not between the broad classes we examined (Azuma et al., 2002). In this analysis, we evaluated plots located

only on lands of the major ownership types in the area (FS, IP, and NIP). The total number of plots examined in this analysis, after photo quality-related and minor ownership class deletions, was 1475.

We stratified and transformed the set of explanatory variables relative to each cover type of interest and used parametric and non-parametric statistics to develop relationships between cover types and explanatory variables. We used Principal Components Analysis to evaluate correlations among the environmental variables that were related to the distribution of the LVL and SHW cover types, and then developed statistical models, using selected environmental variables that were not highly correlated. We transformed elevation using the square root transformation, to meet parametric assumptions of normality, and degrees aspect using a modified Beers transformation, $[\cosine(45\text{-aspect})] + 1$, such that the resulting aspects ranged from 0 (SW) to 2 (NE) (Beers et al., 1966). Variables considered in statistical model development were a subset of those derived from GIS coverages and included: elevation (m, sq. rt.), aspect (Beers transformation), slope (%), slope position (0 (bottom of drainage)–100 (ridgetop)), coast distance (m), stream distance (m), road distance (m), Forest Service ownership, industrial private ownership, and non-industrial private ownership. We used Wilcoxon and Kolmogorov-Smirnov tests (Conover, 1998) and Chi-square tests to detect differences between historical and recent means and distributions of LVL and SHW cover types according to environmental gradients and ownership. We used multiple logistic regression to develop models relating the historical and recent presence of LVL and SHW cover types to environmental gradients, land ownership, and road distance. To choose the best multiple logistic regression model for each response variable, we selected the model that had the lowest AIC score and a non-significant P -value in a drop-in-deviance test (Hosmer and Lemeshow, 1989).

In order to examine the variability of pathways of cover types in this landscape, we calculated metrics of land cover change including diversity and evenness of cover type transitions for plots that changed cover type. We used Shannon's diversity index (H) and Shannon's evenness index (E_H), to evaluate how transitions of 1939 cover types were distributed across the range of recent cover types. In this application, high

values for Shannon's diversity index (H) indicate high richness of transitions across recent cover types, taking relative abundance of transitions into account. High evenness (E_H) of transition pathways might indicate the lack of ecological or anthropogenic constraints on transitions. Low evenness indicates that some transitions are more dominant than others, which might be the consequence of natural or anthropogenic disturbance, as well as the biological or ecological constraints or dynamics of species groups (e.g., hardwoods, conifers). We also used the Chi-square test to determine whether the distribution of destination cover types differed from the expected distribution, with all cover types having equal transition probabilities. Although, we expected that some transitions might predominate, we were not certain what the relative transition probabilities among cover types would be, so we chose to use an even distribution for the Chi-square test to serve as a null model.

We calculated a metric, the stability ratio, to describe landscape elements that remained in or returned to the same state between 1939 and 1993: the number of plots of a given cover type that were the same historically and at recent times divided by the number of plots of that cover type historically. This metric may be most effective for evaluating the stability of the larger mixed and pure coniferous forest types because with our two-date sample it is possible that for other short-lived cover types, net change over the 54-year period could be zero but stability could be low. This is because short-lived cover types may have been disturbed several times and regrown, whereas a very large conifer patch is less likely to have been disturbed and regrown to its former stature during this period.

We also characterized the frequency of transitions from one cover type to another from historical to recent times, at two organizational levels of scale: the individual-cover-type level and the landscape level. At the individual level, we determined the likelihood of one cover type to 'transition' into any of the 14 cover types over the time period (i.e., 1:14). This allowed us to describe the typical and less common transitions for a given cover type. However, we were also interested in determining the relative frequency of occurrence of cover type transitions at the landscape level, in order to characterize dominant long-term landscape patterns of land cover change.

Therefore, we calculated the frequency of a given cover type transition relative to the frequency of all other cover type transitions (i.e., 1:196). This allowed us to characterize the dominant patterns of cover type change across the landscape. Using this combined approach of individual level and landscape level analyses, we determined both what were the typical transitions for a given cover type, and how frequently those transitions occurred in the landscape.

4. Results

4.1. Land cover characteristics

Dominant changes to land cover that occurred from the historical landscape to recent times reflected a shift from older toward younger conifer forest (Table 1; Fig. 1). Very large and large tree cover types experienced the greatest declines, becoming relatively minor landscape components. Very large cover types dropped from 10 to 2% of landscape cover. Large cover had been relatively abundant but declined from 25 to 11% of landscape cover. Hardwood cover declined somewhat (22–20% of landscape cover). Cover of medium-sized trees was high both historically and at present (22–27%). Cover of small trees increased from a negligible presence to become one of the most abundant cover types by present day (0.2–17%). Shrubs and herbs were minor and declining landscape elements (9–7% (shrubs) and 8–4% (herbs)), but bare soil increased from 1.6 to 7.5% of the landscape. The cover

of roads increased more than three-fold, from less than 1–3.5% of the landscape. Both combined cover type classes declined, LVL from 36 to 13% and SHW from 31 to 26% of landscape cover.

4.2. Relationship of cover types to land ownership and environmental gradients

The combined cover classes, large and very large mixed and pure conifer (LVL), and shrub and hardwood (SHW), changed according to land ownership. The percentage of LVL increased on Forest Service lands, decreased on industrial private lands, and stayed the same on non-industrial private lands (Fig. 2a). Conversely, SHW declined on FS lands, increased on NIP lands, and stayed about the same on IP lands (Fig. 2b). The historical distribution of LVL cover reflected the amount of land in each ownership (Fig. 2a). By recent times, the distribution of remaining LVL plots had shifted toward dominance by the FS ownership class (Fig. 2a). In the present-day landscape, LVL cover was over-represented on FS lands and under-represented on IP lands, relative to the amount of land in these two ownerships. The percent of all LVL plots that occurred on NIP lands was low historically relative to the amount of the landscape in this ownership class and did not change appreciably.

The cover types LVL and SHW were unevenly distributed across environmental gradients and these distributions changed over time. Both historically and at the recent date, LVL cover was more common at higher elevations and on steeper slopes (Fig. 3a and c).

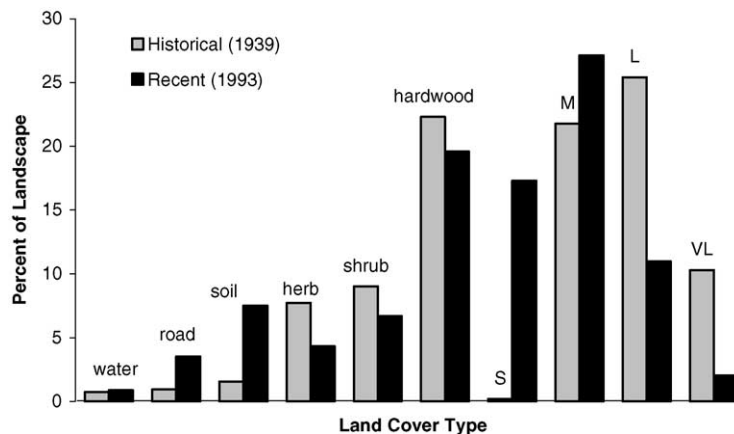


Fig. 1. Percent of land cover type in landscape, by date. S, M, L, and VL are size classes of combined mixed conifer and pure conifer cover types.

Table 1

Transition matrix for landscape change of 14 cover types in the central Oregon Coast Range from historical post-settlement to recent modern forest management times. Matrix cells contain the percent of all plots ($n = 1475$) that changed from one cover type historically (1939) to another by recent times (1993); diagonals (in bold) show the percent of all plots in the landscape that were the same cover type at each date

Recent Cover Type	Historical cover type														Recent percent of total plots in landscape
	Water	Road	Bare soil	Herb	Shrub	Hardwood tree	Small mixed conifer	Small conifer	Medium mixed conifer	Medium conifer	Large mixed conifer	Large conifer	Very large mixed conifer	Very large conifer	
Water	0.68	0.07	0	0.14	0	0	0	0	0	0	0	0	0	0	0.88
Road	0	0.41	0.07	0.47	0.27	0.47	0	0	0.20	0.41	0.68	0.20	0.27	0.07	3.53
Bare soil	0	0.07	0.14	0.41	1.42	2.03	0	0	0.54	0.54	1.15	0.75	0.20	0.27	7.53
Herb	0	0.07	0	1.90	0.68	1.02	0	0	0.14	0.14	0.20	0.14	0.07	0	4.34
Shrub	0	0	0.20	0.54	1.22	1.36	0	0	0.61	0.75	1.15	0.68	0.14	0.07	6.71
Hardwood tree	0.07	0.20	0.34	1.56	1.69	6.98	0.07	0	1.90	1.56	2.58	1.29	0.75	0.61	19.59
Small mixed conifer	0	0	0.27	0.47	0.81	2.44	0	0.07	0.81	1.83	1.29	0.81	0.88	0.61	10.31
Small conifer	0	0	0.14	0.47	0.68	2.24	0	0	0.34	0.81	1.29	0.54	0.34	0.14	6.98
Medium mixed conifer	0	0.07	0.20	1.08	1.42	2.58	0.07	0	1.36	1.36	2.03	1.63	1.15	1.02	13.97
Medium conifer	0	0.07	0.14	0.61	0.61	1.56	0	0	1.56	2.92	1.69	1.76	0.81	1.42	13.15
Large mixed conifer	0	0	0.07	0.07	0.20	1.49	0	0	0.95	1.15	2.03	0.88	0.20	0.34	7.39
Large conifer	0	0	0	0	0	0.14	0	0	0.75	1.02	0.68	0.81	0.14	0.07	3.59
Very large mixed conifer	0	0	0	0	0	0	0	0	0	0	0.75	0	0.27	0.14	1.15
Very large conifer	0	0	0	0	0	0	0	0	0.07	0.07	0.07	0.34	0	0.34	0.88
Historical percent of total plots in landscape	0.75	0.95	1.56	7.73	9.02	22.31	0.14	0.07	9.22	12.54	15.59	9.83	5.22	5.08	100

Column totals are the percent of all plots in each historical cover type class. Row totals are the percent of all plots in each recent cover type class. Mixed classes contained less than 70% coniferous cover. Row and column totals that differ from the sum of cell contents are the result of rounding.

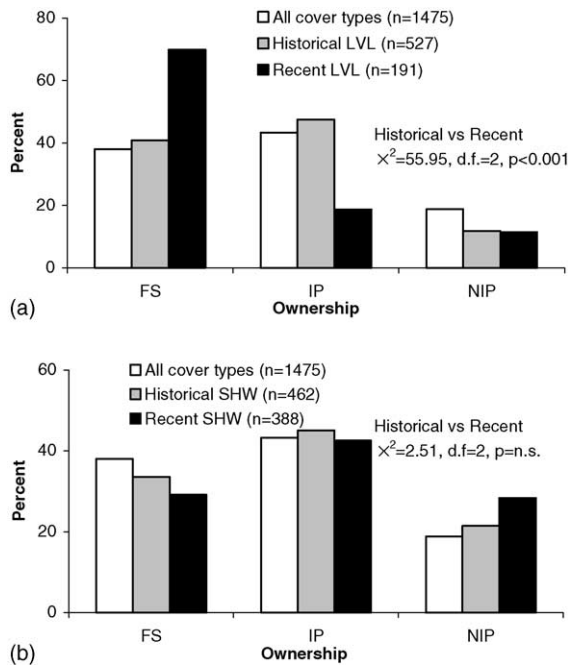


Fig. 2. Percent of total (a) large and very large conifer cover and (b) shrub and hardwood cover, in relation to land ownership class and time period. Percent distribution of ownership classes for the entire landscape (all cover types) is also shown. Percent is relative to the total amount within each class (e.g., historical LVL, etc.). Results of Chi-square tests for differences in distribution between dates are shown with each graph.

Recent LVL cover was distributed at greater distances from streams than in the early logging landscape, and it was also located at greater distances from streams and roads than the overall landscape distribution of all cover types with respect to streams and roads (Fig. 3b and d). Recent SHW cover was located on lower slope positions and closer to streams than either the historical SHW or overall landscape-related distributions of these gradients (Fig. 4).

The relative importance of environment and land use in determining the presence of LVL and SHW cover shifted for both combined cover types over time. Historically, the presence of LVL cover increased with proximity to the coast, slope steepness, elevation, and more northeasterly aspects (Table 2). By recent times, LVL presence was positively associated with forest management-related attributes: Forest Service land ownership and greater distances from roads. The best single predictor (1-variable model) for historical LVL

presence was elevation, and for recent LVL presence, Forest Service land ownership (data not shown). For sites on which LVL cover was present both historically and recently, road distance, FS land ownership, and north-easterly-tending site aspects were the most important characteristics (Table 2); FS ownership was the best single variable determining LVL continued presence (data not shown). The historical occurrence of the SHW cover type was most strongly associated with increasing road distance, higher slope positions, and lower elevations. Recent SHW occurrence was negatively related to elevation and to both Forest Service and industrial private land ownership. Sites on which SHW cover occurred both historically and at the recent date were characterized by relatively low elevations and steep slopes (Table 2). For all three SHW models (historical, recent, both), elevation was the best single predictor of SHW presence (data not shown).

4.3. Cover type transitions—individual level

The likelihood of transition from one cover type to another varied across cover types (Table 3). In general, larger cover types tended to become smaller ones. Exchanges between medium conifer and hardwood tree cover types were common.

The historical vegetation types also differed in the diversity of their transitions (Table 4). Some historical types, such as shrubs and herbs, transitioned to relatively few types while others transitioned to many types by the recent date. Each historical cover type also had an uneven distribution of destination cover types for their plots that changed cover type: for all historical cover types, the observed frequency distribution of plots was strongly different from the expected (even) distribution (Table 4; Chi-square tests, 11 d.f.). In rank order, shrub, herb, and very large conifer cover types in 1939 had the least diverse type transitions. Cover types with the most even distributions of type transitions were the large mixed conifer and large pure conifer types (Table 4).

All cover types showed high levels of change, with even the most stable cover types exhibiting change from the historical cover type as the majority tendency. Average stability for all cover types combined was very low, at 0.12. The hardwood tree, herb, and medium conifer cover types had the lowest percent

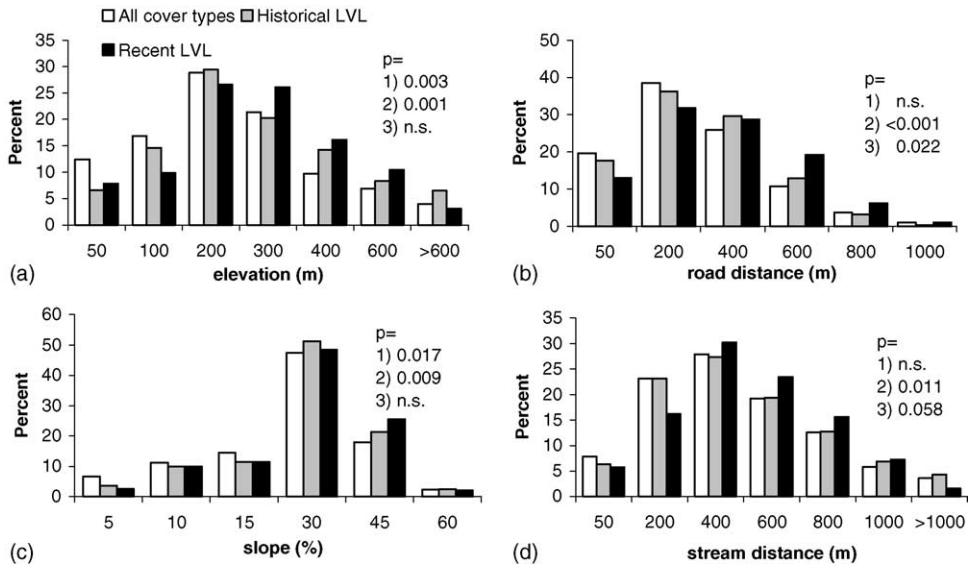


Fig. 3. Percent of total large and very large conifer cover in relation to (a) elevation, (b) road distance, (c) slope, and (d) stream distance historically and at recent times. Percent distribution of environmental classes and road distance for the entire landscape (all cover types) is also shown. Percent is relative to total amount within each class (e.g., historical LVL). Legend for all graphs is in graph a. P-values accompanying each graph are from Kolmogorov-Smirnov tests of difference between cover type distributions for (1) historical LVL vs. all; (2) recent LVL vs. all; (3) historical vs. recent LVL.

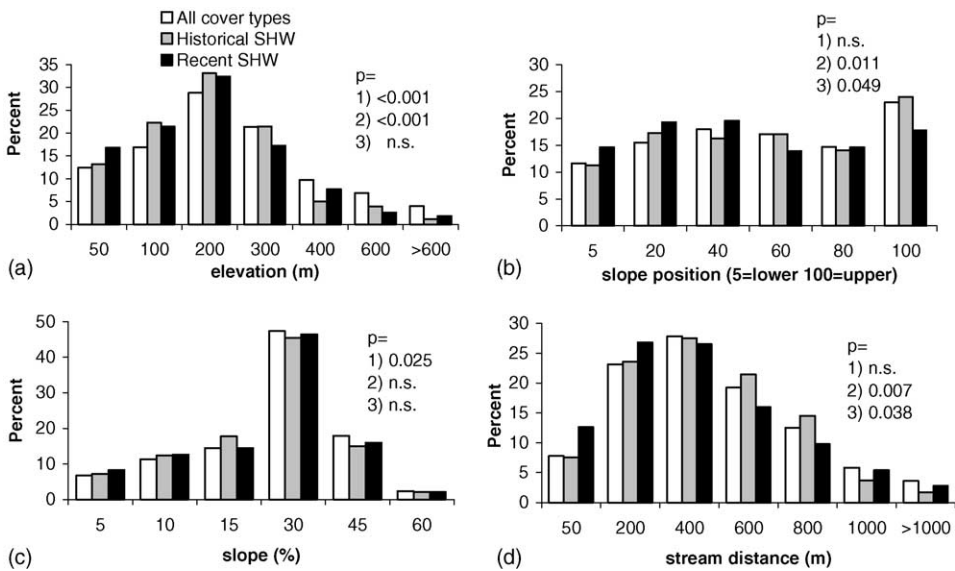


Fig. 4. Percent of total shrub and hardwood cover in relation to (a) elevation, (b) slope position, (c) slope, and (d) stream distance historically and at recent times. Percent occurrence of environmental classes for the entire landscape (all cover types) is also shown. Percent is relative to total amount within each class (e.g., historical SHW, etc.). Legend for all graphs is in graph a. P-values accompanying each graph are from Kolmogorov-Smirnov tests of difference between cover type distributions for (1) historical SHW vs. all; (2) recent SHW vs. all; (3) historical vs. recent SHW.

Table 2
Multiple logistic regression models of factors affecting the presence of historical (1939) and recent (1993) cover types

Cover type	Predictor variable	Parameter estimate	Standard error	Wald's χ^2	P-value
Historical LVL	Intercept	-1.5994	0.1893	71.37	<0.0001
	Slope (%)	0.0147	0.0057	6.73	0.0095
	Coast distance (km)	-2.85E-05	8.331E-06	11.68	0.0006
	Slope position	-0.0029	0.0019	2.30	0.1297
	Aspect (Beers tr.)	0.1933	0.0794	5.93	0.0149
	Elevation (sq. rt.)	0.0808	0.0128	40.01	<0.0001
Recent LVL	Intercept	-2.6141	0.2327	126.24	<0.0001
	Forest Service ownership	1.1948	0.2468	23.43	<0.0001
	Industrial Private ownership	-0.4011	0.2814	2.03	0.1540
	Road distance (m)	0.0010	0.0004	6.44	0.0112
LVL both historically and recently	Intercept	-3.3612	0.3226	108.55	<0.0001
	Road distance (m)	0.0008	0.0005	3.03	0.0819
	Aspect (Beers tr.)	0.3100	0.1488	4.34	0.0372
	Forest Service ownership	0.8632	0.3083	7.84	0.0051
	Industrial Private ownership	-0.5495	0.3574	2.36	0.1241
Historical SHW	Intercept	-0.1356	0.1602	0.72	0.3971
	Road distance (m)	0.0006	0.0003	4.63	0.0315
	Slope position	0.0058	0.0019	8.82	0.0030
	Elevation (sq. rt.)	-0.0822	0.0123	44.62	0.0001
Recent SHW	Intercept	-0.0957	0.1818	0.28	0.5987
	Forest Service ownership	-0.5620	0.1941	8.38	0.0038
	Industrial Private ownership	-0.3931	0.1666	5.57	0.0183
	Elevation (sq. rt.)	-0.0438	0.0138	10.03	0.0015
	Stream distance (m)	-0.0004	0.0002	3.10	0.0785
	Aspect (Beers tr.)	0.1551	0.0861	3.25	0.0715
SHW both historically and recently	Intercept	-1.1856	0.2199	29.07	<0.0001
	Slope (%)	0.0161	0.0083	3.75	0.0527
	Elevation (sq. rt.)	-0.0979	0.0195	25.29	<0.0001

The table lists the statistical significances of the predictor variables. In all analyses, model with lowest AIC value was selected; d.f. = 1 in all cases. For models with ownership variables, non-industrial private ownership is represented by setting both Forest Service and industrial private ownership predictor variables to 0. The fit of each model is significant at $P < 0.0001$.

change from historical to recent times (Fig. 5). The very large mixed and large and very large pure conifer types were the least stable vegetation types. The stability of small mixed and pure conifer cover types was extremely low; this was because there were so few small mixed or pure conifer plots historically relative to the early 1990s number. The SHW combined class was relatively stable, with a ratio of 0.36. By contrast, the LVL combined class had much higher rates of change, with a ratio of 0.20.

4.4. Cover type transitions—landscape level

At the landscape level, the central Coast Range landscape transitioned from late successional types to

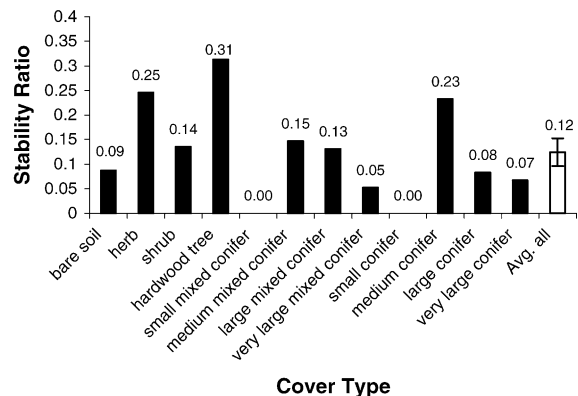


Fig. 5. Stability ratio of cover types. Ratio is proportion of historical (1939) plots that was the same cover type in 1993.

Table 3

Cover type transitions from the historical (1939) to the recent (1993) landscape as percent of total plots within each historical cover type class. Historical n = number of plots in the given historical cover type class

Recent cover type	Historical cover type													
	Water	Road	Bare soil	Herb	Shrub	Hardwood tree	Small mixed conifer	Small conifer	Medium mixed conifer	Medium conifer	Large mixed conifer	Large conifer	Very large mixed conifer	Very large conifer
	Historical n													
	11	14	23	114	133	329	2	1	136	185	230	145	77	75
Water	90.91	7.14	0	1.75	0	0	0	0	0	0	0	0	0	0
Road	0	42.86	4.35	6.14	3.01	2.13	0	0	2.21	3.24	4.35	2.07	5.19	1.33
Bare soil	0	7.14	8.70	5.26	15.79	9.12	0	0	5.88	4.32	7.39	7.59	3.90	5.33
Herb	0	7.14	0	24.56	7.52	4.56	0	0	1.47	1.08	1.30	1.38	1.30	0
Shrub	0	0	13.04	7.02	13.53	6.08	0	0	6.62	5.95	7.39	6.90	2.60	1.33
Hardwood tree	9.09	21.43	21.74	20.18	18.80	31.31	50.00	0	20.59	12.43	16.52	13.10	14.29	12.00
Small mixed conifer	0	0	17.39	6.14	9.02	10.94	0	100.00	8.82	14.59	8.26	8.28	16.88	12.00
Small conifer	0	0	8.70	6.14	7.52	10.03	0	0	3.68	6.49	8.26	5.52	6.49	2.67
Medium mixed conifer	0	7.14	13.04	14.04	15.79	11.55	50.00	0	14.71	10.81	13.04	16.55	22.08	20.00
Medium conifer	0	7.14	8.70	7.89	6.77	6.99	0	0	16.91	23.24	10.87	17.93	15.58	28.00
Large mixed conifer	0	0	4.35	0.88	2.26	6.69	0	0	10.29	9.19	13.04	8.97	3.90	6.67
Large conifer	0	0	0	0	0	0.61	0	0	8.09	8.11	4.35	8.28	2.60	1.33
Very large mixed conifer	0	0	0	0	0	0	0	0	0	0.00	4.78	0	5.19	2.67
Very large conifer	0	0	0	0	0	0	0	0	0.74	0.54	0.43	3.45	0	6.67
Historical percent of total	100	100	100	100	100	100	100	100	100	100	100	100	100	100

Column totals that differ from the sum of cell contents are the result of rounding.

Table 4
Shannon's diversity index (H), Shannon's evenness index (E_H), and Chi-square statistics of cover type transitions for major^a historical (1939) cover types, for plots that changed cover type

Historical cover type	H	E_H^b	χ^2
Herb	1.67	0.139	115.55*
Shrub	1.63	0.136	89.04*
Hardwood tree	1.80	0.150	59.40*
Medium mixed conifer	1.85	0.154	83.16*
Medium conifer	1.92	0.160	62.59*
Large mixed conifer	1.97	0.164	49.58*
Large conifer	1.92	0.160	59.05*
Very large mixed conifer	1.85	0.154	95.34*
Very large conifer	1.74	0.145	121.55*

^a Bare soil, small mixed conifer, and small conifer comprised fewer than 2% of all plots in 1939 and were therefore not considered to be major historical (1939) cover types.

^b Higher numbers indicate more even distribution of recent (1993) cover types.

* P -value < 0.005.

earlier successional types (Table 1). One major change of this kind was the shift from historically common large and very large cover types to medium cover

types (11.5% of the landscape). These larger cover types also transitioned to small cover types, but at lower landscape level frequencies (5.8% of the landscape). With the inclusion of hardwoods and medium-sized cover along with the larger cover types as source cover types, the transition to the small cover types from later successional types was relatively common (12.4% of the landscape). The large increase in roads in this landscape stemmed primarily from losses of the large mixed conifer, hardwood tree, and herbaceous cover types (Table 1).

The cover types most likely to transition to larger forest were the medium-sized cover types, with 17% of their plots becoming large cover types. Nonetheless, this was just 3.9% of the landscape's transitions, and thus, a negligible portion of cover type transitions overall (Table 1). Hardwoods also succeeded to large cover types, but at even lower rates (Table 1).

Landscape level transitional pathways between cover types were distributed among many types and no single transitional pathway was dominant (Fig. 6). Only fourteen out of the 64 possible vegetation-to-

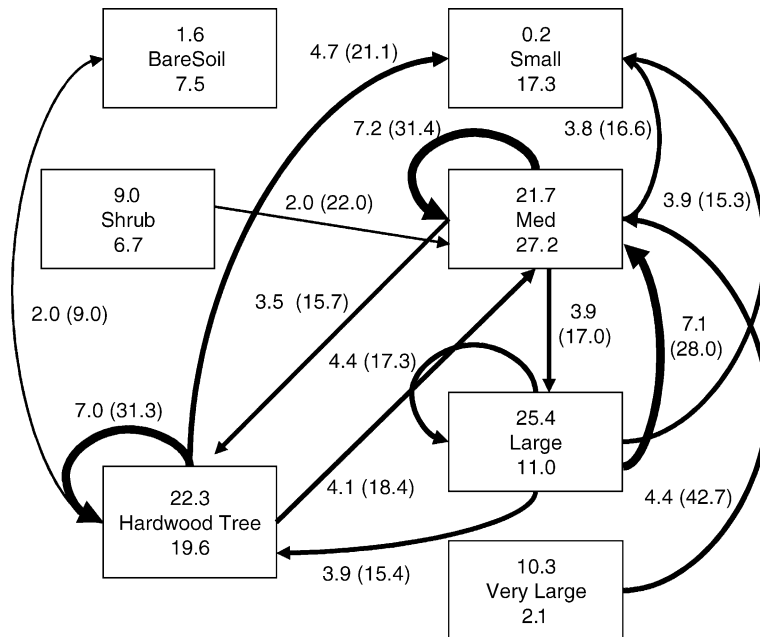


Fig. 6. Major landscape pathways from the early logging landscape (1939) to the recent modern forest management period (1993). All transitional pathways with >2.0% of all landscape plots ($n = 1475$) are shown (shown $n = 913$; 62% of all plots). Arrow thickness is proportional to relative occurrence of pathway, and numbers with arrows are percent of all plots that followed that pathway and, in parentheses, the percent of the source cover type that followed that pathway. Numbers above and below cover types in boxes are, respectively, historical (1939) and recent (1993) total percentages of the landscape in that cover type.

vegetation transitional pathway types contained greater than 2% each of the plots sampled, even after mixed and pure conifer classes for each size class were combined. Sixty-two percent of the plots followed these 14 transitional pathways. The maximum for any trajectory was 7.2% of all plots. Surprisingly, the two most common ‘transition’ types were no-change types, for hardwoods and medium-sized mixed and pure coniferous cover types. The greatest decline, of large mixed and pure conifers, followed three major pathways, to medium mixed and pure conifers (7.1% of landscape plots), to small mixed and pure conifers (3.9%), and to hardwoods (3.9%). The greatest increases, of small mixed and pure conifers and of bare soil, originated from diverse cover types (Fig. 6; Table 1).

5. Discussion

Vegetation cover of the Coast Range landscape was very dynamic between post-settlement historical and recent times. The landscape transitioned from one with an abundance of large and very large conifers, medium-sized conifers and hardwoods, to one in which small- and medium-sized conifers and hardwoods predominated. Transitions among cover types over the 54-year period were multidirectional: no single transition type prevailed. The occurrence of major cover types in the early 1990s landscape was strongly associated with forest management differences, as reflected by patterns of land ownership.

5.1. Declines in large conifers

Declines in large and very large conifers from the historical landscape resulted primarily from timber production in the study area over the last several decades (Garman et al., 1999), as indicated by the replacement of large conifers by managed stands of small-to-medium-sized conifers by present day. Fire and other landscape-level natural disturbances were not common in this area between 1939 and 1993 (Impara, 1997) and therefore, were not responsible for these transitions. The occurrence of large and very large conifers at the recent date primarily on Forest Service lands can be accounted for by differences in land use histories on public and private ownerships

that affected the timing and rates of harvesting. On private lands, harvesting began in the late 1800s with the selective harvest of the largest trees, increased quickly in the early 1940s, and peaked in the 1950s (Azuma et al., 2002). On federal lands, timber harvest began more recently, in the late 1940s, increased gradually, and reached its maximum rate in the 1970s (Garman et al., 1999).

The declines, we found in older coniferous forest in the Coast Range (36 to 13%), are similar to findings of Wimberly and Ohmann (in press), who found that large conifer forests declined from 42 to 18% of the landscape in a study in the Coast Range based on a 1936 historical forest type map and 1996 satellite imagery. Bolsinger and Waddell (Bolsinger and Waddell, 1993) estimated that from the time period between 1933–45 and the early 1980s–1992, old-growth forest area in Oregon declined from 53.2 to 20.5% of productive forest land. Ripple et al. (2000) used 1949 forest type maps and 1988–1991 aerial photography and found a decline in older forest from 63 to 44% of the landscape in the central Coast Range, but said the latter amount was probably inflated because the landscapes they selected were located predominantly on public lands. It is also possible that the higher amount of large conifer forests found by others is in part an artifact of the minimum mapping size of those studies, which would tend to homogenize small areas of younger forest within larger patches of older conifer forest. Our results for the central Coast Range for recent land cover with respect to ownership are somewhat consistent with the findings of Turner et al. (1996) who found that from 1975–1991 in two river basins in the Olympic Peninsula of Washington, coniferous forest cover was predominately found on public lands and deciduous/mixed forest cover was declining throughout much of the landscape. However, in one basin in Washington, unvegetated cover was increasing dramatically on private lands; we saw relatively moderate increases in bare soil in the central Coast Range of Oregon.

Previous studies that did not rely on fine-grained aerial photography were not able to distinguish between large and very large conifers. Our results indicate that very large conifers have declined at a rate that is much higher than that of large conifers, from 10 to 2% of land cover versus from 25 to 11%, respectively. Using aerial photographs we were able to

characterize individual legacy trees (trees that were very large conifers at both dates) and small patches of large trees.

5.2. Dynamism of hardwoods and shrubs

No comparable studies have reported hardwood or shrub dynamics in this area. Although, we found that these two cover types declined somewhat in abundance, both are very competitive after disturbance and their apparent continued relative abundance may have resulted from within-time-period disturbance-related dynamics not captured by this study. Since no fires of significant size occurred in this area during the study period (Impara, 1997), shrubs and hardwoods were most likely maintained primarily by logging, which set back succession and enabled shrub and hardwood establishment, and secondarily by storm-related events (Ruth and Yoder, 1953; Orr, 1963; Strome, 1986), such as floods, windthrow, and landslides. Early logging probably favored hardwoods and shrubs because it created high amounts of soil disturbance and relied on natural regeneration (Hibbs et al., 1994; Garman et al., 1999). More recent intensive forest management includes site preparation, conifer planting, and broadleaf herbicide application, favoring conifer establishment (Lettman and Cannon, 1998).

Shifts in the combined shrub and hardwood cover type toward streams likely reflects both the higher intensity of forest management by industrial owners in upland environments, and the lower intensity of forest management by non-industrial owners whose lands tend to be located along larger streams (Alig et al., 2000). The greater declines in shrubs compared to hardwoods probably resulted from a combination two factors: (1) succession of shrubs to other cover types, including hardwoods and (2) the tendency for hardwood trees, and in particular red alder, to establish along logging roads, which themselves increased substantially.

5.3. Increases in small conifers and roads

Steep increases in small conifers reflected management trends of increased rates of harvesting large conifers and planting young conifers across all ownerships. The virtual absence of small conifers on the landscape of 1939 is probably because (1) logged

areas were not planted in the early 20th century and/or (2) small conifers were not visible using our detection methods because they were overtopped by hardwoods that regenerated after fires and logging prior to 1939.

Generally, increases in small conifer forest that we observed are consistent with prior studies that used aggregated size classes (Cohen et al., 2002). However, the distinction in our study between small versus medium coniferous types illustrates the dramatic increase in small coniferous cover from negligible amounts, as compared to the only moderate increase and relative stability of medium conifer cover. We found that the landscape has shifted to one in which the smallest size class of conifers not only exceeds the prior amount of the largest conifer size class, but also rivals the prior amount of medium conifer forest in a landscape established under a regime dominated by natural disturbance. The harvesting systems typically used in intensive management that allow medium-sized conifers to be cut (40–60-year rotations on private lands; 70–80-year rotations on federal lands) (Garman et al., 1999) account for small conifer cover increasing partly via harvesting medium conifer cover.

The area of roads increased dramatically to provide a transportation network for logging. In a study on the southern Rocky Mountains, a three-fold increase in roads from 1950–1993 had a greater impact on landscape structure than logging (McGarigal et al., 2001). We are not aware of any other studies in the Pacific Northwest region that document changes in cover of roads. Roads have increased throughout forested areas in many parts of the world, in association with human settlement and land conversion to non-forest uses (Guild et al., 2004), and have effects on biodiversity and ecological processes (Haskell, 2000; Trombulak and Frissell, 2000; Forman et al., 2002). In the Coast Range, most of the historically forested area has remained in forest use (Azuma et al., 2002), even with the introduction of roads.

5.4. Ownership-related patterns

Our research corroborates prior work indicating that ownership-related disturbance is an important variable structuring landscape dynamics (Mladenoff et al., 1993; Spies et al., 1994; Turner et al., 1996; Burgi and Turner, 2002; Cohen et al., 2002). At the

landscape level, the LVL and SHW grouped cover types became more concentrated with federal and NIP ownerships, respectively. This reflected differences in the timing and types of management practiced by public and private ownerships and is consistent with prior research in the Coast Range (Alig et al., 2000; Stanfield et al., 2002). Reasons for concentration probably include: (1) removal of LVL on industrial private lands, (2) slower or later-starting removal of LVL on federal lands, (3) reforestation practices and logging reducing SHW on industrial private lands, (4) more partial cutting on non-industrial private lands allowing for more SHW, and (5) non-industrial private ownership location near streams where SHW are competitive.

The relative influence of disturbance and environmental heterogeneity on the distribution of LVL and SHW cover has changed in this area from the early logging landscape to the recent modern forest management period. Historically, environmental heterogeneity played a more important role in the prediction of forest landscape cover. In the modern forest management period, recent disturbance history, as represented by ownership and road construction, had a greater influence on forest landscape cover. The importance of recent disturbance history to present-day vegetation patterns has been noted in other research (Wimberly and Spies, 2001; Ohmann and Gregory, 2002), but, to our knowledge, the shift over time in the relative importance of environmental gradients and disturbance indicators to vegetation patterns has not previously been quantified.

5.5. Cover type transitions

Our findings regarding cover type transitions, which incorporated analyses at the levels of the individual cover type and the landscape, illustrate both the likelihood of change for diverse cover types and the landscape representation of these transitions. By using a multi-scale perspective that combined evaluating individual cover type transition probabilities and landscape patterns of land cover change, we were able to examine the complexity of individual pathways within a landscape context (e.g., Fig. 6). For example, whereas 17.0% of medium conifer cover types became large conifer types during the study period, this was a

minor transition type at the landscape level, comprising only 3.9% of landscape level transitions.

Our results should be considered within the temporal limitations of the data used in this study. Our study sampled aerial photographs from two dates 54 years apart. This limited our ability to detect (1) multiple transitions occurring within this time period and (2) transitions whose natural residence time is longer than 54 years. Consequently, we underestimate the dynamics of this landscape. Given these limitations, we can still draw several conclusions: (1) between 1939 and 1993 change occurred across all cover types, and was multidirectional; (2) timber production that targeted large conifers and post-fire succession were opposing influences, but timber harvest, followed by the planting of conifers, was the dominant influence; (3) a minority of plots succeeded to large and very large coniferous types, as some areas, especially on federal forests, were not cut; (4) succession to conifers most likely occurred where isolated conifers were located in a hardwood matrix or in riparian areas; and (5) increases in roads were not specific to a historical cover type and the road network expanded across all areas of the landscape.

We expected that the large conifer type and the very large conifer type would have similar patterns of evenness of cover type transitions because both were intensively logged, but the large conifer type was the least constrained in terms of the diversity of transitional pathways they followed, and the very large conifer type was among the most constrained. This difference probably occurred because of the logging history of the area. The largest conifer trees were harvested first (Strome, 1986; Garman et al., 1999) and these stands naturally developed into medium-sized coniferous forest by the 1990s. Stands of large conifer trees were typically logged more recently, after the largest trees, and so fewer of these stands would reach the medium-size class. In addition, cover type transitions for the very large conifers might have lower evenness because they can only move into smaller classes.

The low average stability of cover types indicates the landscape was dynamic and change was widespread across cover types. Even the most stable cover types in this landscape (hardwood trees and herbs) had low absolute stability. Shrubs and hardwoods can be

alternate stable vegetation states on some individual sites (Tappeiner et al., 1991), but our results indicate that this process was uncommon at broader spatial and temporal scales. The least change of hardwood trees and herbs (which included meadows and grassy areas) tended to occur in valleys where agriculture (Azuma et al., 2002) and larger streams would promote the occurrence of these cover types (Harrington, 1987; Harrington, 1990; Kennedy and Spies, in press). The lack of increase in hardwoods found in this study can be attributed at least in part to intensive management-related inhibition of hardwood tree growth and establishment following harvest and reforestation with conifers. However, the fact that conifer cover types showed similar transitional tendencies toward other cover types across all conifer size classes, regardless of whether the plots were mixed or pure conifer, indicates that the presence of hardwoods and shrubs in mixed conifer plots may not have much effect in the long-term trajectories of these cover types.

5.6. Ecological consequences and management implications

Our results have several implications for forest management and biodiversity conservation. The loss of large and very large conifers eliminated habitat at multiple scales, including whole stands of old-growth forest and individual trees that can provide refugia in early successional landscapes. Large old tree refugia are biological legacies that may stabilize food webs and provide refuge for some species (Neitlich and McCune, 1997; Perry and Amaranthus, 1997; Hazell and Gustafsson, 1999). Large old trees also provide residual older forest structure when retained in managed forests (Franklin et al., 1997). In highly dynamic landscapes such as this, species with slow dispersal and recolonization potential (e.g., western hemlock (*T. heterophylla*), Pacific yew (*Taxus brevifolia*), and the epiphytic lichen *Lobaria oregana*) will be reduced. Increases in roads, such as those we observed, may affect stream quality and wildlife and fish habitat because roads may be closely linked to the hydrologic flows of the stream network and thereby influence a large area of the landscape (Wemple et al., 1996; Jones et al., 2000), and may increase fragmentation of intact patches. The increased distance between patches of older forest types, the losses of older trees that serve as

biological legacies, and the landscape-wide shift to younger forest conditions are likely to reduce the habitat quality of numerous wildlife species, such as the red tree vole (*Arborimus longicaudus*), fisher (*Martes pennanti*), American marten (*Martes americana*), pileated woodpecker (*Dryocopus pileatus*), and marbled murrelet (*Brachyramphus marmoratus*) (Csuti et al., 1997).

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