HISTORICAL RANGE OF VARIABILITY IN LANDSCAPE STRUCTURE: A SIMULATION STUDY IN OREGON, USA

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Abstract. We estimated the historical range of variability (HRV) of forest landscape structure under natural disturbance regimes at the scale of a physiographic province (Oregon Coast Range, 2 million ha) and evaluated the similarity to HRV of current and future landscapes under alternative management scenarios. We used a stochastic fire simulation model to simulate presettlement landscapes and quantified the HRV of landscape structure using multivariate analysis of landscape metrics. We examined two alternative policy scenarios simulated by two spatially explicit simulation models: (1) current management policies for 100 years into the future and (2) the wildfire scenario with no active management until it reached the HRV.

The simulation results indicated that historical landscapes of the province were dynamic, composed of patches of various sizes and age classes ranging from 0 to >800 years including numerous, small, unburned forest islands. The current landscape was outside the HRV. The landscape did not return to the HRV in the 100 years under either scenario, largely because of lack of old-growth forests and the abundance of young forests. Under the current policy scenario, development of landscape structure was limited by the spatial arrangement of different ownerships and the highly contrasting management regimes among ownerships. As a result, the vegetation pattern after 100 years reflected the ownership pattern. Surprisingly, the wildfire scenario initially moved the landscape away from the HRV during the first 100 years, after which it moved toward the HRV, but it required many more centuries to reach it. Extensive forest management and human-caused fires in the 20th century have left legacies on the landscape that could take centuries to be obliterated by wildfire.

Departure from the HRV can serve as an indicator of landscape conditions, but results depend on scale and quantification of landscape heterogeneity. The direct application of the concept of HRV to forest policy and management in large landscapes is often limited since not all ownerships may have ecological goals and future climate change is anticipated. Natural disturbance-based management at large scales would not show the projected effects on landscape structure within a typical policy time frame in highly managed landscapes.

Key words: disturbance; fire; forest management; historical range of variability (HRV); landscape dynamics; landscape metrics; presettlement; principal component analysis; Oregon Coast Range; scenario; stochastic simulation model.

INTRODUCTION

Landscape assessments require reference conditions, but objectively defined references are difficult to obtain. The historical range of variability (HRV) in forest landscape structure created by natural disturbances has been proposed as a guide for biodiversity conservation in the past decade (e.g., Morgan et al. 1994, Montreal Process Working Group 1998, Aplet and Keeton 1999, Landres et al. 1999). Despite the attention and theoretical appeal, studies that rigorously quantify HRV are limited (but see Cissel et al. 1999, Tinker et al. 2003, Wimberly et al. 2004).

Much has been learned about the application of HRV in forest management from studies in the Pacific Northwest (Cissel et al. 1999, Wimberly et al. 2000, Agee 2003). Wimberly (2002) and Wimberly et al. (2004) investigated the HRV in landscape structure for the 2 million ha Oregon Coast Range province and concluded that old-growth forest (>200 years) was the dominant forest type prior to Euro-American settlement, occupying at least 40% of the landscape on average. Wimberly et al. (2004) found that the current landscape is outside the HRV for major seral stages ranging from young to old growth, and for basic spatial patterns such as mean patch size and edge density. The amount of old-growth forest has been considerably reduced and fragmented, while the area of young forest has strongly increased and now comprises the matrix of the landscape. However, previous HRV studies in the province have not examined the full diversity of stand development, especially young, open-canopy (<20 years)
and very old stages (>450 years). These extreme ends of the distribution of stand development provide distinctive habitats, but their landscape dynamics have not been characterized by using simulation models.

We are aware of only a few studies from other parts of North America or the world that quantitatively analyzed the variability of historical landscape structure. Tinker et al. (2003) quantified the HRV of landscape structure of Yellowstone National Park for the last 300 years by using six major landscape metrics. They compared the pre- and post-harvest landscapes of an adjacent national forest and concluded that 30 years of clearcutting moved the landscape outside the HRV of the Yellowstone landscape. Other studies used fire-simulation models and landscape metrics to estimate the HRV for landscapes in the southern Rocky Mountains (Roworth 2001) and in northern Idaho and nearby areas in Washington and Montana (Keane et al. 2002) but did not compare the current conditions with the HRV. The concept of HRV, however, has been discussed for the potentials for providing reference conditions for management in other regions, including boreal forests in Fennoscandia (Kuuluvainen 2002, Kuuluvainen et al. 2002) and Canada (Andison and Marshall 1999, Bergeron et al. 1999, 2002), mixed forests in Minnesota (Baker 1989, 1992) and Wisconsin (Mladenoff et al. 1993, Bolliger et al. 2004), and diverse landscapes in the southwestern USA (Swetnam et al. 1999).

Several studies have used HRV to evaluate alternative future management scenarios (Wallin et al. 1996, Andison and Marshall 1999, Hemstrom et al. 2001, Swanson et al. 2003). Andison and Marshall (1999) compared landscape compositions in British Columbia, Canada, under four management scenarios against those under the natural fire regime and demonstrated that resultant managed landscapes would stay within the HRV but with much reduced temporal variability. Wallin et al. (1996) examined how alternative management scenarios differed in their potentials to return relatively small landscapes to the HRV of the central Oregon Cascade Range. Hemstrom et al. (2001) assessed “landscape health” of the historical landscape and that of three alternative management scenarios in the interior Columbia River Basin based on the amount of land within the major forest types. The latter two studies found that some management approaches can bring landscapes back toward HRV. No studies, however, have examined how current and alternative future policies would change large multi-ownership landscapes relative to HRV.

Previous work on HRV has also been limited to examination of only a small number of landscape metrics. Numerous landscape metrics are available, and many of them are known to be correlated (Riitters et al. 1995, Gustafson 1998, Hargis et al. 1998). Estimates of variability in landscape structure are sensitive to classifications and the type of metrics used (Keane et al. 2002). Also, sensitivity to landscape change differs among metrics (Baker 1992). Complex landscape structure and changes are more likely to be captured by collectively using multiple metrics (Li and Reynolds 1994, O’Neill et al. 1996).

The main objective of this study was to evaluate the use of the HRV approach for assessing the effects of forest management in a large, province-scale landscape. We studied the Oregon Coast Range because we had a good foundation of ecological studies and simulation models upon which to advance our knowledge of HRV and its relevance to forest management (Wimberly et al. 2000, Spies et al. 2002a). Although the study area is defined as a physiographic province, we considered it a “landscape” in the sense that it is a heterogeneous area in which the spatial pattern of vegetation is affected by a distinctive pattern of topography, fire, and management activities (Turner et al. 2001). Throughout this paper, when the term “landscape” is used for the Oregon Coast Range, it refers to the entire extent of the province. We defined HRV in this study as the variability in the amount and spatial characteristics of forests of various ages under the pre-settlement fire regime. The specific objectives of this study were to (1) establish the HRV of landscape structure using a wide array of age classes and landscape metrics, (2) compare the current landscape condition with the HRV, and (3) evaluate the similarity of alternative future landscapes to HRV.

**Methods**

**Study area**

The Oregon Coast Range is a 2 million-ha physiographic province in Oregon, USA (Fig. 1). The climate is characterized by mild, wet winters and dry, cool summers and affected by the Pacific Ocean to the west (Franklin and Dyrness 1988). As a result of the orographic effects, the western half of the region has a moister climate than the eastern half. The topography is characterized by highly dissected mountains, steep slopes, and a high density of streams. The soils are deep to moderately deep and fine to medium texture, derived from sandstone, shale, or basalt (Franklin and Dyrness 1988). Two major vegetation types are the Picea sitchensis (Sitka spruce) zone and Tsuga heterophylla (western hemlock) zone, juxtaposed with Willamette Valley foothills along the eastern margin (Franklin and Dyrness 1988). The forests are dominated by relatively few species and are highly productive. The modern vegetation composition started to form about 5000 years ago (Whitlock 1992, Worona and Whitlock 1995). Forest less than 80 years in age currently occupies the majority of the landscape, and large old conifer forests are rare (Ohmann and Gregory 2002). About 27% of the landscape has been clearcut at least once in the last 30 years (Cohen et al. 2002).

**Disturbance regimes**

Large-scale wildfire is the most important disturbance that has shaped forests of the Oregon Coast
Range (Agee 1993, Impara 1997). The fire regime was relatively stable for the 1000 years prior to Euro-American settlement (Long et al. 1998). In this presettlement time, the estimated mean fire-return interval ranged from 150 to 350 years for high-severity fires in this landscape (Agee 1993, Ripple 1994, Long and Whitlock 2002). Moderate-severity fires occurred often in mixture with high-severity fires (Impara 1997). High-severity fires often led to stand replacement, while moderate-severity fires left unburned forest patches and single trees (Agee 1993, Impara 1997), which influenced subsequent stand development (Goslin 1997, Weisberg 2004). Fires were set by Native Americans in the coastal valleys and adjacent Willamette Valley for agriculture and hunting (Boyd 1999); some of these fires may have occasionally burned into the coastal foothills, but the evidence for this is not strong (Agee 1993, Whitlock and Knox 2002). The landscape experienced more extensive fires following Euro-American settlement in the mid-1800s (Impara 1997, Weisberg and Swanson 2003), and high-severity fires were prevalent from the mid-1800s to the mid-1900s (Morris 1934, Arst 1983). Effective fire suppression efforts began in the 1940s in western Oregon (Weisberg and Swanson 2003).

In the Pacific Northwest, extensive logging has occurred on private lands, starting during the first half of the 1900s and continuing up to the present. Dispersed patch cutting or a checkerboard pattern of clearcutting (30–50 acres per patch) began after the mid-1940s on the federal lands and was common until the early 1990s (Franklin and Forman 1987, Swanson and Franklin 1992). The prevalence of dispersed patch cutting altered the landscape structure by increasing edge and decreasing interior forest habitat in Pacific Northwest forests (Franklin and Forman 1987). Since the implementation of the Northwest Forest Plan (FEMAT 1993) in the early 1990s, timber harvest on federal lands has nearly ceased. Clearcuts are still common on private lands, but they now must be less than 48 ha in size on state and private forest lands.

The Oregon Coast Range is a mosaic of five major land ownership types: U.S. Department of Agriculture Forest Service (USFS), U.S. Department of Interior Bureau of Land Management (BLM), the State of Oregon, private industrial, and private nonindustrial (Fig. 1). The two federal agencies (USFS and BLM) collectively manage about 21% of the study area (ownership proportion values are based on data from the Coastal Landscape Analysis and Modeling Study [available online]) and operate under the Northwest Forest Plan (USDA and USDI 1994). Current management goals on the federal lands emphasize the protection of late-successional forest and aquatic habitat. Consequently, most of these lands are in late-successional and riparian reserves where timber production is prohibited except through thinning aimed at promoting late-successional habitat structure in <80-year-old stands (USDA and USDI 1994). In matrix land, where most of timber harvesting occurs, relatively long rotations (~80 years) with green-tree and deadwood retentions are used (USDA and USDI 1994).

The State of Oregon lands, about 10% of the province, are managed under specific forest plans (Oregon Department of Forestry 2001). For example, the forest plan developed for the state forests in northwestern Oregon aims at maintaining diversity in forest stand structure and landscape structure (Bordelon et al. 2000). Management goals are to sustain healthy forests, produce abundant timber, and maintain productivity, fish and wildlife habitat, air and water quality, and other forest uses.

Private industrial landowners control ~33% of the region, and private nonindustrial landowners own the remaining 36%. Both types of private landowners also comply with the Oregon Forest Practices Act. Timber production is the highest priority of management on private industrial lands, and the protection of environment for fish and wildlife required by the act may constrain the actions of management on these lands. Private industrial landowners often use clearcutting and

Fig. 1. Distribution of land ownership in the Oregon Coast Range Province and location of the province in the region.
timber rotations of 40–50 years. Private nonindustrial landowners have diverse management objectives but commonly manage their lands for timber. However, they use partial cutting and somewhat longer rotations than industrial owners (Lettman and Campbell 1997).

The locations of large tracts of federal and state lands (Fig. 1) reflect the patterns of large fires in the mid-1800s and early to mid-1900s in the western and central parts of the Coast Range (Teensma et al. 1991). In addition, the BLM manages sections that alternate with private lands in a checkerboard pattern, reflecting historical land management policies by the U.S. government (Fig. 1).

Model simulations

Historical landscapes.—Historical landscapes were simulated by using the Landscape Age-Class Dynamics Simulator (LADS), version 3.1 (Wimberly 2002). LADS is a spatially explicit, stochastic cellular-automata model designed to simulate forest landscape dynamics under fire regimes specified by the user. We applied this model to ask how forest age composition and spatial pattern in the Oregon Coast Range landscape varied historically. We constructed the HRV of those characteristics from the Monte Carlo simulations in LADS. Large-scale fire was historically the key process driving the landscape dynamics of the province, and time since fire is a good descriptor for characterizing general stand structure of the forests (Franklin et al. 2002). LADS simulates fire patterns based on the probabilities of fire ignition, spread, and extinction, which vary with topography and fuel accumulation inferred from time since fire. LADS does not simulate the physical processes of fire. Efficiency in computation simulating over a large landscape was achieved by using a coarse-grained representation of the landscape, which also reduced the number of input parameters. Therefore, fine-scale heterogeneity such as canopy gaps and fire breaks cannot be inferred from the model outputs. The simulation requires quantitative data on the fire regime, natural fire rotation, size and shape distributions of burned patches, and the effects of slope position, vegetation age, and wind on the direction and probabilities of fire ignition and spread. Wimberly (2002) estimated these parameters from dendrochronological data collected in the central part of the province (Impara 1997) aided by paleoecological data from lake sediment cores (Long et al. 1998).

The landscape of the Oregon Coast Range was represented in LADS as a grid of 9-ha cells (300 × 300 m). LADS was parameterized to the historical fire regimes prior to Euro-American settlement around the mid-1800s (Wimberly 2002). Fire frequency, severity, and size were modeled as random variables drawn from appropriate probability distributions estimated from data in order to reflect variability in fire and uncertainty in the data. The probabilities of fire ignition in randomly selected initiation cells and spread of fire from adjacent cells increased with elevation and elevation and that fuel loads are high in early- and late-successional stages (Agee and Huff 1987). Shapes of fire were calibrated to match the boundaries of fire events depicted on historical fire maps and satellite imageries. The landscape was subdivided into two climate zones, coastal (northwestern two-thirds) and interior (southeastern one-third) (Fig. 1 in Wimberly 2002). The climate of the coastal zone is moist and characterized by a longer natural fire rotation (NFR), while that of the interior zone is drier and historically more frequently burned (Impara 1997). Fires were likely to be larger and more severe in the coastal zone than in the interior because of the greater fuel accumulation and less frequent occurrence of climatic conditions that favor fire. Because simulated fires spread from cell to cell depending on each cell’s fire susceptibility, unburned or partially burned forest “islands” are left behind within larger burns.

We used output from 200 model simulations for 1000 years with 10-year intervals. Numerous model runs were necessary to represent the full range of possible landscape patterns from stochastic models (Keane et al. 2002, Wimberly 2002). Forest stand development was indexed by the time since the last high-severity fire, and disturbed stands were assumed to recover deterministically through stand development (Table 1). To ensure independence among maps (200 total), we randomly selected one time step from each simulation for estimating HRV.

Current and alternative future landscapes.—The Coastal Landscape Analysis and Modeling Study (CLAMS) provided the current (as of 1996) and alternative future landscape vegetation maps for this study. The vegetation of the current landscape was estimated from a statistical model that uses satellite imagery, inventory plots, and GIS layers (Ohmann and Gregory 2002). For comparison with the outputs from LADS, we resampled the map from 25-m (0.625-ha) to 300-m (9-ha) cell size using the RESAMPLE command in ARC/INFO GRID with the nearest-neighbor assignment (ESRI 1995). The accuracy of the map at the 9-ha resolution was 69% with seven classes (J. L. Ohmann and M. J. Gregory, unpublished data).

Two alternative future management scenarios were modeled: a current policy scenario (CPS) and a wildfire scenario (WFS). The CPS was simulated by using the Landscape Management and Policy Simulator (LAMPS), a spatially explicit, dynamic simulation model that projects future forest development with both deterministic and stochastic processes (Spies et al. 2002b, Bettinger and Lennett 2003, Bettinger et al. 2005). LAMPS tracks forest structure, development, and disturbance in a grid with a minimum resolution of 0.06 ha. Management activities are projected by using simulated harvest units whose size, shape, and spa-
TABLE 1. Age classes used to characterize coastal coniferous forests in the Pacific Northwest and descriptions of their forest structure.

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>Age class</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–10</td>
<td>very open</td>
<td>The canopy is very open and may contain very high amounts of down wood and snags created by fire and carried over from the previous stand. A new cohort of live trees may be establishing at different rates across the various locations. A few large residual trees may have survived the fire.</td>
</tr>
<tr>
<td>11–20</td>
<td>patchy open</td>
<td>The stand can contain very high amounts of down wood and snags created by the last fire and carried over from the previous stand. The canopy is not yet closed, and small trees may be patchily distributed. Trees may be establishing, but the canopy is mostly single story. There may be few large residual trees.</td>
</tr>
<tr>
<td>21–80</td>
<td>young</td>
<td>The canopy is closed and typically single story. Tree regeneration is low, and trees are small to medium size. Stand structure is relatively homogeneous. There can be accumulations of well-decayed deadwood from previous stands.</td>
</tr>
<tr>
<td>81–200</td>
<td>mature</td>
<td>The canopy is dominated by shade-intolerant species with low to moderate amounts of shade-tolerant species. Some canopy gaps may form, creating heterogeneity in the canopy, but stand structure is relatively homogeneous; diseases and insects can create many gaps. The trees are medium to large size, and the amount of deadwood is relatively low.</td>
</tr>
<tr>
<td>201–450</td>
<td>early old growth</td>
<td>The canopy, which is dominated by shade intolerants, is heterogeneous with gaps where shade-tolerant species are regenerating and adding vertical structural diversity. Very large (&gt;100 cm diameter at breast height) trees are common. Down wood and snags are often abundant, with old-growth characteristics becoming well developed during this stage.</td>
</tr>
<tr>
<td>451–800</td>
<td>mid-old growth</td>
<td>The canopy is a mixture of shade-intolerant and tolerant species and is increasingly heterogeneous; gaps add both vertical and spatial diversity. Very large trees are common. The original cohort of trees gradually disappears and is replaced by shade-tolerant species, with down wood and snags abundant. Structural development is slower in this age class than in the younger classes.</td>
</tr>
<tr>
<td>≥801</td>
<td>late old growth</td>
<td>The canopy is composed mainly of shade-tolerant trees and is heterogeneous with trees at various ages. There may be a few very large survivors of the original cohorts, but they are senescent. Down wood and snags are abundant. The initial cohort of shade-intolerant species is largely lost from the stand and replaced by shade-tolerant species.</td>
</tr>
</tbody>
</table>

Note: Age indicates time (in years) since the last stand-replacing fire.

tential distribution are based on historical information and policy rules that limit adjacency and size of clearcuts. Harvests are scheduled (or not scheduled) depending on landowner goals. Regeneration and subsequent stand development are projected from a look-up table created by running stand-level models that emulate the silvicultural practices of the different landowners. Small (<2 ha) natural disturbances (e.g., due to disease, wind, or insects) are stochastically simulated, and the resulting gaps are regenerated by using a probabilistic regeneration routine.

The CPS simulated forest management for 100 years into the future under the policies currently in force in the province. The CPS assumed that federal land managers would comply with the Northwest Forest Plan (USDA and USDI 1994), which is largely based on reserve strategies aimed at maintaining or restoring old-growth forests. State lands were simulated under current plans that use a combination of long rotations and limited reserves to achieve both biodiversity and timber goals (Oregon Department of Forestry 2001). Private industrial and nonindustrial owners, who manage primarily for timber production, were assumed to follow the Oregon Forest Practices Act (Oregon Department of Forestry 2001). To reduce the complexity of the analysis, we used only outputs for years 50 and 100 (the midpoint and final simulation years) from the CPS simulation. The output maps were resampled to a 9-ha resolution with the same procedure as the current vegetation map. LADS was used to simulate the WFS, with the current landscape used as the initial condition. This scenario was selected to provide hypothetical reference dynamics based on the natural disturbance regimes. Using forestry practices that emulate natural disturbance regimes has been advocated as a strategy for maintaining landscape conditions within the historical range (e.g., Hunter 1993, Perera et al. 2004), but no studies have explicitly examined the effectiveness of a pure representation of this strategy on human-dominated landscapes. We ran the model 10 times for 1500 years and calculated the mean results of the 10 runs at every fiftieth simulation year.

Age classes.—Douglas fir—western hemlock and Douglas fir—silver fir forests of western Oregon and Washington are often described as having several developmental stages (e.g., Franklin et al. 2002). We grouped the decadal age classes from LADS into seven age classes based on structural development and ecological functions (Spies and Franklin 1991, Franklin et al. 2002; Table 1). To assign an age class to each cell,
Table 2. Metrics used to quantify the landscape structure of simulated landscapes in the Oregon Coast Range.

<table>
<thead>
<tr>
<th>Categories, metrics, and acronyms</th>
<th>Level measured at:</th>
<th>Descriptions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amount of forest</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percentage of landscape (PLAND)</td>
<td>no</td>
<td>total area of landscape occupied by patches</td>
</tr>
<tr>
<td>Total core area (TCA)</td>
<td>yes</td>
<td>total area of landscape occupied by core area of patches</td>
</tr>
<tr>
<td>Patch size/abundance</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean patch area (MPA)</td>
<td>yes</td>
<td>mean of the distribution of patch size</td>
</tr>
<tr>
<td>Coefficient of variation of patch area (PACV)</td>
<td>yes</td>
<td>cv of patch area distribution expressed as percentage of mean</td>
</tr>
<tr>
<td>Largest patch index (LPI)</td>
<td>yes</td>
<td>percentage of the landscape occupied by the largest patch</td>
</tr>
<tr>
<td>Patch density (PD)</td>
<td>yes</td>
<td>number of patches per 100 ha</td>
</tr>
<tr>
<td>Edge abundance</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Edge density (ED)</td>
<td>yes</td>
<td>edge length of patches per hectare</td>
</tr>
<tr>
<td>Total edge contrast index (TECI)</td>
<td>yes</td>
<td>degree of structural contrast along patch edges</td>
</tr>
<tr>
<td>Patch shape</td>
<td>yes</td>
<td>degree of patch shape complexity</td>
</tr>
<tr>
<td>Perimeter-area fractal dimension (PAFRAC)</td>
<td>yes</td>
<td></td>
</tr>
<tr>
<td>Diversity of forest age</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Simpson's evenness index (SIEI)</td>
<td>yes</td>
<td>evenness in proportional abundance of classes</td>
</tr>
<tr>
<td>Patch isolation/connectivity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean nearest neighbor distance (MNN)</td>
<td>yes</td>
<td>mean of Euclidean nearest neighbor distance distribution between patches</td>
</tr>
<tr>
<td>Coefficient of variation of nearest neighbor distance (NNCV)</td>
<td>yes</td>
<td>cv of Euclidean nearest neighbor distance distribution as expressed percentage of mean</td>
</tr>
<tr>
<td>Patch cohesion index (COHESION)</td>
<td>yes</td>
<td>physical connectedness of patches</td>
</tr>
<tr>
<td>Mean proximity index (PROX)</td>
<td>yes</td>
<td>mean isolation of patches based on proximity to and size of patches of the same class within the search window [radius = 1000 m]</td>
</tr>
<tr>
<td>Mean similarity index (SIMI)</td>
<td>yes</td>
<td>mean isolation of patches based on proximity to and size of patches of the same class within the search window [radius = 1000 m] for class level; values are weighted by similarity between classes</td>
</tr>
<tr>
<td>Patch contagion/interspersion</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interspersion and juxtaposition index (IJI)</td>
<td>yes</td>
<td>juxtapositioning of patches with other classes</td>
</tr>
<tr>
<td>Aggregation index (AI)‡</td>
<td>yes</td>
<td>degree of cell aggregation</td>
</tr>
</tbody>
</table>

Notes: See McGarigal et al. (2002) for complete description and definitions of metrics. Landscape-level metrics quantify landscape structure with all classes together, while class-level metrics quantify it by class. † TECI requires an edge contrast matrix, which contains edge contrast weights. We selected values so that the weights reflected the degree of structural contrasts between age classes. For example, the edges between old-growth forests and open stands were assigned the highest weight. ‡ AI was measured for both levels, but because it was perfectly correlated with edge density for the landscape level, it was not included in the analysis.

we used the age of the overstory cohort, as represented by time since the last high-severity fire (AGE), for the historical landscapes, and the age of the dominant trees for current and future landscapes.

Landscape metrics

We used both “landscape-level” and “class-level” metrics available in FRAGSTATS, version 3.0 (Table 2; McGarigal et al. 2002). The landscape-level metrics describe overall landscape structure with all classes together, and the class-level metrics describe landscape structure by class (McGarigal et al. 2002). We chose 16 landscape-level and class-level metrics that are commonly used in ecological literature or are identified as important in parsimonious sets of landscape metrics (see Table 2 for descriptions; McGarigal and McComb 1995, Riitters et al. 1995, Gustafson 1998). The categories of metrics were (1) amount of forest, (2) patch size/abundance, (3) edge abundance, (4) patch shape, (5) diversity of forest age, (6) patch isolation/connectivity, and (7) patch contagion/interspersion (Table 2). Categories 1 and 5 focus on landscape composition and the others on configuration, although these categories are all interrelated. Previous studies on avian (Mc-
Garigal and McComb 1995, Cushman and McGarigal 2002, 2003) and small mammal (Martin and McComb 2002) diversity in the Oregon Coast Range have found that both landscape composition and configuration are important for explaining variations in species richness and abundance, although composition is generally more important. Two of the avian diversity studies also demonstrated that species responded to landscape configuration differently depending on their habitat association (McGarigal and McComb 1995, Cushman and McGarigal 2003). In addition to these measurements, we added connectivity measures because connectivity influences dispersal and metapopulation persistence and can be dramatically affected by land management (e.g., With and Crist 1995, Gustafson and Gardner 1996, With 1999). We used the eight-neighbor rule to define connectivity of adjacent cells (e.g., Milne et al. 1996, Turner et al. 2001).

Data analysis

Principal component analysis of the landscape metrics.—We used principal component analysis (PCA) with the Pearson correlation coefficients in PC-ORD (McCune and Mefford 1999) to reduce the number of metrics into the major components of landscape structure and to facilitate visualizing HRV and positions of managed landscapes in relation to HRV (McGarigal et al. 2000, McCune and Grace 2002). We chose PCA because (1) most of the variables were linearly correlated, and transformations (log, square root, and arcsine) reasonably linearized any remaining nonlinear relationships, and (2) our purpose was to condense the redundant information and extract new variables that captured variation in the data in order to contrast landscapes with different patterns. The operations in PCA are transparent and well understood, which makes the method ideal for data with linear relationships (McCune and Grace 2002). Previous studies also used PCA to ordinate landscapes using landscape metrics (Milne 1992, Cushman and Wallin 2000, Roworth 2001). We used the first two principal components (PCs) for ease of interpretation. To facilitate interpretation among different ordinations, the resultant ordinations were rotated by a multiple of 90°, which did not change the amounts of variation explained by the component axes. We calculated the PC scores for the current and future landscapes using the principal component structure (i.e., eigenvectors or loadings) from the corresponding PCA and projected them onto the ordinations. To determine the statistical significance of the axes in PCA, we used the broken-stick criterion, which is based on eigenvalues from random data (Jackson 1993).

Quantifying the HRV.—We delineated 50, 75, 90, and 95% HRV likelihood for each ordination on the two-dimensional space defined by the first two PC axes using the kernel density estimation method (Seaman and Powell 1996). The method was performed in ArcView 3.2 by using the extension program, Animal Movement SA, version 2.04 beta (Hooge et al. 1999). The least-square cross-validation option was applied for the smoothing parameter because it gives very little bias in area estimates (Seaman and Powell 1996). This method estimates the density surface from the spatial distribution of data points and encloses the specified density within the range. Lundquist et al. (2001) and Roworth (2001) used this method to delineate the range of variability in landscape structure on their ordinations. The HRV likelihood can be considered as a confidence range of historical landscape conditions that could have occurred under the historical fire regime (Roworth 2001, Wimberly 2002). We used the 90% likelihood as the reference condition. Because 95% HRV likelihood did not differ much from 90%, we did not show it in the figures. We calculated mean, minimum, and maximum for individual metrics measured on the landscapes that fell within the 90% HRV likelihood for each analysis.

Results

The HRV of landscape structure and comparison with current conditions

Analysis of landscape structure and comparison with current conditions—The first PC (PC1) explained 63% of the variation and was highly correlated with many of the metrics that are related to patch size (LPI, MPA, PACV, TCA), connectivity (COHESION, PROX, SIMI), patch proximity (MNN, NNCV), and abundance of edge (ED) and patches (PD) (Table 3). This axis represented class aggregation and large patch dominance. The second PC (PC2) explained an additional 14% of the variation and was moderately correlated with edge contrast (TECI) and patch juxtaposition (IJII) (Table 3). This axis suggested a gradient of intermixing and contrasts among patches of different classes. The eigenvalues of the first two axes were greater than the broken-stick eigenvalue, indicating that these axes are meaningful and should be considered for interpretation (Jackson 1993, McGarigal et al. 2000, McCune and Grace 2002; Table 3).

The current landscape was outside the HRV in terms of PC1 but not PC2 (Figs. 2a and 3). The current landscape had a more aggregated patch configuration than would be expected under the historical disturbance regime. Patches were more simply shaped (perimeter-area fractal dimension; PAFRAC) and distributed at distances of greater variation from the nearest patch of the same class (NCCV) than in the simulated historical landscapes. Of 16 individual landscape metrics, 15 were outside of the corresponding HRV for the current landscape (Appendix A). Perimeter-area fractal dimension (PAFRAC) was especially important for both of the PC scores of the current landscape (Appendix B), suggesting that patch shape on the current landscape was considerably simpler than on the simulated historical landscapes.
TABLE 3. Eigenvalues of the principal components and the Pearson correlations of the original variables with the PC axes for the ordinations of the simulated historical landscapes of the Oregon Coast Range.

<table>
<thead>
<tr>
<th>Metrics</th>
<th>Landscape level</th>
<th>Very open</th>
<th>Patchy open</th>
<th>Young</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>PC2</td>
<td>PC1</td>
<td>PC2</td>
</tr>
<tr>
<td>Eigenvaleut†</td>
<td>9.39</td>
<td>2.05</td>
<td>8.04</td>
<td>2.50</td>
</tr>
<tr>
<td>Variance explained (%)</td>
<td>62.5</td>
<td>13.6</td>
<td>50.9</td>
<td>15.7</td>
</tr>
<tr>
<td>Correlations with the PC axes</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PLAND‡</td>
<td>NA</td>
<td>NA</td>
<td>0.96</td>
<td>-0.11</td>
</tr>
<tr>
<td>TCA</td>
<td>0.87</td>
<td>-0.32</td>
<td>0.97</td>
<td>0.12</td>
</tr>
<tr>
<td>MPA</td>
<td>0.86</td>
<td>-0.16</td>
<td>0.94</td>
<td>0.22</td>
</tr>
<tr>
<td>PACV</td>
<td>0.86</td>
<td>0.21</td>
<td>0.91</td>
<td>0.12</td>
</tr>
<tr>
<td>LPI</td>
<td>0.80</td>
<td>0.27</td>
<td>0.97</td>
<td>0.12</td>
</tr>
<tr>
<td>PD</td>
<td>-0.86</td>
<td>0.17</td>
<td>0.06</td>
<td>-0.82</td>
</tr>
<tr>
<td>TECI</td>
<td>-0.92</td>
<td>-0.27</td>
<td>0.87</td>
<td>-0.36</td>
</tr>
<tr>
<td>PAFRAC</td>
<td>0.34</td>
<td>-0.65</td>
<td>0.18</td>
<td>-0.21</td>
</tr>
<tr>
<td>SIEI§</td>
<td>-0.78</td>
<td>-0.47</td>
<td>0.24</td>
<td>-0.50</td>
</tr>
<tr>
<td>MNN</td>
<td>0.91</td>
<td>-0.31</td>
<td>-0.23</td>
<td>0.86</td>
</tr>
<tr>
<td>NNCV</td>
<td>0.68</td>
<td>-0.31</td>
<td>-0.23</td>
<td>0.67</td>
</tr>
<tr>
<td>COHESION</td>
<td>0.91</td>
<td>0.14</td>
<td>0.95</td>
<td>0.13</td>
</tr>
<tr>
<td>PROX</td>
<td>0.81</td>
<td>0.39</td>
<td>0.94</td>
<td>0.07</td>
</tr>
<tr>
<td>SIMI</td>
<td>0.87</td>
<td>0.34</td>
<td>0.00</td>
<td>-0.14</td>
</tr>
<tr>
<td>IJI</td>
<td>-0.49</td>
<td>-0.62</td>
<td>-0.04</td>
<td>0.00</td>
</tr>
<tr>
<td>AI†</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

Note: Correlations >0.6 (positive or negative) are in boldface type. Descriptions of metrics are listed in Table 2.
† The broken-stick criterion suggested that all the axes were meaningful and should be considered for interpretation except the second axis for the young class, whose eigenvalue was very close to the broken-stick criterion. The eigenvalue for the third PC axes were all <2. The percentage of variance explained by PC3 ranged from 9.2% to 12.3%.
‡ PLAND is not applicable at a landscape level.
§ SIEI was not available for the class-level analysis.
∥ AI was not used for the landscape-level analysis because of the near perfect correlation with ED.

Very open and patchy open classes.—PC1 explained 51% of the variation for very open and 52% for patchy open classes. It was highly correlated with many metrics, including the amount of class area (PLAND), patch size (LPI, MPA, PACV, TCA), edge density (ED), and connectivity of classes (COHESION, AI, PROX) (Table 3). This axis represented an area and aggregation gradient. PC2 explained an additional 16% of the variation for very open and 13% for patchy open classes and was strongly correlated with mean nearest neighbor distance (MNN) and patch density (PD) (Table 3). This axis suggested a gradient of patch proximity and density. The eigenvalues for the first two axes were greater than the broken-stick eigenvalues for both classes.

The current conditions of very open and patchy open types were outside the HRV in terms of PC2 only (Figs. 2a and 4a, b). There were more patches and shorter mean nearest neighbor distances on the current landscape than would be expected within HRV. The ordination suggested that the current landscape had very high patch density (PD) in these two classes. High patch density was the major factor that put the current landscape outside the HRV along PC2 for both the classes (Appendix B). Of 16 individual metrics, 4 metrics for very open and 6 for patchy open classes were outside the corresponding HRV (Appendix A).

Young, mature, and early old-growth classes.—PC1 explained 52% of the variation for young and 53% for both mature and early old-growth classes. It had correlated variables similar to those for the youngest two classes, representing area and aggregation gradient (Table 3). PC2 explained an additional 13% of the variation for young and mature and 17% for early old-growth classes (Table 3). PC2 was moderately correlated with mean nearest neighbor distance (MNN), coefficient of variation of nearest neighbor distance (NCCV), and patch shape (PAFRAC) (Table 3). This axis represented a gradient of patch proximity and patch shape complexity. Except for the PC2 for young class, whose eigenvalue was just below the broken-stick value, the eigenvalues for the first two axes were greater than the broken-stick eigenvalues.

The current landscape was outside the HRV of both PC1 and PC2 for all three age classes (Figs. 2a and 4c, d, e). In the current landscape, young forests were more connected and had larger patch areas and simpler patch shapes than in the historical landscapes. Mature and early old-growth forests were less abundant and occurred in fewer and smaller patches that were more isolated and simpler in shape than expected under the historical fire regime. Many individual metrics were outside the HRV (Appendix A). For all three classes, many metrics were important for the PC1 scores of the current landscape, suggesting that many patch characteristics of the three classes in the current landscape differ from those in the simulated historical landscapes.
Table 3. Extended.

<table>
<thead>
<tr>
<th>Class level</th>
<th>Mature</th>
<th>Early old growth</th>
<th>Mid-old growth</th>
<th>Late old growth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>PC2</td>
<td>PC1</td>
<td>PC2</td>
</tr>
<tr>
<td></td>
<td>53.4</td>
<td>12.7</td>
<td>52.6</td>
<td>17.3</td>
</tr>
<tr>
<td>0.97</td>
<td>-0.11</td>
<td>0.97</td>
<td>-0.10</td>
<td>0.95</td>
</tr>
<tr>
<td>0.95</td>
<td>0.11</td>
<td>0.94</td>
<td>0.15</td>
<td>0.93</td>
</tr>
<tr>
<td>0.95</td>
<td>-0.08</td>
<td>0.96</td>
<td>0.03</td>
<td>0.97</td>
</tr>
<tr>
<td>0.79</td>
<td>0.33</td>
<td>0.77</td>
<td>0.44</td>
<td>0.79</td>
</tr>
<tr>
<td>0.93</td>
<td>0.18</td>
<td>0.88</td>
<td>0.30</td>
<td>0.86</td>
</tr>
<tr>
<td>-0.71</td>
<td>-0.07</td>
<td>-0.67</td>
<td>-0.27</td>
<td>0.43</td>
</tr>
<tr>
<td>-0.74</td>
<td>-0.47</td>
<td>0.77</td>
<td>-0.53</td>
<td>0.92</td>
</tr>
<tr>
<td>0.13</td>
<td>0.40</td>
<td>0.13</td>
<td>0.44</td>
<td>-0.20</td>
</tr>
<tr>
<td>-0.23</td>
<td>-0.58</td>
<td>-0.17</td>
<td>-0.71</td>
<td>0.26</td>
</tr>
<tr>
<td>-0.47</td>
<td>0.78</td>
<td>-0.56</td>
<td>0.74</td>
<td>-0.83</td>
</tr>
<tr>
<td>-0.43</td>
<td>0.62</td>
<td>-0.56</td>
<td>0.62</td>
<td>-0.74</td>
</tr>
<tr>
<td>0.91</td>
<td>0.15</td>
<td>0.80</td>
<td>0.04</td>
<td>0.90</td>
</tr>
<tr>
<td>0.95</td>
<td>0.03</td>
<td>0.90</td>
<td>0.23</td>
<td>0.95</td>
</tr>
<tr>
<td>-0.25</td>
<td>0.14</td>
<td>-0.48</td>
<td>0.59</td>
<td>-0.60</td>
</tr>
<tr>
<td>0.30</td>
<td>0.28</td>
<td>0.28</td>
<td>-0.11</td>
<td>0.32</td>
</tr>
<tr>
<td>0.94</td>
<td>0.18</td>
<td>0.93</td>
<td>0.22</td>
<td>0.94</td>
</tr>
</tbody>
</table>

(Appendix B). For the young class, mean nearest neighbor distance (MNN) and coefficient of variation of nearest neighbor distance (NNCV) were relatively important for the PC2 score (Appendix B). For the mature and early old-growth classes, mean nearest neighbor distance (MNN) and patch shape (PAFRAC) were important for the PC2 scores.

Mid- and late old growth classes.—PC1 explained 53% of the variation for mid-old growth and 61% for late old growth. It had correlated variables similar to those for the previous classes and represented an area and aggregation gradient (Table 3). PC2 explained an additional 14% of the variation for both classes. PC2 was moderately correlated with patch density (PD) and represented a patch density gradient (Table 3). The eigenvalues for the first two axes were greater than the broken-stick eigenvalues for both classes.

The current landscape was outside the HRV of both PC1 and PC2 for mid-old growth (Figs. 2b, c and 3). The CPS, however, brought the landscape condition within HRV in terms of class aggregation and large patch dominance (PC1) but not patch contrast and intermixing (PC2). Edge contrast (TECI), patch juxtaposition (IJI), and patch shape (PAFRAC), which were important variables for the ordination, either did not move much toward HRV (IJI) or moved away (TECI and PAFRAC) from the HRV.

The wildfire scenario (WFS) continuously moved the landscape away from the HRV in terms of class aggregation and large patch dominance in the first 100 years (Fig. 3). After 100 years, the landscape gradually moved back toward HRV, falling within the marginal scatter of simulated historical landscapes by 200 years. By 500–700 years, it nearly reached 90% HRV, stabilizing at the center by 800 years. The simulation sequence showed that under the WFS, the landscape became more homogeneous and were occupied by large patches of mature forests in the first 100 years (Fig. 2e, f); after this, fire dissected large mature patches into smaller patches of various ages.

Analyses of class-level metrics.—Under the CPS, none of the age classes returned to the HRV in the 100-year simulation. However, landscape condition moved toward the HRV with the exception of the very open class (Figs. 2b, c and 4). The very open class moved further from the HRV because it increased in patch density (PD) and area (PLAND). The patchy open class approached the HRV mainly because of the considerable decrease in patch density. The landscape pattern of the young class moved substantially toward the HRV because many metrics, with the exception of patch density and patch shape (PAFRAC), approached their

to the HRV within 100 years (Figs. 2b, c and 3). The CPS, however, brought the landscape condition within HRV in terms of class aggregation and large patch dominance (PC1) but not patch contrast and intermixing (PC2). Edge contrast (TECI), patch juxtaposition (IJI), and patch shape (PAFRAC), which were important variables for the ordination, either did not move much toward HRV (IJI) or moved away (TECI and PAFRAC) from the HRV.

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HRV. After 100 years, the density of young forest patches was higher and the shapes were simpler than those on the current landscape. For the mature class, most metrics, with the exception of patch shape, moved substantially toward HRV. As a result, the landscape noticeably approached the HRV in terms of area and aggregation, but not in the direction of patch proximity and shape complexity. Patch shape of mature forests consistently became simpler over time. All old-growth classes were very rare on the current landscape so that change in landscape pattern was more sensitive to increases in area than to changes in configuration. The late old-growth class did not appear in this 100-year simulation.
FIG. 3. Historical range of variability (HRV) represented by PC1 and PC2 of landscape-level metrics. Lines indicate trajectories of simulated landscapes under the current policy scenario (CPS; solid line) and the wildfire scenario (WFS; dashed line). The shaded areas are the 50%, 75%, and 90% HRV likelihoods (from inner to outer) delineated by the density estimation method. The star represents the current landscape; simulated landscapes are as follows: under HRV (WFS), solid circles; CPS year 50, solid square; CPS year 100, solid triangle; and WFS, open circles (with simulation year noted). The characteristics indicated by the axes increase with the axis values.

Under the WFS, there were three general trajectories. The very open and patchy open classes returned to the HRV by year 50 (Fig. 4a, b). The young, mid-, and late old-growth classes more or less moved consistently toward the HRV, reaching it by year 200, 450, and 800, respectively (Fig. 4c, f, g). The mature and early old-growth classes overshot the HRV at year 50 and 200 and then returned to the HRV by year 200 and 450, respectively (Fig. 4d, e). The different trajectories reflected the changes associated with the development of existing young forests into older forests during simulation time. The large patches of young forests became large patches of mature and early old-growth forests in the first few centuries of the simulation. A couple of centuries of the wildfire regime were needed to break these large patches into smaller patches of various age classes that were characteristic of the simulated historical landscapes.

**DISCUSSION**

*Historical landscape dynamics of forests in the Oregon Coast Range*

The simulations indicated that the landscapes under the historical disturbance regime during 1000 years prior to Euro-American settlement were characterized by high structural diversity over time and space. The proportions of the seven age classes fluctuated from uneven to relatively even distributions as indicated by Simpson's evenness index (SIEI). Patch shapes were quite complex, and all age classes occurred in large patches. The high values for physical connectivity (COHESION) and patch juxtaposition (JJI), as well as inspection of the output maps, suggest that the historical landscapes had many large patches (coarse-grained pattern) and much intermixing of patch types. Patchiness and juxtaposition of different habitat types are important characteristics of landscapes for regional biodiversity (Angelstam 1997, Pickett and Rogers 1997). Patchiness and juxtaposition also create different types of ecotones and edge habitats by various combinations of edges (Hunter 1990, McGarigal and McComb 1995). Studies have shown that a mixture of forest conditions is associated with higher species diversity in this region (e.g., McGarigal and McComb 1995, Martin and McComb 2002, Cushman and McGarigal 2003).

The very open and patchy open classes tended to be infrequent components of the historical landscapes, each occupying ~3% of the province, on average. These two extreme age classes had not been separately quantified by the previous studies. Those studies (Wimberly 2002, Wimberly et al. 2004) reported a median of 17% for early-successional forests (<30 years). The difference arose because the previous studies not only used different age class definitions but also considered that both high severity and moderate severity fires reset the stand development. In this study, moderate severity fire did not affect age. These two young classes were ephemeral on the historical landscapes and blinked on and off as fires burned and vegetation filled in.

The dominant cover type on the historical landscapes was early old-growth forests (201–450 years), occupying 28% of the Oregon Coast Range, on average. Together with mid- and late old growth, these forests (>200 years) historically comprised 54% of the province, on average. The previous studies (Wimberly 2002, Wimberly et al. 2004), which used different age class definitions (see previous paragraph), found that oldgrowth forest was the most dominant cover type and covered 42%, on average (29–52% for the 90% interquartile range). Other studies showed that old-growth forests covered about 40% of the province around 1850 (Teensma et al. 1991, Ripple 1994) and approximately 61% before the widespread fires associated with human settlement in 1840s (Ripple 1994).

Mid- and late old-growth forests were consistently present on the historical landscapes although the fire rotation periods were shorter than the ages of the forests. Differentiating old-growth forests revealed that the early old-growth class was two to three times as abundant as the two oldest classes, but those two clas-
ses were not uncommon under the historical fire regime. The patches of mid- and late old-growth forests, which can be considered "remnant patches" (Forman 1995), collectively occupied 26% of the province, on average. Remnant patches can be created either by chance or because they occur in environments that are not fire-prone (Zackrisson 1977, Angelstam 1997). Angelstam (1997) suggested that landscapes with infrequent fire regimes (<1 fire per century) may have both types of remnant patches. The parameters of LADS did not simulate strict fire refugia (i.e., with a zero probability of fire), but the wetter climate zones and lower slope positions had lower probabilities of fire. Even without true fire refugia, the landscapes still had a considerable number of remnant patches, sometimes very large in size.

The patch characteristics of mid- and late old-growth classes were somewhat different from those of other classes. These two oldest classes had the highest patch density for the relatively small area they occupied.
These metrics imply that these two classes were often more isolated and occurred in smaller patches than other classes. Patch shape (PAFRAC) of late old growth was simpler than that of other classes, on average. Late old-growth forests tended to occur in small patches scattered across the landscapes, where forests escaped from fire for more than 800 years. Scattered remnant patches can be important habitat refugia on landscapes characterized with infrequent, high severity fires (DeLong and Kessler 2000) and may provide critical source habitat from which individuals that survived fires can disseminate to colonize younger patches around them (Peterken and Game 1984, Matlack 1994). Wimberly and Spies (2001) showed in their simulation study that post-fire recruitment of fire-sensitive western hemlock was sensitive to the abundance and locations of remnant patches in a small watershed in the Oregon Coast Range. Remnant patches are especially important for the persistence of low-mobility species associated with old growth, such as certain lichens, in landscapes characterized by large-scale fires (Sillett et al. 2000).

Comparison between current landscape and HRV

More than a century of various logging practices has strongly altered the abundance and spatial pattern of forest age classes in the Oregon Coast Range relative to the HRV. The results suggested that the major differences on the current landscape from the historical
landscapeeds are abrupt patch edges, simple patch shapes, fewer forest islands, the reduced variety of patch juxtaposition, altered interpatch distances, the skewed age distribution toward young forests, and the shortage of older forests. Short rotations on private lands, which cover almost two-thirds of the province, and human-caused wildfires have created a matrix of young, relatively uniform forests with scattered patches of old forest. It was anticipated that some characteristics of the current landscape of the Oregon Coast Range were outside of HRV (Wimberly et al. 2004), but this analysis demonstrated that a large number of landscape characteristics are outside of HRV (Appendix A). Currently, forests <80 years old cover >75% of the landscape, whereas they historically occupied 21%, on average. The total core area of mature and older forests has decreased to about one twenty-seventh of the mean historical level. In addition to patch size, distances between younger forests have decreased by two- to threefold, on average, and those of older forests have substantially increased. Although forests <20 years old increased in area, they are more fragmented as indicated by the mean patch area and the patch density. These fundamental changes in landscape structure have ecological consequences on the flows of energy, materials, and organisms (Saunders et al. 1991, McGarigal and McComb 1995, Richards et al. 2002). The influences of the changes on functioning of the landscape to maintain ecological processes (e.g., carbon cycle) and diversity need a synthesis of existing knowledge and further study. The quantitative HRV and the comparison with the current condition help identify altered structures and the degrees of alteration.

Comparisons between the current policy (CPS) and wildfire scenarios (WFS)

The simulations indicated that 100 years was not long enough to return the overall condition of the landscape to the HRV under either scenario. First, the 100-year period was too short for old forests to reach the HRV. On the current landscape, the amount of forest older than 80 years is well below the historical level especially because old-growth forests (>200 years) are very rare. Second, patch shape moved away from the HRV over the 100-year period under the CPS, offsetting changes toward the HRV in other attributes of landscape structure. Patch shape became simpler over time, and the vegetation map after 100 years resembled the ownership pattern.

Under the CPS, ownership pattern indirectly constrained development of landscape structure because of the contrasting forest management regimes used by different ownership types. The three general ownership groups (federal, state, and private) have different management goals and regulatory constraints, and the ranges of forest conditions that can be produced within a particular ownership may be limited (Wimberly et al. 2004). For example, young forests will occur primarily on private lands, and mature and old forests will occur primarily on state and federal lands.

Multiple studies have reported the strong influence of ownership patterns on the vegetation and disturbance patterns in western Oregon (e.g., Spies et al. 1994, 2002b, Cohen et al. 2002, Stanfield et al. 2002). This study indicates that ownership boundaries can affect patch characteristics at the broad scale. Shapes of ownership tracts are considerably simpler than those of fire patches. The decreasing trend in fractal dimension of patch shape may reflect in part the constraints imposed by the underlying ownership pattern. For example, the checkerboard pattern of forest industry and BLM ownerships in the southeastern part of the study area became more evident on the simulated landscapes over time. Although forest conditions within ownerships can be heterogeneous, ownership boundaries may lead to simpler patch shapes at broad scales if management practices are highly contrasting.

Ownership boundaries may also control the location and characteristics of edge types. Because general patch types (e.g., age) are likely to be fixed by ownership, certain combinations of edge types can be reduced or increased. For example, edges between old growth and open, very young stands may be found only in or around reserves where federal lands abut private lands. Also, the ownership pattern may reduce intermingling of forest types compared with that in historical wildfire landscapes. According to the analysis of landscape-level metrics, patch juxtaposition (IJ) did not reach HRV over the 100-year management scenario. Altered patch adjacency may lead to differential disruption or enhancement in source–sink movement of organisms and materials across different forest types (Forman 1995, With and King 2001, Spies et al. 2002b, Loreau et al. 2003). For example, elk move across patch boundaries between forests for hiding and shading and open habitats for foraging (Thomas et al. 1979, Witmer and deCalesta 1983), so that increased adjacency of forests to open habitats may increase their flows between the two patch types. Large wood in streams through patches of lowland young forest may originate from upper streams in old forests where debris flows deposit large trees into the streams. These dead trees may be later redistributed to downstream patches by flood events (May 2002, May and Gresswell 2003). If the juxtaposition of source and sink patches is reduced, the flows of organisms and materials between these patches will be altered in the landscape and may impair the functional integrity of the landscape (Reiners and Driese 2001).

In contrast, the WFS took the landscape away from the HRV, with its direction almost opposite that of the trajectory of the management scenario. This result was somewhat surprising because emulating natural disturbance regimes is hypothesized as a way of conserving biodiversity and maintaining landscape conditions within HRV (e.g., Hunter 1993, Bergeron et al. 2002,
Kuuluvainen 2002, Perera et al. 2004). In the simulations, the large young forest patches on the current landscape developed into massive, highly connected patches of mature forests within several decades. It took a couple of centuries in the simulation for these patches to be broken up by wildfire and to develop into various age classes. Other studies have also noted the lag effects in landscape pattern development (Baker 1993, 1995, Wallin et al. 1994, Landres et al. 1999). Wallin et al. (1994) demonstrated that landscape dynamics may show inertia in response to change in disturbance regimes because of the legacy effects of altered landscape structure caused by dispersed patch cuts in the Pacific Northwest. Swanson et al. (2003) found that the time required to attain the HRV was shorter in a much less altered landscape. The legacy of past management can affect the amount of time it takes for a landscape to reach a particular structural condition.

**Limitations of HRV approaches**

To quantify HRV, we chose the 1000-year time period prior to the change in land use that occurred after Euro-American settlement. This time period was chosen because the fire regime and vegetation composition were relatively stable over that period (Worona and Whitlock 1995, Long et al. 1998). This choice of a reference period is, however, somewhat arbitrary, given the fact that fire regimes changed as climate and vegetation changed in the past and will change again in the future (Whitlock et al. 2003, McKenzie et al. 2004). This study focused on changes due to stochasticity in fires but not on stationary trends in fire regimes over a longer time span. Inclusion of different climatic conditions will increase the estimated range of variability and reduce accuracy because of scarcity in data for the distant past. Increased temperature and summer drought and change in fire activity are anticipated in the future, especially on the valley margin of the Oregon Coast Range, although the effects on vegetation is uncertain because the forests are not water-limited (JISAO 1999, Mote et al. 2003, Whitlock et al. 2003). Under the anticipated climate change, the HRV estimated from the recent past could become less relevant as a reference for future management (Whitlock et al. 2003).

Quantitatively estimating HRV imposes many challenges because available data are often insufficient and the methodology is not well established. Existing literature on HRV indicates a wide variety of approaches (Humphries and Bourgeron 2001) and suggests that analysis methods are study specific. Estimating HRV of landscape structure by using simulation models requires considerable information on fire regimes. To parameterize the model, we needed data for disturbance frequency, size, shape, severity, pattern of spread, and effects of topography and vegetation on forest susceptibility to fire. Empirical data are sparse for these variables at this broad scale, and the simulation model used in this study was calibrated by using only a few studies conducted in the Oregon Coast Range. A dendrochronological study (Impara 1997), which provided input data for fire return intervals, examined only the middle portion of the region, for example.

Multivariate analysis (PCA) was useful for condensing landscape metrics that could otherwise be difficult to comprehend as a whole. It was also useful for visualizing the relative conditions of the landscapes and changes over time in relation to the HRV. PCA relies on correlational structure within a particular system of variables. Therefore, if a managed landscape has a different correlational structure from historical landscapes, the synthetic axes obtained from the ordination of historical landscapes might not effectively describe the difference between the HRV and the managed landscape. In other words, a landscape with highly different landscape structure can be cryptic in the ordination, although the combination of the values for variables indicates that it is a multivariate outlier from HRV. The limitations of the multivariate analysis make it important to interpret multivariate results with reference to the original variables for comparisons with HRV.

HRV is also affected by scale (Morgan et al. 1994, Aplet and Keeton 1999, Wimberly et al. 2000, Agee 2003). Although studies have not investigated the effects of grain size (i.e., cell size) on HRV estimation, this factor can potentially influence the characterization of landscape structure by landscape metrics (Turner et al. 1989, Wu 2004, Wu et al. 2004). The scale problem also applies to time, and Keane et al. (2002) found that long simulations relative to fire frequency were needed to capture full variation and that summary intervals of output data influenced apparent variability. The HRV estimated in this study applies specifically to the particular spatial and temporal scale investigated.

The HRV of landscape conditions depends on classification schemes and metrics used (Li and Reynolds 1994, 1995). How stand age was binned into classes probably has substantial effects on estimated variability, and this uncertainty has not been explored in landscape ecology literature. This is one of the weaknesses of categorizing variation in order to use landscape metrics. Furthermore, if we lumped all old-growth forests (>200 years) into one class, the landscape would not take more than 500–800 years to reach the 90% HRV. Some of the metrics also differed in time required to reach HRV. Baker (1992, 1995) found in his simulation analyses that metrics differed in the time required to depart from historical conditions. He attributed these differences to different sensitivities of the metrics to changes in fire frequency and size although full explanations need further study. We found that, in general, metrics that take into account patch arrangement surrounding a focal patch type (e.g., IJI and TECI) respond
more slowly to change in disturbance regime than metrics that measure only a single type.

In this study, we did not quantify the durations of certain landscape conditions or examine the sequence and rates of landscape changes over time, but these metrics are potentially important for maintaining ecological processes and biodiversity in the landscape. Some populations of organisms might be able to persist in refugia for a limited amount of time when landscape condition is not optimal. Also, even within HRV, drastic changes in landscape structure (e.g., from the margin of HRV to the other margin) might not have occurred in the historical landscapes. As we learn more about habitat relationships at the broad scale, more appropriate characterization of landscape structure may be needed. In this study, we did not differentiate partially burned forests from even-aged forests, but the differences in forest structure created by the different fire histories could have substantial effects on habitat quality. In a companion study (E. Nonaka, T. A. Spies, M. C. Wimberly, and J. L. Ohmann, unpublished manuscript), we characterized the landscape in terms of live and dead wood biomass, which is more indicative of structural differences in forests affected by different disturbance histories.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This study confirms the findings of previous work that several components of the current forest landscape structure are outside the HRV that probably occurred in the pre-Euro-American landscape (Wimberly et al. 2000). It goes beyond the previous work to demonstrate that additional characteristics of the landscape, such as current amounts of very old forest (>450 years old) and young, open-canopy forest (<20 years old), along with several ecologically important landscape metrics, also lie outside the HRV. The results also indicate that the major components of variation in the set of landscape structure metrics fell into two groups: measures of structure associated with area, edge, and connectivity, and measures of structure associated with contrast and juxtaposition of vegetation types. Simulations of alternative scenarios reveal that after 100 years, current policies would move landscape structure toward HRV for the first group of metrics but not for the second. Under the wildfire scenario, the historical fire regime would move landscape structure away from HRV for the first 100 years before sending it back toward HRV. It would require several more centuries of the historical fire regime for landscape structure to reach the edge of the HRV for both groups of landscape metrics.

The application of the HRV concept to forest policy and management is problematic in the Oregon Coast Range. First, no current federal or state policies or management plans use HRV as an explicit goal, although both federal and state plans use HRV as a reference in developing general goals (FEMAT 1993, Oregon Department of Forestry 2001). The use of HRV as an explicit goal for management is also problematic because climate change may alter disturbance regimes in the Pacific Northwest (JISAO 1999, Whitlock et al. 2003, McKenzie et al. 2004). For example, wildfires are expected to become more extensive and more severe, especially along low-elevation transition zones such as the eastern margins of the province. Such a change would result in a new disturbance regime with a new range of variation of forest types. However, it is not clear how different it would be from the historical range of variation. A further major limitation is that not all landowners have the same ecological goals. Consequently, even if public lands had a goal of achieving the HRV of landscape structure, it would not be possible to reach it using those lands alone.

Despite these significant limitations, knowledge of HRV can be useful in understanding how humans have altered landscapes, and if the goal is to retain or restore desired native species and ecosystems, HRV can provide insights that can help managers formulate biodiversity goals for inherently dynamic forest ecosystems. The use of HRV in developing federal and state forest plans (FEMAT 1993, Oregon Department of Forestry 2001) is evidence that managers can find the concept useful without making it a specific goal.

This study provides some additional insights about the concept of HRV and landscape analysis that may be useful to managers and policy makers. First, the potential future landscapes will have less juxtaposition of patch types than under HRV. Current policies and land ownership patterns will act to segregate old and young forests into large blocks, probably influencing biodiversity. Some species and processes may benefit from a more interspersed mix of old and young forests. For example, fitness of northern spotted owl (Strix occidentalis caurina) populations in northern California is higher in landscapes with a mixture of old and open brushy stages than in landscapes with complete old-growth cover (Franklin et al. 2000). Policy makers and land managers may want to more carefully evaluate the ecological effects of policies that lead to reduced connectivity of old and young forest in space and time.

Second, the finding that it would take many centuries to return to HRV, even under a historical wildfire regime, means that this landscape is both slow to change and quite altered from the pre-Euro-American landscapes. Consequently, policies and plans that typically have a lifetime of years or at most a decade may not be in place long enough to recover many of the landscape structures of the historical disturbance regime. Nevertheless, this analysis indicates that current policies, which were not specifically designed to return the landscape to HRV, will in fact move it in that direction for several components of landscape structure. Policy makers could use the relative rate and direction of the trend toward HRV as one indicator for evaluating the differences between alternative biodiversity policies.
Third, the oldest old-forest age classes, 450–800 years and >800 years, which are largely absent from the Coast Range today, probably occupied a significant portion of this landscape under the HRV. Without a long-term commitment to growing old growth, this structurally distinctive stage of old growth (Spies and Franklin 1991) will not occur.

Fourth, many landscape metrics are highly correlated. Where managers use them as indicators, they should be careful to evaluate the correlational structure of the metrics and select those that convey fundamentally different information about landscape structure. The use of many highly correlated landscape metrics without consideration for the problem to monitor or compare landscape plans can give a false impression of a comprehensive understanding of landscape structure.

Fifth, as mentioned above, it will be impossible to develop the HRV of landscape structure in a multi-ownership landscape by means of the actions of a single ownership. Not all owners use HRV in the process of setting management goals. However, it may be possible to cost-effectively incorporate some of the elements of natural disturbance regimes on lands managed primarily for timber production. For example, leaving wildlife trees or patches of older forest around riparian areas could move the structural diversity of these landscapes more toward the diversity that would have occurred following wildfires and windthrow. There are many economic and legal barriers to ecological planning across ownerships, but there are also incentives for private landowners to move in this direction as well (Thompson et al. 2004).

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LITERATURE CITED


ESRI (Environmental Systems Research Institute). 1995. ARCInfo. Redlands, California, USA.


McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MJM software design, Gleneden Beach, Oregon, USA.


McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS, version 3.0: spatial pattern analysis program for categorical maps computer software program produced by the authors at the University of Massachusetts, Amherst, Massachusetts, USA. (http://www.umass.edu/landeco/research/fragstats/fragstats.html)


Rowe, T. L. 2001. Quantifying the variation in landscape structure under a natural fire regime in the southern Rocky Mountains. Thesis. University of Massachusetts, Amherst, Massachusetts, USA.


agement planning documents within the range of the northern spotted owl. USDA Forest Service and US Department of the Interior Bureau of Land Management, Portland, Oregon, USA.


APPENDIX A

A table showing the mean, minimum, and maximum of the metrics from the simulated historical landscapes that fell in the 90% historical range of variability (HRV) likelihood of the age classes, along with values of the metrics measured on the current and potential future landscapes under current policy scenario (CPS) of the Oregon Coast Range, Oregon, USA, is available in ESA’s Electronic Data Archive: Ecological Archives A015-050-A1.

APPENDIX B

A table showing the elements of linear combinations and PC scores for the current, year-50, and year-100 landscapes under CPS for the Oregon Coast Range, Oregon, USA, is available in ESA’s Electronic Data Archive: Ecological Archives A015-050-A2.