Spatial simulation of historical landscape patterns in coastal forests of the Pacific Northwest

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Abstract: Concerns about the fragmentation of Pacific Northwest forests are based on the assumption that these landscapes historically contained large, contiguous patches of old growth. However, this supposition appears to conflict with disturbance history research, which shows that wildfire was an important component of pre-settlement forest ecosystems. To better quantify historical forest patterns, a spatial simulation model of wildfire and forest succession was used to simulate pre-settlement landscape dynamics in the Oregon Coast Range, U.S.A. The model was parameterized to simulate fire regimes over 1000 years prior to Euro-American settlement using data from paleoecological, dendroecological, and historical sources. A simple fire-spread algorithm produced mosaics of variable fire severity and allowed simulated fires to be calibrated to match the shapes of real fires. The simulated landscape was spatially heterogeneous and highly dynamic. Old growth was the dominant patch type occupying a median of 42% of the total area. The relatively long fire return intervals, highly skewed fire size distributions, and mixed severities characteristic of the historical fire regime generated a landscape mosaic with large (> 100 000 ha) patches of old-growth forest, although smaller patches (<100 ha) were the most numerically abundant. Both small and large patches of old forest have important ecological roles in a dynamic ecosystem, and future landscape management efforts should consider the implications of altering these historical patterns.

Résumé : L'inquiétude engendrée par la fragmentation des forêts du Nord-Ouest du Pacifique est basée sur l'hypothèse que ces paysages renfermaient historiquement de grandes parcelles contiguës de forêts anciennes. Cette supposition semble toutefois contredire les résultats des travaux de recherche sur l'historique des perturbations qui montrent que le feu était une composante importante des écosystèmes forestiers avant la colonisation. De façon à mieux quantifier la répartition originale des forêts, un modèle spatial de simulation du feu et de la succession forestière a été utilisé pour simuler la dynamique du paysage avant la colonisation dans la chaîne côtière de l'Oregon, aux États-Unis. Le modèle a été paramétré pour simuler des régimes de feu sur le millier d'années précédant la colonisation euro-américaine à partir de données d'origine paléoécologique, dendroécologique et historique. Un algorithme simple de propagation du feu a produit une mosaïque de feux de sévérité variable et a permis de calibrer les feux simulés pour les faire correspondre à la forme des feux réels. Le paysage simulé était hétérogène dans l'espace et fortement dynamique. Les forêts anciennes correspondaient au type dominant d'écosystème, dont la médiane représentait 42 % de la superficie totale. Les intervalles relativement longs entre les feux, les distributions fortement asymétriques de la taille des feux ainsi que les sévérités mixtes, caractéristiques du régime de feu historique, génèrent un paysage diversifié avec de grandes parcelles (> 100 000 ha) de forêts anciennes, quoique les parcelles plus petites (<100 ha) soient numériquement les plus abondantes. Les parcelles petites et grandes de forêt ancienne ont un rôle écologique important dans un écosystème dynamique, et les efforts futurs d'aménagement du paysage devraient considérer les conséquences reliées à l'altération de ces structures historiques.

[Traduit par la Rédaction]

Introduction

The field of landscape ecology studies the effects of human activities on ecological systems at large spatial scales. However, most ecological assessments have not considered human-induced changes in the context of the natural variability characteristic of historical landscapes. Disturbances such as wildfire, wind, and flooding were common in pre-settlement forests, creating a shifting mosaic in which the amounts and spatial patterns of seral stages continually fluctuated (Bonnicksen 2000). Understanding historical landscape dynamics may provide a key to assessing human impacts on disturbance regimes and landscape patterns (Morgan et al. 1994; Landres et al. 1999; Swetnam et al. 1999). Pre-settlement landscapes are assumed to have supported the native biodiversity that we currently wish to preserve, including many species that have adapted to disturbance-driven fluctuations in their habitats over past millennia (Bunnell 1995). Therefore, if disturbance rates, sizes, and effects are similar to those that occurred historically, the resulting forest mosaic should support the diversity of species that existed in the past (Hunter 1993).

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Landscapes that differ substantially from historical conditions may indicate a decreased capacity for sustaining native species.

Much of the landscape-scale forest research in the Pacific Northwest has been grounded in the assumption that pre-settlement landscapes were dominated by a late-successional forest matrix. Ecological studies have examined the influences of timber harvesting on forest landscape patterns (Franklin and Forman 1987; Spies et al. 1994), the effects of clearcuts on old-growth habitats along the forest edge (Chen et al. 1992, 1995), and the impacts of habitat fragmentation on populations of native birds and mammals (Carey et al. 1992; McGarigal and McComb 1995; Perault and Lomolino 2000). Current forest management policies on federal lands are focused on preserving and restoring large blocks of old-growth habitat (FEMAT 1993). Disturbance history studies, however, have provided evidence of fire-return intervals shorter than 100 years in drier Douglas-fir forests (Morrison and Swanson 1990; Impara 1997; Weisberg 1998) and the occurrence of catastrophic burns larger than 100 000 ha in coastal forests (Teensma et al. 1991). These findings call for a re-examination of current assumptions about historical landscape patterns. Could these fire regimes have produced landscapes with large, contiguous areas of old forest?

Our understanding of historical landscapes is largely derived from data on forest conditions in the late 19th and early 20th centuries (Teensma et al. 1991; Rasmussen and Ripple 1998; Ripple et al. 2000) and from estimates of the forest age distribution based on simple, equilibrium models of fire frequency (Ripple 1994). This assumption of a steady-state landscape is unrealistic in ecosystems characterized by large disturbances and long recovery times (Turner et al. 1993). It is, therefore, necessary to characterize a range of possible patterns over a long time period rather than simply estimate static landscape conditions. Because earlier landscape records are gradually overwritten by more recent disturbances, it is difficult to reconstruct landscape patterns more than a few centuries into the past (Wallin et al. 1996). However, it is possible to obtain estimates of frequencies, sizes, and severities of past disturbances (Morrison and Swanson 1990; Teensma et al. 1991; Impara 1997; Long et al. 1998; Weisberg 1998).

Computer modeling has emerged as a promising framework for integrating disturbance history data with information about disturbance processes and ecological responses. By simulating disturbance patterns in time and space and tracking the resulting successional changes, landscape models can estimate forest patterns and dynamics. Several spatial simulation models have been used to explore the influences of fire frequency and size on forest age structure. These models have been used to demonstrate the sensitivity of landscape variability to the scale of analysis (Baker 1993; Boychuk and Perara 1997; Wimberly et al. 2000), examine changes in landscape pattern following shifts in the fire regime (Baker 1992, 1995), and estimate ranges of landscape variability under historical fire regimes (Andison 1998; Andison and Marshall 1999; Wimberly et al. 2000). Other studies have used landscape models to link fire regimes with forest community dynamics (He and Mladenoff 1999; Roberts and Betz 1999) and geomorphic processes (Benda and Dunne 1997).

The objective of this study was to estimate historical variability in the landscape patterns of pre-settlement forests in the Oregon Coast Range. Previous research used the landscape age-class demographics simulator (LADS) to assess historical amounts of old-growth forests in the Coast Range (Wimberly et al. 2000). A new, spatially explicit version of LADS was developed for the present study. This enhanced model simulates spatial variability in fire frequency and size using a cellular automata based fire-spread subroutine that allows fire patterns to be calibrated to the shapes of real fires. Additional features include a mixed-severity fire regime in which fire severity is linked to fire size, a multiple-pathway succession model that allows old growth to develop more rapidly after moderate-severity fires than after stand-replacing burns, and a buffer zone to model fire spread from outside the simulated landscape. The landscape simulator was used to predict the relative abundance of forest structure classes; the size distribution of forest patches; and the spatial patterns of fire frequencies, fire severities, and structure classes under the pre-settlement fire regime.

Model overview

Landscape representation

This Oregon Coast Range was simulated as a grid of 9 ha (300 × 300 m) cells. The study area encompassed approximately 23 000 km^2 in western Oregon, bounded by the Pacific Ocean to the west, the Klamath Mountains to the south, the Willamette Valley to the east, and the Columbia River to the north (Fig. 1). Coastal areas have high annual precipitation and relatively cool growing season temperatures, with a natural fire regime characterized by large, infrequent, stand-replacing burns. Areas along the Willamette Valley margin receive less precipitation and have higher growing season temperatures, and fires are smaller, more frequent, and less severe than in the coastal areas. Maps of annual precipitation and mean growing season temperature were used to delineate these two zones by extrapolating fire regime boundaries from a dendroecological field study in the central Coast Range (Impara 1997) (Fig. 1*a*).

Physiography in the Coast Range is characterized by deeply dissected terrain with steep slopes and high stream densities. Topographic patterns were modeled using a slope position index that classified the landscape into three topographic units: valley bottom – lower hillslope, middle hillslope, and upper hillslope – ridge (Fig. 1*b*). Fire susceptibility was assumed to be highest on upper hillslopes, reflecting drier conditions and the tendency for fire to burn more rapidly uphill than downhill. Because the eastern and southern edges of the study area did not correspond with any natural firebreaks, some historical fires were assumed to have initiated outside these boundaries and burned into the study area. Fire spread from the Willamette Valley was particularly likely given evidence of widespread burning by Native Americans (Boyd 1986). To account for these external ignition sources, a buffer zone was included outside the core simulation area (Fig. 1). Fires were allowed to burn across the boundary between the buffer and the core simulation area, but landscape pattern analyses were applied only to the core.

Fig. 1. Location of the Oregon Coast Range study area, along with (*a*) climate zones and (*b*) topographic classes used in the LADS model. Solid borders encompass the core simulation area.

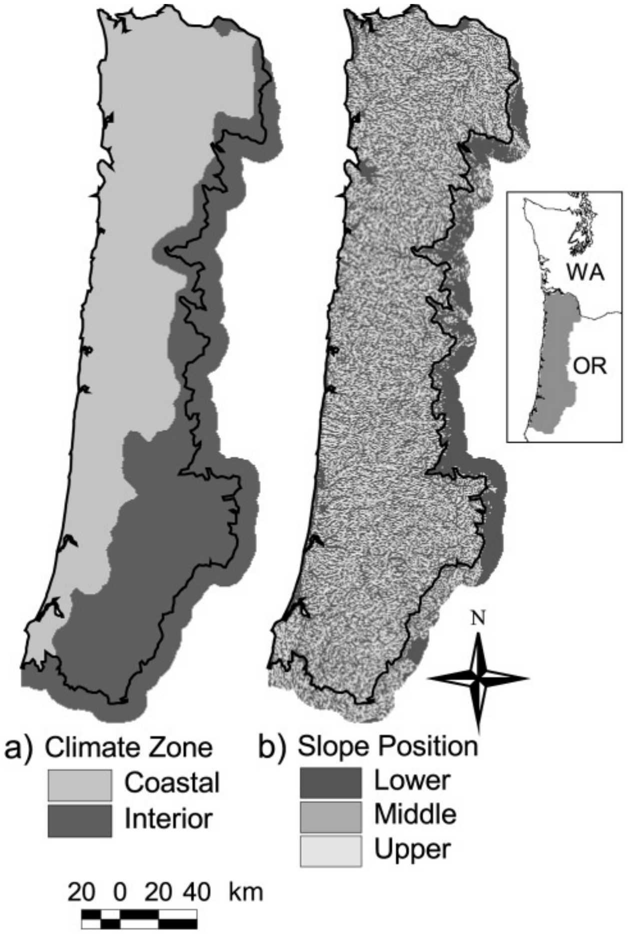
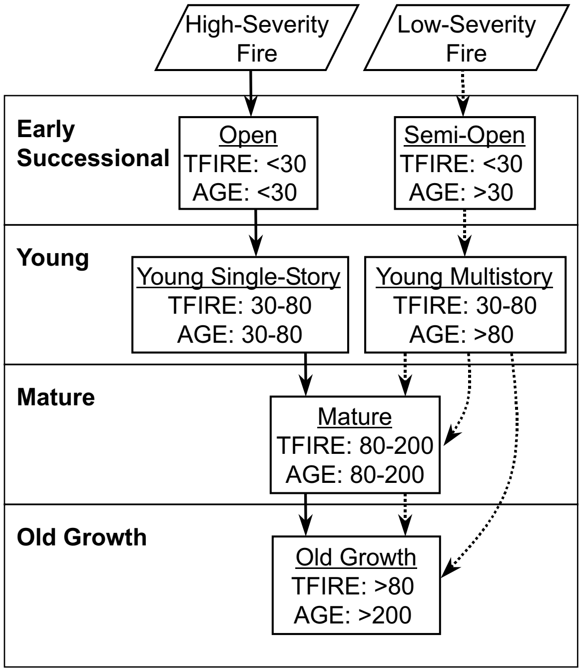


Fig. 2. Forest structure classes used in the LADS model, classified based on stand age (AGE) and time since last fire (TFIRE). Developmental stages (small boxes) can be aggregated into broader structure classes (large boxes). Solid arrows illustrate succession following a high-severity fire. High-severity fires reset both AGE and TFIRE to 0, and the post-fire stand follows a pathway through open, young, mature, and old-growth stages. Broken arrows illustrate possible successional pathways following a moderate-severity fire. Moderate-severity fires reset only TFIRE to 0, leaving a remnant cohort of older trees. Depending on the value of AGE, the stand can transition into the mature or old-growth class 80 years after the moderate-severity fire.



Stand dynamics

An age-based model of forest structure development was used to simulate stand dynamics. Although species composition of Coast Range forests varies with climate and topographic position, structural development is closely linked to stand age and has a comparatively weak relationship with environmental heterogeneity (Spies and Franklin 1991; Wimberly and Spies 2001). Immediately after a stand-replacing fire, early successional patches (<30 years) are dominated by herbaceous plants, shrubs, and seedlings with high levels of snags and down logs from fire-killed trees. Most young stands (30–80 years) have little understory vegetation and are characterized by dense canopies of *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) or *Picea sitchensis* (Bong.) Carrière (Sitka spruce), often in mixture with *Alnus rubra* Bong. (red alder). Mature forests (80–200 years) are distinguished by the re-initiation of understory tree recruitment and often have low volumes of snags and down logs. Old-growth forests (>200 years) are characterized by large live trees, multi-layered canopies, prevalence of cavities, broken tops, or other defects, and high levels of snags and down logs. Douglas-fir often survives ground fires because of its thick, fire-resistant back, leaving a cohort of live remnant trees on the disturbed site (Agee 1993). Because of the large live trees, snags, and down wood that remain after these moderate-severity fires, old-growth characteristics can develop in less than 100 years after the burn (Goslin 1997; Wimberly and Spies 2001).

Each cell was assigned a forest structure class based on the number of years since the last high-severity, stand-replacing fire (AGE), and the number of years since the last moderate- or high-severity fire (TFIRE). Thus, high-severity fires reset both AGE and TFIRE to zero, whereas moderate-severity fires reset only TFIRE to zero (Fig. 2). Following a high-severity fire, forests passed though open, young single-story, mature, and old-growth stages. Following a moderate-severity fire, forests typically passed through semi-open and young multi-story stages. Then, if a remnant cohort of older trees was present (as represented by the AGE variable), the forests could move directly into the old-growth stage 80 years after the moderate-severity burn. For the purposes of this study, we combined open and semi-open classes into an “early successional” class, and young single-story and young multi-story classes into a “young” class (Fig. 2). Vegetation-related variability in fire susceptibility was modeled as a function of time since the last fire, following the U-shaped relationship described by Agee and Huff (1987). Fire susceptibility was assumed to be highest immediately after fire because of high fuel levels from the fire-killed trees.

Fire susceptibility then decreased in the young age-class as these fuels decayed and increased again as stands gradually accumulated more dead fuels in the mature and old-growth classes (Wimberly et al. 2000).

Fire regimes

The rate of burning for each climate zone was specified by the natural fire rotation (NFR), which equaled the mean number of years required to burn an area equal in size to the climate zone (Heinselman 1973). Published data from a dendroecological study of fire history in the central Coast Range were used to compute a NFR of 200 years for the coastal–interior zone and 100 years for the valley margin zone over the 366 years preceding Euro-American settlement (Impara 1997). These NFR estimates were assumed to be representative of the Coast Range fire regime over the past 1000 years, based on an analysis of macroscopic charcoal in sediments from Little Lake, in the central Coast Range (Long et al. 1998). This study showed that mean fire return interval at this site was relatively stable over 1000 years prior to Euro-American settlement, ranging from 192 to 220 years. Although these results were obtained from a single sediment core, comparisons with the dendroecological data indicated that this charcoal record reflected regional fire events in the coastal zone more than smaller, local fires (Impara 1997).

To model the occurrence of discrete fire events, the overall rate of burning specified by NFR was converted to the frequency of individual fires

$$[1] \qquad \mathrm{FF} = 10\left(\frac{A}{\mathrm{NFR} \times \mathrm{MFS}}\right)$$

where FF is the mean number of fires per decade in a given climate zone, A is the total area of the climate zone, MFS is the mean fire size, and NFR is the natural fire rotation (Boychuk et al. 1997). The temporal pattern of fires per decade in each climate zone was modeled as a Poisson random variable, with the parameter λ equal to 1/FF.

The size of each fire was randomly determined from a lognormal probability distribution, parameterized using four historical vegetation maps from 1850, 1890, 1920, and 1940 (Teensma et al. 1991). These maps included the boundaries of recently burned patches that had been identified using multiple historical data sources. A separate fire size distribution was computed for each climate zone. Both the negative exponential distribution (Boychuk et al. 1997; Wimberly et al. 2000) and the lognormal distribution (He and Mladenoff 1999) were examined as potential models. The lognormal probability distribution had the closest fit to the empirical size distributions, and was therefore used to simulate historical fire sizes (Fig. 3). Parameters were computed as the mean (μ) and variance (r) of the log-transformed fire sizes. The mean (MFS) and standard deviation (SDFS) of the untransformed fire sizes were then computed for each climate zone from μ and r (Ott 1995).

Fire patterns

The LADS model was designed to simulate landscapes over large temporal (hundreds of years) and spatial (millions of hectares) extents. These constraints necessitated a fire-spread algorithm that was computationally efficient, was sensitive to spatial variation in fire susceptibility, and could be calibrated to change the fire shapes. Fire-behavior models such as BEHAVE (Andrews 1986) and FARSITE (Finney 1999) have been incorporated into landscape dynamics simulators but operate at finer spatial and temporal scales than those used in LADS. Although these physical models produce reasonable estimates of the shapes of small fires when sufficient data is available, they are less well suited for predicting the behavior of very large, high-severity conflagrations (Turner and Romme 1994). Cellular-automata models do not predict spread rates as well as physical models, but they have proved useful for efficiently simulating fire patterns similar to those observed in nature. A cellular automata based fire simulator was developed for LADS by adapting the algorithms of Clarke et al. (1994) and He and Mladenoff (1999).

Each fire initiated at random cell in the appropriate climate zone, with ignition probabilities weighted so that fires were more likely to start in more flammable vegetation types and topographic positions. Fire propagated outward from each ignition site, burning along a string of connected cells or "run" (Clake et al. 1994). Maximum run length was specified by the FRUN parameter. The terminal cell of each run then served as a new ignition site for fire spread in subsequent iterations. An additional parameter, FEXT, specified the probability of an ignition site becoming extinguished.

Fig. 3. Cumulative frequency distribution of Coast Range fires occurring in the (*a*) coastal and (*b*) valley margin climate zones. Fire sizes were computed from the maps of Teensma et al. (1991). Broken lines represent the best-fit negative exponential probability distribution. Solid lines represent the best-fit lognormal probability distribution.

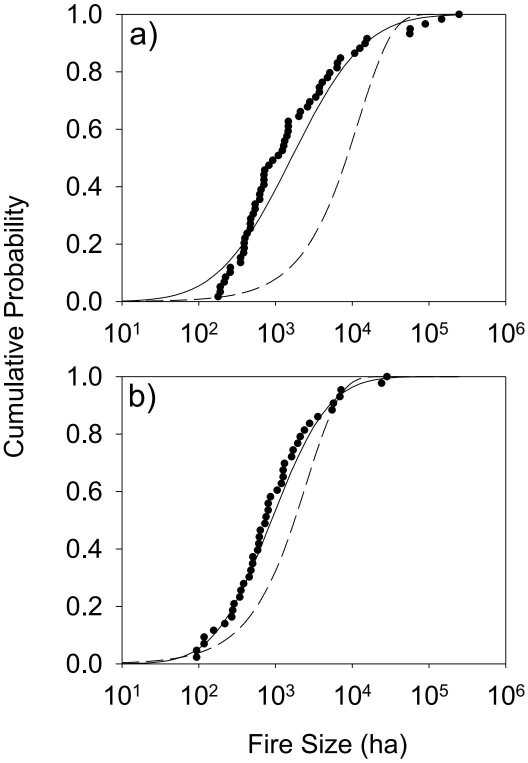


Fig. 4. Elongation indices of simulated fires compared with elongation indices computed from the Teensma et al. (1991) fires.

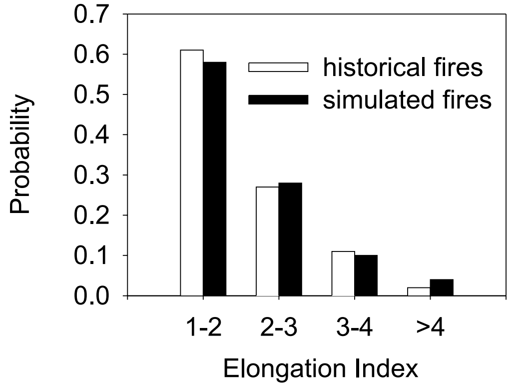
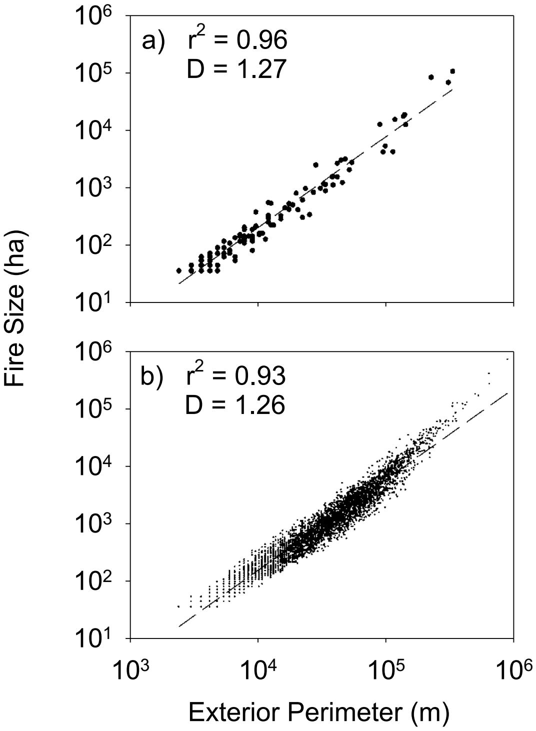


Fig. 5. Double-log fractal dimension of (*a*) mapped historical fires and (*b*) simulated fires.



Once a cell was burned and extinguished, fire could no longer burn into or out of that cell. This algorithm was repeated until the total number of burned cells was equal to the randomly determined fire size.

Direction of fire movement was chosen randomly, with the probability of spread into each neighboring cell computed as

$$[2] \qquad p(\mathrm{SPR}_i) = \frac{\mathrm{FSUSC}_i}{\sum_{i=1}^{8} \mathrm{FSUSC}_i}$$

where $p(\mathrm{SPR}_i)$ is the probability of spread into neighboring cell i, and FSUSC_i is the susceptibility of neighboring cell i. FSUSC was computed by multiplying susceptibility factors for topography, vegetation, and wind. Wind effect on fire spread was modeled as a function of the fire-spread direction, a randomly chosen wind direction, and a wind-velocity parameter (WIND). When WIND was set to 0, wind effects were negligible, and fires were generally circular. As WIND increased, wind direction had a stronger effect on fire susceptibility, and fire shapes became more elongated.

Fire-shape calibration

Fire shapes were calibrated by simulating fires over a range of FRUN, FEXT, and WIND values and comparing the predicted fire shapes with historical fire maps. Patch elongation was computed as

$$[3] \qquad E = l/w$$

where l is the length of the longest patch axis and w is patch width perpendicular to the long axis. Axis lengths were obtained from the best-fit ellipse of each burned patch using the ZONALGEOMETRY command in ARC/INFO GRID. Values of E close to 1 indicated a circular patch shape, whereas larger values denoted more elliptical shapes. Elongation indices of the simulated fires were compared with elongation indices computed from the Teensma et al. (1991) fire maps.

The fractal dimension of the simulated fires was also calculated by computing the regression of the logarithm of patch perimeter against the logarithm of patch size and calculating the fractal dimension as

$$[4] \qquad D = 2b_1$$

where b_1 is the slope of the regression equation. Values of D close to 1 indicated geometric shapes with simple perimeters. Increasing values of D denoted increasingly complex shapes with convoluted, plane-filling perimeters (McGarigal and Marks 1995). It was not possible to use the Teensma et al. (1991) maps to compute fractal dimension, because they were made at a relatively coarse spatial resolution. Instead, historical maps of fires in the Tillamook area between 1900 and 1945 (Chen 1997) and remote-sensing maps of recent fires in western Oregon derived from multi-date Landsat imagery (Cohen et al. 1998) were used. Digital maps from both of these sources were rescaled to 300-m grids to make them comparable with the simulated fires. Simulated fires generated with WSUSC = 6, FRUN = 2, and FEXT = 0.78 had a distribution of elongation indices similar to that of the historical fires (Fig. 4). In addition, fires simulated with these parameters had complex fractal shapes, similar to real fires, as measured by the fractal dimension (Fig. 5). These parameter values were used in all subsequent simulations.

Fire severity

Fires in the Pacific Northwest are typically mosaics of variable fire severity, which can be classified into low-, moderate-, or high-severity patches (Morrison and Swanson 1990; Agee 1993). Low-severity patches are remnant islands within larger burns where fire did not spread or where overstory mortality was minimal. Estimates of percent unburned interior area ranged from 9% for the Tillamook fire of 1933 (ODF 1983) to 30% or more for smaller fires in the Oregon Cascades and the Valley Margin Zone of the Coast Range (Morrison and Swanson 1990; Impara 1997; Kushla and Ripple 1997). Percent unburned islands from simulated fires generally fell within this range. Small fires tended to

Table 1. Parameters used in the LADS baseline and sensitivity runs.

Parameter	Description	Baseline run	Sensitivity runs –	Sensitivity runs +
NFR_c	Natural fire rotation for coastal zone (years)	200	160	240
NFR_v	Natural fire rotation for valley margin zone (years)	100	80	120
MFS_c	Mean fire size for coastal zone (km^2)	73	58.4	87.6
MFS_v	Mean fire size for valley margin zone (km^2)	22.2	17.8	26.6
$SDFS_c$	SD of fire size for coastal zone (km^2)	320.5	218.1	384.6
$SDFS_v$	SD of fire size for valley margin zone (km^2)	51.0	34.9	61.2
SEV(1)	Minimum severity of fires <100 km^2	0.0	0.0	0.05
SEV(2)	Maximum severity of fires <100 km^2	0.5	0.4	0.55
SEV(3)	Minimum severity of fires 100–500 km^2	0.1	0.01	0.18
SEV(4)	Maximum severity of fires 100–500 km^2	0.8	0.71	0.9
SEV(5)	Minimum severity of fires >500 km^2	0.7	0.535	0.98
SEV(6)	Maximum severity of fires >500 km^2	0.95	0.785	1.0
FEXT	Fire shape calibration parameter (see text)	0.78	0.624	0.93
FRUN	Fire shape calibration parameter (see text)	2	2	2
WIND	Wind strength index (see text)	0.6	0.48	0.72

have the highest amounts of unburned interior, whereas the largest, high-severity fires typically had less than 20% unburned interior.

The area actually burned by each fire was a mixture of moderate- and high-severity fire. Data from several fire-history studies suggest that the ratio of high- to moderate-severity disturbance increased with fire size but was highly variable at all fire sizes (Morrison and Swanson 1990; Impara 1997). This relationship between size and severity reflects the occurrence of large burns under extremely dry and windy conditions, which often lead to widespread crown fires with high levels of overstory mortality (Agee 1993; Turner and Romme 1994). The probability of high-severity disturbance (SEV) within each fire was modeled as a uniform random variable for three fire size classes (Table 1) with the minimum and maximum values for each size class based on published fire-severity data (Impara 1997). Each pixel was assumed to burn at high severity with probability equal to SEV and at moderate severity otherwise. SEV values were also weighted by topography and vegetation such that high-severity fires were most likely to occur on upper hillslopes and in forests less than 30 years old (Agee and Huff 1987; Impara 1997).

Landscape analysis

The range of possible historical landscape patterns was examined by making a 50 000 year simulation of landscape dynamics. The model was run for an initial 1000-year period to overwrite arbitrary initial starting conditions, and landscape summaries were computed at 200-year intervals thereafter. Running the model for 50 000 years does not mean that the simulation reflected the 50 000 year period prior to Euro-American settlement. Rather, the lengthy simulation period was necessary to estimate the full range of variability in landscape conditions that could have occurred during the 1000-year time frame of the model.

We selected four easily interpretable landscape metrics to describe the spatial structure of the simulated historical landscapes: percentage of total area, size of largest patch, patch density, and edge density. These indices were calculated for each of the four structure classes using the APACK program (Mladenoff and DeZonia 2000). The simulated historical variability of each index was summarized as a boxplot. In addition, the mean and SD of the number and total area of patches were computed for six patch size classes and summarized as histograms. Spatial patterns of fire occurrence were described by computing the mean fire return interval and the percentage of high-severity fires for each cell. The spatial distribution of forest structure classes was also summarized by computing the percentage of time that cells were occupied by each structure class.

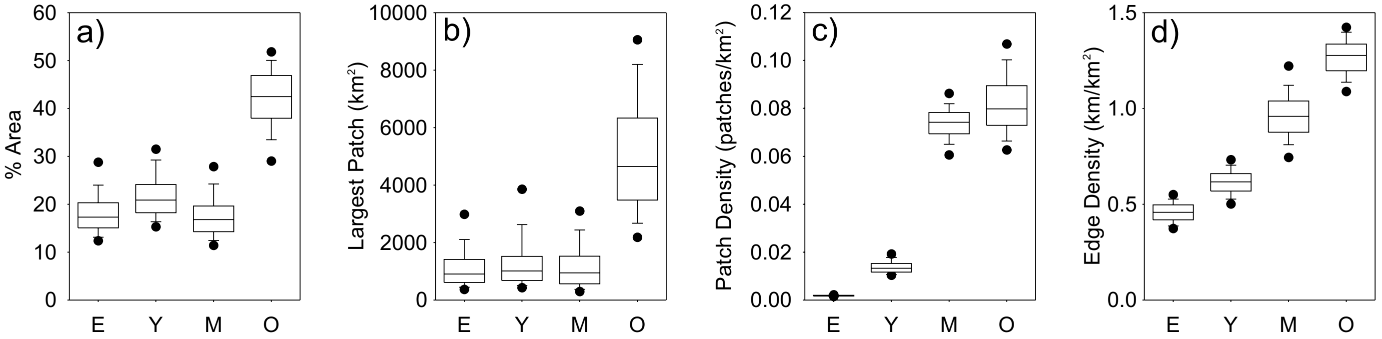
A sensitivity analysis was carried out to assess the potential for changes in the parameters to affect the simulated landscape patterns. Sets of input parameters were altered one at a time and model results were compared with values obtained from a baseline simulation. The NFR, MFS, WIND, and FEXT parameters were each varied ±20% of their baseline values (Table 1). NFR and MFS were varied simultaneously across climate zones to examine the aggregate response over the entire landscape. SDFS was varied simultaneously with MFS, reflecting the strong correlation between these two parameters. The SEV parameters were varied simultaneously to vary the proportion of high-severity fires in each size class by ±20%. Ten independent model runs were made for each parameter set. Each run was 1000 years in length, following a 1000-year initialization phase, with landscape summaries computed at 10-year intervals. Results were expressed as the percent changes in the mean values of the landscape indices relative to the baseline run.

Results

Historical ranges of variability

Despite the large study area, the simulated landscapes were far from equilibrium. The amounts and spatial arrange-

Fig. 6. Historical ranges of variability from 250 simulated landscapes, based on fire regimes characteristic of the Oregon Coast Range over the 1000 years prior to Euro-American settlement. Landscape metrics include (*a*) percentage of total area, (*b*) largest patch size, (*c*) patch density, and (*d*) edge density computed separately for early successional (E), young (Y), mature (M), and old-growth (O) patches. Boxplots display the median (centre line), 25 and 75% quantiles (box), 10 and 90% quantiles (whiskers), and 5 and 95% quantiles (solid circles) of each landscape metric.



ments of the forest structure classes varied over time, reflecting the spatial patterns of the simulated fires. Old growth was the most abundant structure class in the simulated historical landscapes, occupying a median 42% of the total area and typically ranging from 29 to 52% (Fig. 6*a*). Young forest was the next most common structure class, varying between 15 and 31% with a median of 21%. Early successional forests occupied between 12 and 29% of the landscape with a median of 17%. Mature forests were the least abundant, covering 12–28% of the landscape with a median of 16%. The largest old-growth patch had a median size of 4300 km^2 but varied widely from 2100 to 8500 km^2 (Fig. 6*b*). Largest patches of the other structure classes were generally smaller than 2000 km^2. Densities of mature and old-growth patches were always much higher than the densities of early successional and young patches (Fig. 6*c*). Edge density was lowest for early successional patches and increased for young, mature, and old-growth patches (Fig. 6*d*)

Two distinctive scales of spatial heterogeneity were noted in the simulated landscapes (Fig. 7). Small patches dominated the patch-size distributions (Figs. 8*a*–8*d*), with more than 80% of patches in the young class and nearly 95% of patches in the mature and old-growth stages less than 100 ha in size. Most of these small patches were created by the heterogeneous fire patterns that left many low-severity islands within larger burned areas, and created mosaics of high- and moderate-severity fire that led to different successional trajectories. A coarser scale mosaic of large patches was created by the spatial pattern of the large fires. Proportions of total area occupied by each size class were heavily skewed toward the larger patches (Figs. 8*e*–8*h*). Seventy-two percent of the total mature forest area was concentrated in patch sizes larger than 1000 ha, and 75% of early successional and young forest occurred as patches larger than 10 000 ha. More than 70% of the total old growth area was clustered into patches larger than 100 000 ha.

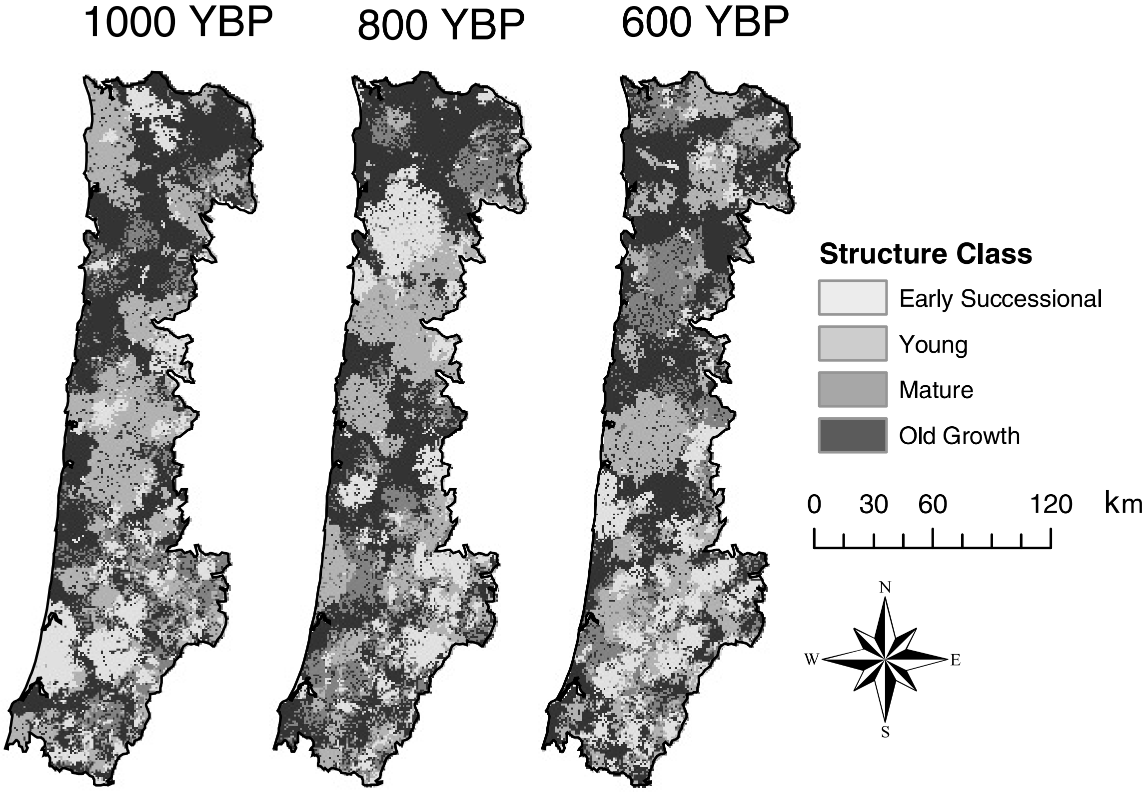
Spatial patterns of fire frequency and severity

The simulated pattern of fire-return intervals reflected the underlying climate zones. Fire-return interval was longest and fire severity highest in the northern and western portions of the Coast Range (Figs. 9*a* and 9*b*). Fire-return interval and severity both decreased to the east and south. Finer scale patterns reflected topographic variation in fire susceptibility with fire-return intervals longer and incidence of high-severity fires lower in valley bottoms than on adjacent ridges. The landscape distribution of old growth was predominantly controlled by the fire-return interval. Old growth occurred most frequently in the coastal and northern areas where fire-return intervals were long, even though high-severity fires were most prevalent in these areas (Fig. 9*f*). Early successional and young forests occurred most frequently in valley-margin areas with short fire-return intervals (Figs. 9*c* and 9*d*). Mature forests were slightly more frequent in coastal areas than along the valley margin (Fig. 9*e*).

Sensitivity analysis

The percent area in each size class responded most strongly to changes in NFR, with early successional, young, and mature areas decreasing and old-growth area increasing at higher NFR values (Table 2). The sizes of the largest early successional, young, and mature patches decreased and the size of the largest old growth patch increased with NFR. Patch densities and edge densities generally decreased with increasing NFR. The largest patch sizes of early successional, young, and mature forests increased with MSIZE, whereas the densities of early successional, young, and mature forest patches decreased with increasing MSIZE. Changes in SEV had a particularly strong influence on the area and spatial pattern of mature forests. As SEV decreased, larger areas of moderate-severity fire occurred, and more forests moved directly from the young to old-growth classes without passing through the mature class (Fig. 2). The size of the largest early successional patch increased considerably when FEXT was raised 20% above its baseline value. Patch density and edge density also increased with FEXT, reflecting more complex patch perimeters and more unburned islands in the simulated fires. The effects of varying the FEXT parameter were nonlinear; the 20% increase typically had a much greater effect than the 20% decrease. All landscape indices exhibited relatively weak responses to changes in WIND, although largest patch size tended to decrease with increasing WIND.

Fig. 7. Simulated landscape mosaics at (*a*) 1000, (*b*) 800, and (*c*) 600 years before present (YBP) from a single 1000-year run of the LADS model. Because the occurrences and spatial patterns of fires are stochastic, these maps are not predicted landscape configurations for the specified points in time. Instead, they illustrate the variability in landscape patterns that arises from the simulated pre-settlement fire regime.



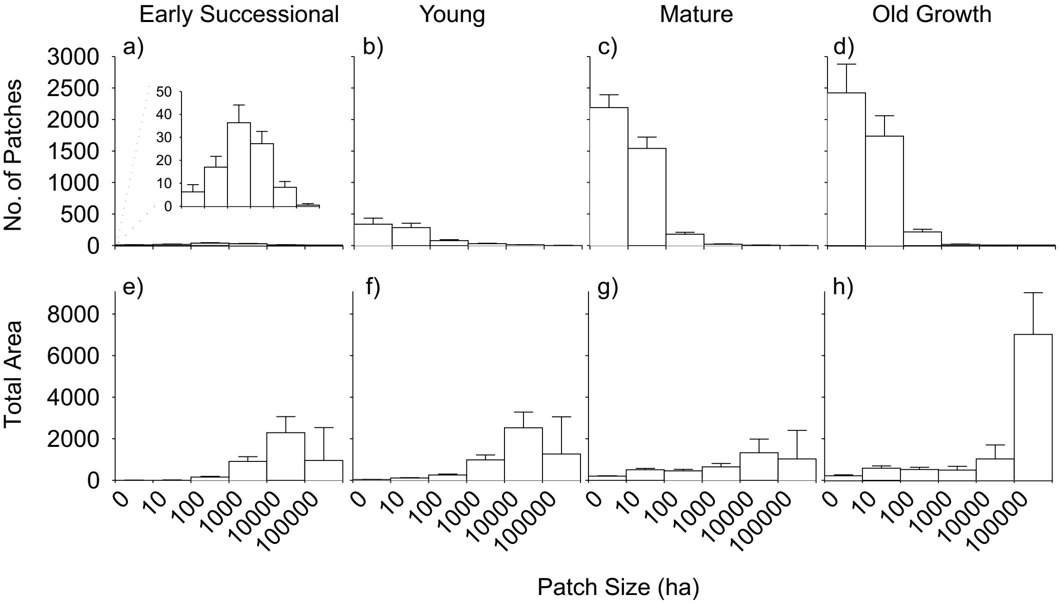
Discussion

As noted by Johnson et al. (1998), suppositions about landscape patterns derived from simplistic assumptions about disturbance regimes are often misleading. Temporal variability in fire occurrence, highly skewed fire size distributions, successional time lags, and the gradual erasure of past landscapes all combine to produce a complex and unpredictable dynamic mosaic. Spatially explicit simulations of landscape dynamics provide more rigorous, quantitative estimates of landscape structure and represent a major advance over previous assessments of historical landscapes in the Pacific Northwest (Ripple 1994; Wallin et al. 1996; Wimberly et al. 2000). Simulation results suggest that old growth was the dominant structure class in pre-settlement landscapes, with the majority of old growth concentrated into large (> 100 000 ha) patches. The model produces a multi-scale pattern in which small patches (<100 ha) are numerically the most abundant, but large patches (> 10 000 ha) cover the majority of the landscape. Despite the limited area covered by small patches, they may still influence the long-term persistence of disturbance-sensitive species. Small patches of old growth can provide refugia for late-successional species within larger burned areas and then serve as foci for later recolonization (Sillett et al. 2000; Wimberly and Spies 2001).

These conclusions about landscape patch structure under natural fire regimes contrast with findings from other parts of western North America. In boreal forests, old growth has been found to be relatively rare, typically occurring as small patches embedded in a mosaic of younger forests (Andison 1998; Johnson et al. 1998; Weir et al. 2000). Because mean fire-return intervals in the Oregon Coast Range (100–200 years) are longer than those typically reported for boreal forests (<100 years), a larger proportion of the landscape is expected to survive 200 years or longer. In forested landscapes of the northern Rocky Mountains, estimates of mean old-growth percentage derived from natural fire regimes were mostly lower than 40%, with many landscapes having less than 20% old growth (Lesica 1996). Reported fire intervals in the northern Rockies spanned a range of values similar to those in the Oregon Coast Range. However, the methods used by Lesica (1996) to compute old-growth percentage assumed that all fires were stand-replacing burns. Coast Range forests have a mixed-severity disturbance regime that includes a significant proportion of moderate-severity fire. Because old-growth structure develops more rapidly following moderate-severity fire than after a high-severity fire, old-growth levels in the Coast Range are higher than would be expected under a comparable stand-replacement fire regime.

Even within the Oregon Coast Range there is considerable spatial variability in the simulated patch mosaic. Although many areas in the coastal climate zone are old growth, more than 50% of the time, other sites in the valley margin zone are old growth less than 30% of the time, with a correspond-

Fig. 8. Patch size distributions by structure class generated from 250 simulated landscapes, based on fire regimes characteristic of the Oregon Coast Range over the 1000 years prior to Euro-American settlement: (*a*–*d*) proportion of the total number of patches in each size class and (*e*–*h*) proportion of total area covered by each size class. Error bars are SDs. Note the logarithmic scale.



ing increase in the prevalence of early successional and young forests. Because of higher fire frequencies and smaller fire sizes in the valley margin zone, patch sizes are generally smaller and the landscape more heterogeneous than in the coastal zone. These contrasts should caution that inferences about forest dynamics derived from a particular disturbance regime are not necessarily transferable to different forest ecosystems, or even to different landscapes within a particular region. Estimates of fire-return intervals in coastal Douglas-fir forests range from less than 100 years (Morrison and Swanson 1990) to over 400 years (Hemstrom and Franklin 1982), suggesting that a considerable variety of forest patterns could emerge despite the generally similar climate, physiography, and dominant species across this region.

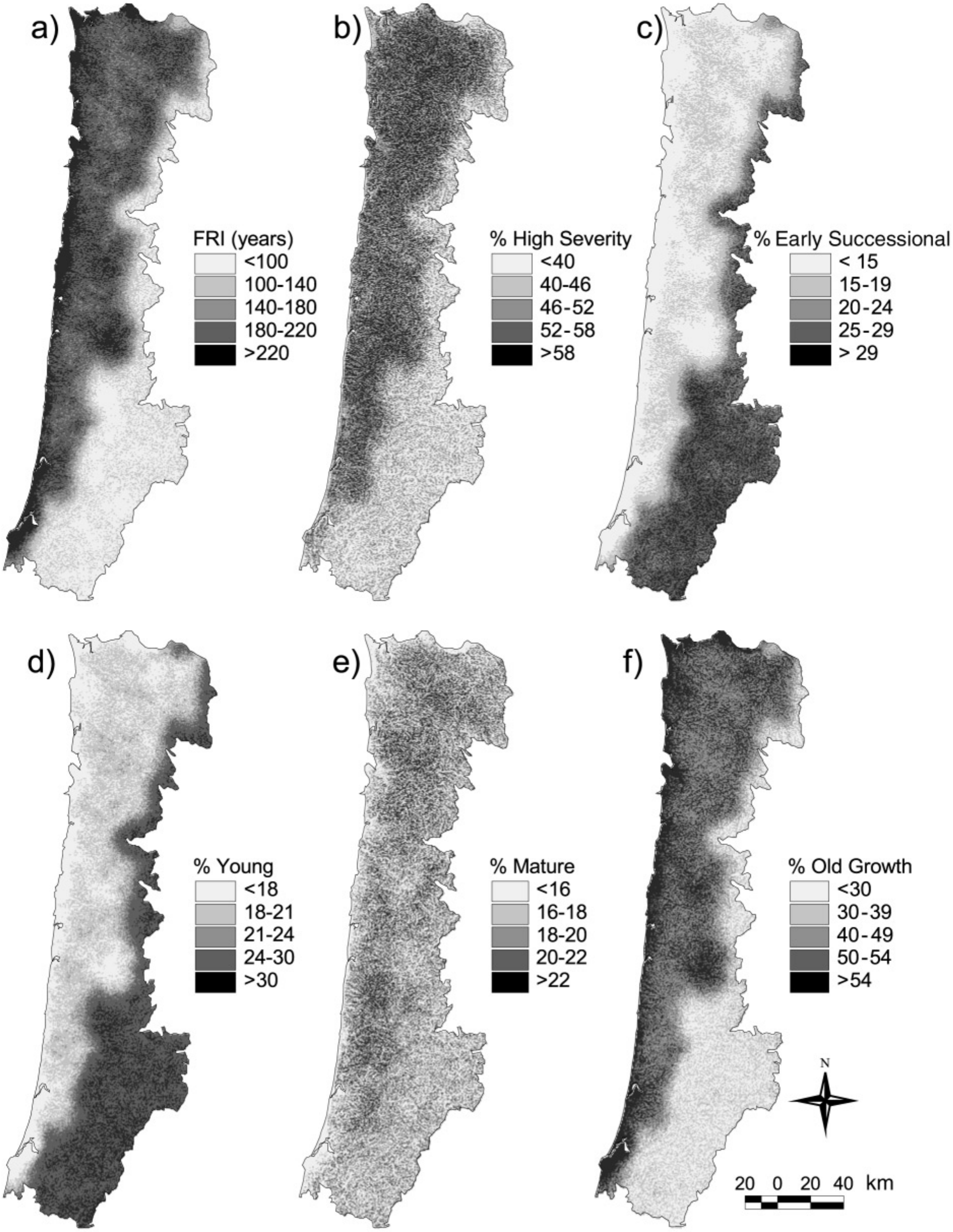
Assumptions and limitations

The simulations presented here must be interpreted in light of their underlying assumptions. Succession was simulated using a simple model that categorized forests into broad structure classes. Vegetation and fire patterns were modeled at a relatively coarse spatial scale (9-ha cells) to limit the number of parameters and increase simulation efficiency. Because edge effects can influence the microclimate and forest structure of old growth ≥100 m from the stand edge (Chen et al. 1992, 1995), 9 ha represents a reasonable minimum mapping unit for delineating old-growth stands. Although patches are presumed to be structurally distinct from surrounding vegetation, each patch also encompasses a finer scale mosaic of varied forest conditions including species gradients related to climate and topography (Ohmann and Spies 1998; Wimberly and Spies 2001), canopy gaps caused by insects, disease, or windthrow (Spies et al. 1990), and riparian corridors (Pabst and Spies 1999). Thus, range of historical variability estimates generated using LADS are most applicable to large-scale studies based on broad habitat classes rather than fine-grained, site-specific assessments.

Simulations of historical variability are also highly dependent on spatial and temporal extent. Historical variability was modeled across the entire Coast Range province, rather than for individual watersheds or ecoregions, because a previous study demonstrated that historical ranges of variability computed at smaller extents were too broad to be of practical use (Wimberly et al. 2000). Similarly, if too short a temporal window is considered, landscape conditions may reflect short-term variations in climate or disturbance that are not representative of longer time periods. As the temporal extent lengthens, however, it will encompass climate, species compositions, and disturbance regimes that are increasingly uncharacteristic of the present day. The selection of the past 1000 years to model historical variability is a compromise between these two extremes. Assessments of climate, fire regimes, and species composition suggest that this period had ecological conditions generally similar to the present day but is also long enough to incorporate disturbance-driven fluctuations and a variety of different landscape patterns (Worona and Whitlock 1995; Long et al. 1998).

Several major assumptions were necessary to estimate model parameters using available data. Estimates of natural fire rotation and fire severity were obtained by extrapolating results from a fire-history study with a limited spatial (1375 km^2) and temporal (366 years) window to the 23 000 km^2 Coast Range over a 1000-year period. Although fire size and shape estimates were obtained from a much larger area, they only encompass a relatively short time period (90 years). Even though the paleoecological record suggests that fire regimes were fairly stable over the past 1000 years, the degree of error resulting from these extrapolations is unknown. Results from the sensitivity analysis emphasize that accurate estimates of the natural fire rotation are particularly critical for modeling the areal distribution of the forest structure classes, as well as largest patch size, patch density, and edge density

Fig. 9. Landscape pattern summaries from a 50 000 year simulation of Oregon Coast Range landscape dynamics, based on fire regimes characteristic of the 1000 years prior to Euro-American settlement. (*a*) mean fire return interval (FRI), (*b*) percentage of fires that were high severity, (*c*–*f*) percentage of time each cell was in the (*c*) early successional, (*d*) young, (*e*) mature, and (*f*) old-growth stage.



for certain structure classes. Fire-shape calibration does not greatly affect the relative area or largest patch size of most structure classes but does have a strong influence on patch density and edge density.

The LADS model was designed to be flexible enough to incorporate new information as it becomes available. As more research on historical fire regimes is carried out, it will either corroborate the current assumptions or be used to up-

Table 2. Results from sensitivity analysis of LADS model simulations of historical Coast Range landscape patterns.

	NFR		MSIZE		SEV		FEXT		WIND	
	–	+	–	+	–	+	–	+	–	+
% Area										
Early successional	23	–14	3	4	1	–1	4	1	5	–2
Young	13	–11	1	2	0	–2	2	1	2	–1
Mature	4	–9	–5	3	–15	28	3	0	3	3
Old growth	–18	16	1	–4	6	–11	–4	–1	–4	3
Largest patch										
Early successional	27	–19	–5	16	1	0	1	43	12	–9
Young	13	–17	–6	13	–3	–3	1	16	2	–8
Mature	3	–12	–7	19	–19	34	16	–18	13	–6
Old growth	–32	38	–1	–4	12	–12	–1	–17	–11	1
Patch density										
Early successional	4	–6	14	–13	0	1	4	–15	1	1
Young	34	–18	12	1	3	0	–23	48	5	–1
Mature	3	–3	9	–4	7	–18	–18	36	–2	4
Old growth	9	–12	–2	0	–9	–5	–12	13	3	–1
Edge density										
Early successional	17	–12	9	–3	0	–1	–24	49	–2	1
Young	13	–10	8	–2	0	0	–23	48	–2	2
Mature	1	–7	0	–3	–2	4	–10	17	0	0
Old growth	–5	–1	4	–5	4	–9	–14	27	–2	3

Note: Values are the percent changes in the mean values of landscape indices relative to the baseline run. See Table 1 for definitions of variables.

date model specification and parameterization. In particular, more work is needed to characterize the spatial and temporal variability of fire regimes. Simulated landscape patterns were strongly influenced by the stratification of the landscape into discrete climate zones. Additional data on patterns of fire frequency, severity, and size could be used to develop more sophisticated spatial models of fire regimes (McKenzie et al. 2000). Several fire-history studies have found temporal shifts in fire frequency at the scale of centuries (Johnson and Larsen 1991; Weir et al. 2000), and this temporal variability can be readily incorporated into landscape simulations (Baker 1992; Wimberly et al. 2000). Temporal variability in fire size and severity is also of interest; given evidence suggesting that regional occurrence of large, stand-replacing fires may be associated with periods of warm climate (Weisberg 1998).

Conclusions

Simulation results demonstrated that the expectation of a landscape mosaic dominated by large patches of old forest is consistent with fire history of the Oregon Coast Range. Old-growth forests usually occupied at least 40% of the landscape. At least one old-growth patch larger than 200 000 ha was present on the landscape at all times, along with a large number of small mature and old-growth patches that were distributed in areas of younger forests. Both of these pattern elements are ecologically significant. Large patches of old forest are important habitat for some species such as the northern spotted owl (Carey et al. 1992), whereas smaller fragments may provide habitat for other old-growth associated species such as the marbled murrelet (Raphael et al. 1995) or serve as refugia for disturbance-sensitive species (Sillett et al. 2000). Simulated landscape maps emphasized the dynamic nature of the landscape mosaic, with the spatial arrangement of habitat patches continually shifting through time. Given the comparatively small area of old growth in the Coast Range today (<5%), it is reasonable to predict that current landscape patterns have shifted outside the range of historical variability that occurred under pre-settlement fire regimes (Wimberly et al. 2000).

Although the historical range of variability concept has emerged as an important paradigm in conservation biology, many of its underlying assumptions require a more thorough examination. Several key questions remain to be addressed. How much do spatial patterns of forest structures on the current landscape differ from those that occurred historically? What are the implications of these changes for the persistence of native species and maintenance of key ecosystem processes? Will current land-management policies move us closer to or further from the range of historical variability? To what extent is our ability to restore historical disturbance regimes and forest patterns constrained by the 150-year legacy of Euro-American land use and landscape alteration?

Landscape simulation models such as LADS can provide a basis for examining some of these questions. Simulated ranges of historical variability can be compared with estimates of current landscape conditions as well as projections of future landscape conditions under various management strategies. Landscape dynamics could also be linked to habitat indices for species or functional groups based on the spatial patterns of structure classes, community types or individual habitat features. In addition, spatially explicit population models could be used to examine species persistence in these dynamic landscapes. These types of assessments may eventually provide baseline information for designing and testing new management strategies that reproduce ecologically significant elements of historical landscape patterns.

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