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Spatially explicit modeling of mixed-severity fire regimes and landscape dynamics

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Abstract

Simulation models of disturbance and succession are being increasingly applied to characterize landscape composition and dynamics under natural fire regimes, and to evaluate alternative management strategies for ecological restoration and fire hazard reduction. However, we have a limited understanding of how landscapes respond to changes in fire frequency, and about the sensitivity of model predictions to assumptions about successional pathways and fire behavior. We updated an existing landscape dynamics model (LADS) to simulate the complex interactions between forest dynamics, fire spread, and fire effects in dry forests of the interior Pacific Northwest. Experimental model runs were conducted on a hypothetical landscape at fire rotations ranging from 5 to 50 years. Three sensitivity analyses were carried out to explore the responses of landscape composition to (1) parameters characterizing succession and fire effects on vegetation, (2) the probability of fire spread into different successional stages, and (3) the size and spatial pattern of static fire refugia. The area of old open-canopy forests was highest at the shortest fire rotations, and was particularly sensitive to the probability of stand-replacement fire in open-canopy forests and to the fire-free period required for ingrowth to occur in open-canopy forests. The area of old closed-canopy forests increased with lengthening fire rotation, but always comprised a relatively small portion of the landscape (<10%). The area of old closed-canopy forests increased when fire spread was more rapid in open-canopy forests than in closed-canopy forests, and when the physical landscape incorporated large ‘‘fire refugia’’ with low fire spread rates. Old closed-canopy forests appear to comprise a relatively minor landscape component in mixed-severity fire regimes with fire rotations of 50 years or less. However, these results are sensitive to assumptions about the spatial interactions between fire spread, landscape vegetation patterns, and the underlying physical landscape.

Keywords: Interior Pacific Northwest; Simulation; Fire; Succession; Late-successional forests

1. Introduction

Decades of fire suppression and forest management have caused a widespread shift in landscape patterns across much of the interior Pacific Northwest (Hessburg and Agee, 2003; Hessburg et al., 2005). Historically, low- and mixed-severity fire regimes maintained heterogeneous mosaics of open and semi-open forests dominated by fire-resistant tree species. In contrast, the modern landscape has much larger patches of dense forest dominated by shade-tolerant, fire sensitive tree species. These changes in species composition and connectivity can contribute to the occurrence of uncharacteristically large and destructive stand-replacement wildfires (Hessburg et al., 2005). Considerable efforts are currently being directed toward developing strategies for restoring historical stand structure and reducing the hazard of high-severity wildfire (Agee and Skinner, 2005). However, these efforts are hampered by a limited understanding of historical fire regimes and landscape dynamics in mixed severity fire regimes that historically included both high- and low-severity fires. In particular, there are unanswered questions about the historical abundance of late-successional forests characterized by large dominant trees, accumulations of down and standing dead wood, and dense multilayered canopies (Spies et al., 2006). Are late-successional forests in the modern landscape entirely an artifact of fire suppression, or could historical fire regimes have produced significant areas of late-successional forests?

Spatially explicit computer simulation models of natural disturbances, land management activities, and ecological processes are useful for reconstructing fire regimes in historical

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landscapes and evaluating the impacts of alternative fire management strategies on modern landscapes (Wimberly et al., 2000; Keane et al., 2002). In these models fire affects the spatial pattern of vegetation, and this pattern in turn constrains fire spread and fire effects. These interactions create strong positive and negative feedbacks, resulting in complex ecological responses to changes in the fire regime. Non-spatial models such as the Vegetation Development Dynamics Tool (Beukama et al., 2003; Wondzell et al., 2007), and spatially explicit models such as LADS (Wimberly, 2002; Nonaka and Spies, 2005), LANDSUM (Keane et al., 2002, 2003, 2006), LANDIS (He and Mladenoff, 1999; Gustafson et al., 2004), SELES (Fall and Fall, 2001; Fall et al., 2004), and SEM-LAND (Li et al., 2005; Barclay et al., 2006) have all been used for these types of assessments in a variety of landscapes. However, few studies have explored more general questions about how simulated landscapes respond to changes in fire regimes, uncertainties in parameterization, and decisions to include or exclude spatial interactions in the model.

To address these issues, we implemented a landscape modeling experiment to examine influences of fire frequency on landscape composition in dry mixed-conifer forests with mixed-severity fire regimes, and to assess sensitivity of these results to underlying model assumptions about forest succession and fire spread. The main objectives of this study were to (1) adapt an existing landscape model to simulate fire regimes and forest dynamics in mixed-severity fire regimes of the interior Pacific Northwest, (2) test the sensitivity of the model to uncertainties in key parameters characterizing successional pathways, and (3) assess the sensitivity of the model to fire spread interactions with two spatially explicit landscape features: (a) the dynamic mosaic of successional stages, and (b) the static distribution of landtypes that serve as fire refugia.

1.1. Background

Previous modeling research into the influences of disturbance regimes on forest landscape composition has focused on stand-replacement fire regimes. In these regimes, fires produce a shifting mosaic of predominantly even-aged forest stands (Johnson et al., 1998). Weather-driven fires are presumed to account for the majority of the area burned, and thus forest age is considered to have only a minor influence on fire spread and the fire size distribution (Fryer and Johnson, 1988; Bessie and Johnson, 1995). The fire rotation, or fire cycle, is defined as the number of years required for one or more fires to burn a given area (Heinselman, 1973; Agee, 1993). Theoretically, if the probability of fire remains constant at all stand ages, the resulting forest age distribution has a negative exponential distribution with a mean age equal to the fire rotation (Johnson et al., 1995). Old forests occupy the tail of this distribution, and increase in spatial extent with increasing fire rotation length. The expected age-class distribution remains negative exponential regardless of the fire-size distribution as long as the rate of spread remains independent of stand age (Boychuk et al., 1997). However, variability over time in the landscape age class distribution increases when the fire rotation is held constant, but fire size is increased and the number of fires is decreased (Boychuk and Perera, 1997). The result is that when the majority of the burned area is accounted for by a relatively small number of large fires, the age-class distribution at any point in time may be very different from the long-term expected exponential distribution.

When models of even-aged stand dynamics are modified to incorporate spatial feedbacks in the form of increasing rates or probabilities of fire spread with stand age, both the distribution and spatial arrangement of forest age classes are affected. The expected forest age structure can be modeled as a Weibull distribution with a monotonically increasing probability of fire as a function of stand age (Johnson and VanWagner, 1985). This model predicts that increasing fire hazard with stand age will lead to a smaller area of older forests than under the exponential model. A simulation experiment similarly found that mean stand age decreased with increasing dependence of ignition probabilities on stand age, although the shapes of the resulting age-class distributions were unaffected (Barclay et al., 2006). As the dependence of fire spread rates on stand age increases, the pattern of age classes on the resulting landscape becomes increasingly autocorrelated in both time and space (Peterson, 2002). In this situation, fires act to maintain landscape patterns rather than to erase them.

In comparison, considerably less is known about how landscape vegetation patterns respond to mixed-severity fire regimes that include both stand-replacement disturbances and lower severity disturbances that initiate different successional pathways. A model simulating old growth forest dynamics under historical fire regimes in coastal Oregon, USA, incorporated both moderate-severity and stand-replacement fires (Wimberly, 2002). Burned stands recovered old growth characteristics more rapidly after a moderate-severity fire than after a stand-replacement fire, and old growth levels were consequently higher than would be expected under a stand-replacement fire regime with an equivalent fire rotation. A simulation experiment examining fire effects on landscape-level species composition in the Georgia Piedmont using the LANDIS model incorporated variable fire severity as a function of stand age and species composition and examined species-specific feedbacks between fire regimes and landscape patterns (Wimberly, 2004). A simulation study of boreal forest dynamics in Fennoscandinavia also used LANDIS and found that fire severity was as important as fire return interval in determining the amount of old growth in the landscape (Pennanen, 2002). To date, no modeling studies have specifically addressed the influence of fire regimes on old forests in mixed-conifer forests of the western United States characterized by mixed-severity fire regimes, where old forests may vary considerably from open savannah-like forests to closed-canopy forests with multilayered, late-successional structure.

2. Model description

The model used in this research was the landscape dynamics simulator (LADS), a spatially explicit grid-based model originally developed to study historical variability of old-growth forests in the coastal Pacific Northwest (Wimberly et al., 2000, 2004; Wimberly, 2002). The current version of LADS has been updated to reflect forest dynamics in mixed-severity fire regimes of the interior Pacific Northwest. The fire spread subroutine has been modified to more comprehensively model variability in fire spread and fire effects as a function of fuels, forest structure, site moisture, and topography. The forest succession subroutines have also been updated to capture multiple pathways of forest development, with transitions among successional stages resulting from overstory tree growth, fire-induced tree mortality, and establishment of shade-tolerant cohorts in the absence of fire.

2.1. Fire spread

The effects of environmental heterogeneity on fire are represented at two spatial scales. Fire regime zones encompass areas that have characteristic fire frequencies, sizes, and severities. The spatial distribution of fire regimes is related to climate, vegetation, and physiography. Landtype zones delineate finer-scale environmental variability that influences the spread and effects of individual fires. For example, in some landscapes particular topographic settings may be associated with fire refugia where high soil and fuel moisture reduce fire frequency and severity (Camp et al., 1997). Landtypes can also be used to delineate non-flammable land cover such as exposed rock and water.

For each fire regime zone, the fire rotation (FR) parameter specifies the mean number of years required to burn an area the size of the fire regime zone. To model the occurrence of discrete fire events, the rate of burning specified by FR is converted to the frequency of individual fires per year.

$$\mathrm{FF} = \frac{\mathrm{SIZE}}{\mathrm{FR} \times \mathrm{MFS}} \tag{1}$$

where FF is the mean number of fires per year, SIZE is the total area of the fire regime zone, FR is the fire rotation in years, and MFS is the mean fire size. If estimates of fire rotation are not available, it is also possible to parameterize the model by directly specifying the fire frequency. The size of each fire is randomly generated from a lognormal probability distribution, with mean fire size (MFS) and standard deviation of fire size (SDFS) specified as input parameters (Wimberly, 2002).

Each fire is initiated as a single burning cell. A potential initiation cell is randomly selected in the appropriate fire regime zone, and the probability of fire ignition in that cell is computed as

$$\mathrm{PINIT} = \mathrm{VIF} \times \mathrm{LIF} \tag{2}$$

where VIF is the vegetation initiation factor and LIF is the landtype initiation factor. VIF is specified for each successional stage and LIF is specified for each landtype. Both VIF and LIF can range from zero to one, with higher values indicating higher probabilities of fire initiation. If a uniform (0, 1) random variable is less than PINIT, the fire initiates in the cell. Otherwise, another cell is randomly selected and the algorithm continues until the fire is initiated. The effect of this algorithm is to weight ignition probabilities so that fires are more likely to start in particular topographic positions and successional stages.

Fire spread is modeled using a modified cellular automata algorithm. This approach builds on the probabilistic approaches that have been applied in previous studies (Hargrove et al., 2000; Wimberly et al., 2000), but incorporates a two-stage process that allows for greater flexibility in simulating disturbance shapes. There are two main subroutines that (1) model fire spread from burning cells into adjacent cells and (2) model fire extinction in the burning cells. Each cell has a fire spread modifier, FSMOD, calculated as

$$\mathrm{FSMOD} = \mathrm{SSF} \times \mathrm{WSF} \times \mathrm{VSF} \times \mathrm{LSF} \tag{3}$$

where SSF is the slope spread factor, WSF is the wind spread factor, VSF is the vegetation spread factor, and LSF is the landtype spread factor. SSF is based on the relative elevations of the source cell and the adjacent unburned cell, along with user-specified parameters characterizing the sensitivity of fire spread to slope angle. WSF is based on user-supplied parameters describing prevailing wind direction, variability in wind direction, and wind speed. VSF is specified for each successional stage, and LSF is specified for each landtype. For these modifiers, a value of 1 indicates no influence on fire spread, values less than one decrease the probability of fire spread, and values greater than one increase the probability of fire spread.

For each burning cell, the eight neighboring cells are candidates for fire spread. The probability of fire spread is computed as

$$\mathrm{ODDS} = \frac{\mathrm{FSPR}}{1 - \mathrm{FSPR}} \tag{4}$$

$$\mathrm{ODDS2} = \mathrm{ODDS} \times \mathrm{FSMOD} \tag{5}$$

$$\mathrm{FSPR2} = \frac{\mathrm{ODDS2}}{1 + \mathrm{ODDS2}} \tag{6}$$

where FSPR is the base fire spread probability, ODDS is the odds of fire spread, FSMOD is the fire severity modifier, ODDS2 is the modified odds of fire spread, and FSPR2 is the modified probability of fire spread.

Once a neighboring cell is ignited it also can serve as a new source for fire spread, so fire has the potential to move through multiple unburned cells during a single iteration of the fire spread subroutine. An iteration of the fire spread subroutine is completed once all burning cells in the fire have been processed. The fire extinction subroutine then operates by randomly extinguishing fires in the burning cells. Each burning cell has an independent probability of being extinguished, specified by the FEXT parameter. Once a cell burns out, it can no longer propagate fire into surrounding cells or have fire spread into it. Fires grow through multiple iterations until the fire reaches the predetermined fire size, or until there are no more actively burning cells within the fire perimeter. The FSPR and FEXT parameters can both be used to adjust fire shapes, and fire patterns can thus be calibrated by computing one or more spatial metrics for the simulated fires and comparing them with the spatial pattern of real fires (e.g. Wimberly, 2002).

2.2. Vegetation dynamics

Forest succession is modeled as a series of discrete successional stages, defined as a pathway. Each pathway is parameterized by specifying the events that trigger transitions among these stages (Fig. 1). Pathways can be specified for one or more community types, which are spatially linked to community zones on the landscape. Fire effects are modeled by specifying successional stage transitions for three fire severity classes: high, moderate, and low. High-severity fires are assumed to be stand-replacement disturbances that kill the majority of trees on a site. Moderate-severity fires are assumed to primarily kill smaller subcanopy trees, but not larger dominant trees. Low-severity fires are assumed to primarily kill seedlings and saplings. The probability of high-severity fire is defined by specifying a separate PHS parameter for each successional stage. For example, a fire burning in a successional stage with low fuel loads and large, fire-resistant trees would be expected to have a low PHS, whereas a fire burning in a successional stage with high accumulations of ladder fuels or particularly fire-sensitive species would be expected to have a high PHS. A uniform (0, 1) random variable is generated for each burned cell, and the fire burns at high severity if the value is less than PHS. Otherwise, the fire burns at either low or moderate severity depending on the successional stage (Fig. 1).

Forest succession is modeled using two state variables. Stand age (AGE) is the number of years since the last high-severity fire. Time since fire (TSFIRE) is the number of years since the last fire of any severity. Thus, a high-severity fire resets both AGE and TSFIRE to zero, whereas a moderate- or low-severity fire only resets TSFIRE to zero. The number of years that a cell has spent in the current successional stage is also monitored. Overstory succession is modeled by specifying the AGE at which transition to a new successional stage occurs. When low- and moderate-severity fires occur frequently, continual mortality in the shrub, sapling, and small tree layers maintains an open understory. In the absence of fire, tree regeneration occurs in the understory vegetation layers and triggers a change in successional stage. This ingrowth is modeled by specifying a maximum TSFIRE after which a transition to a new successional stage occurs.

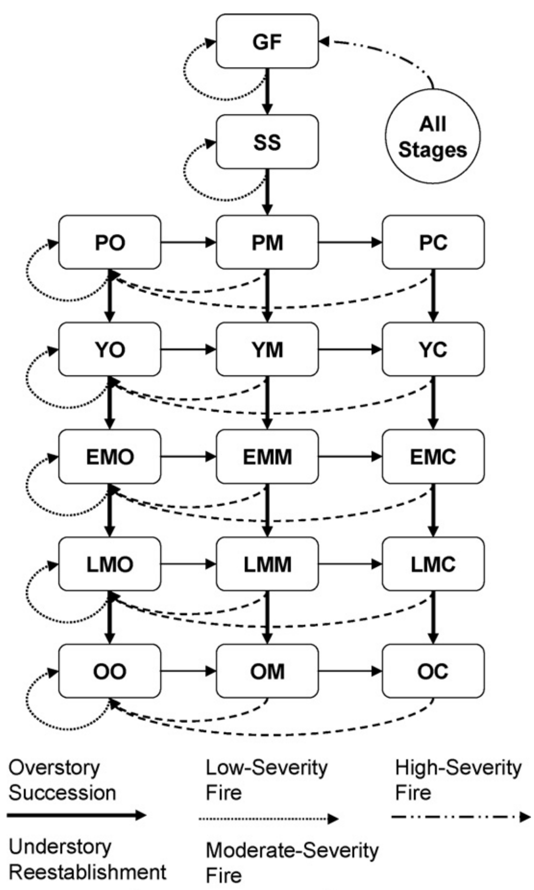

Fig. 1. Hypothetical successional pathway diagram for a mixed-conifer community type. For definition of codes see Table 1. High-severity fires can occur in any successional stage, initiating a transition to the grass/forb stage.

3. Methods

3.1. Sensitivity analysis of successional pathways

Simulations were carried out on artificial landscapes using a single successional pathway in a single community zone. The successional pathway was a modification of one initially developed for mixed-conifer forest communities in the Deschutes National Forest, on the east side of the Cascade Mountains, Oregon, USA (Fig. 1, Table 1). Parameters for the transition lags and fire severity modifiers were adapted from a state-and-transition model originally developed for the Deschutes National Forest based on the expert opinion of local ecologists and land managers and literature review. Ponderosa pine (*Pinus ponderosa*) is assumed to be the predominant tree

Table 1
Baseline parameters for successional pathways

Code	Overstory age class	Canopy closure	Max Age	Max TSFIRE	PHS
GF	Grass/forb	Early-successional	10	10	0.5
SS	Seedling/sapling	Early-successional	25	35	0.5
PO	Pole	Open	60	25	0.1
YO	Young	Open	90	25	0.05
EMO	Early mature	Open	120	25	0.02
LMO	Late mature	Open	180	25	0.01
OO	Old	Open	NA	25	0.01
PM	Pole	Medium	60	50	0.5
YM	Young	Medium	90	50	0.2
EMM	Early mature	Medium	120	50	0.2
LMM	Late mature	Medium	180	50	0.05
OM	Old	Medium	NA	50	0.05
PC	Pole	Closed	60	NA	0.95
YC	Young	Closed	90	NA	0.9
EMC	Early mature	Closed	120	NA	0.8
LMC	Late mature	Closed	180	NA	0.8
OC	Old	Closed	NA	NA	0.8

Max Age: stand age at which transition to the next overstory age class occurs; Max TSFIRE: time since fire at which transition to the next canopy closure class occurs; and PHS: probability that a fire will be high severity.

species establishing after high-severity fire. In contrast, Douglas-fir (*Pseudotsuga menziesii*) and true fir (*Abies* spp.) are the principal species that establish in the forest understory. PHS was lowest in open forests, slightly higher in medium-canopy forests, and highest in closed-canopy forests (Table 1). Within each canopy cover class, the probability of high-severity fire was highest in pole stands and decreased with increasing stand age. High-severity fire could occur in any successional stage, and always caused a transition to the grass/forb stage (Fig. 1). Low-severity fires occurred in the open-canopy and early-successional forests, and did not cause a change in successional stage. Moderate-severity fires occurred in medium- and closed-canopy forests, and caused a transition to an open canopy class.

Six scenarios examined parameters controlling critical portions of the successional pathway (Table 2). In scenario 1, the age at which patches transitioned from the grass/forb to the seedling/sapling stage was increased to 15 and decreased to 5. In scenario 2, the time since fire at which forests transitioned to closed-canopy stages was increased to 60 and decreased to 40. In scenario 3, the stand age at which forests transitioned from the late mature age class to old age class was increased to 200 and decreased to 160. In the next three scenarios, PHS parameters were modified to increase by 100% and decrease by 50% the odds of a high-severity fire (Table 2). In scenario 4, the PHS value for the grass/forb stage was modified. In scenario 5, the PHS values for the open-canopy stages were modified. In scenario 6, the PHS values for the closed-canopy stages were modified. All other parameters were held at baseline levels.

The simulations were carried out on a hypothetical 200 × 200 cell landscape. This landscape was flat, and was comprised of a single community type, a single landtype, and a single fire regime zone. The landscape was modeled as a torus to avoid edge effects—fire spreading off one side of the landscape reentered the landscape from the opposite side. Parameters of FSPR, FEXT, and WSF were selected to generate fires that had realistic elliptical shapes based on visual comparisons with the patterns of recent fires. Runs were conducted for fire rotations ranging from 5 to 50 years at 5-year intervals. This range was chosen to span the reported range of fire rotations for dry forest habitats in the interior Pacific Northwest (Agee, 2003). Each run was initialized from a random starting configuration, and was run for a 2000-year initialization period. Then landscape composition was sampled 100 times at 100-year intervals for a total main simulation length of 10,000 years. Analysis of the results focused on four successional classes that were of particular interest from an ecological standpoint: the early-successional (grass/forb + seedling/sapling stages), old open canopy, old medium canopy, and old closed canopy stages.

When fire initiation and spread are not affected by successional stage or environmental characteristics the expected percentage of the landscape occupied by each successional stage is not affected by fire size, whereas temporal variability in the proportion of the landscape occupied by each successional stage decreases with fire size (Boychuk et al., 1997). Therefore, running simulations with small fire sizes served as a variance reduction technique (Ross, 1990) that resulted in highly efficient estimates of the percentage of the landscape occupied by each successional stage. We used a mean fire size of 100 cells and a standard deviation of 50 cells in the sensitivity analysis of successional pathways. Because the resulting standard errors were extremely low (<0.2% of the landscape for all estimates), no statistical analyses were carried out on these runs.

Table 2
Parameters modified in the sensitivity analysis of successional pathways

Scenario	Parameters modified[a]	Successional stages affected[b]	Low value	High value
1	Max AGE	GF	5	15
2	Max TSFIRE	PM, YM, EMM, LMM, OM	40	60
3	Max AGE	LMO, LMM, LMC	160	200
4	PHS	GF	0.333	0.667
5	PHS	PO	0.053	0.182
	PHS	YO	0.026	0.095
	PHS	EMO	0.010	0.039
	PHS	LMO, OO	0.005	0.020
6	PHS	PC	0.905	0.974
	PHS	YC	0.818	0.947
	PHS	EMC, LMC, OC	0.667	0.889

[a] See Table 1 footnotes for definitions of parameters.
[b] See Table 1 for a list of abbreviations.

3.2. Sensitivity analysis of fire spread

The baseline scenario assumed that fire had an equal probability of spreading into neighboring cells regardless of successional stage (VSF = 1 for all stages). Three scenarios examined the effects of varying spread rate with successional stage (Table 3). In scenario 7, we assumed that fire spread rates were related to the development of ladder fuels and the potential for crown fire spread, and were therefore higher in the closed-canopy stages (VSF = 1.2) than in other successional stages (VSF = 0.8). In scenario 8, we assumed that fire spread rates were highest in open stands dominated by grassy fuels, and were therefore higher in open- and medium-canopy forests (VSF = 1.2) than in other forest types (VSF = 0.8). In scenario 9, we assumed that fire spread rates were higher in grass/forb and seedling/sapling stages (VSF = 1.2) than in other stages (VSF = 0.8) because of a pulse of fuels resulting from post-fire mortality.

Four additional scenarios assumed that fire spread rate was independent of successional stage but was lower in landtypes characterized as fire refugia than in other parts of the landscape (Fig. 2). Fire refugia were assigned an LSF of 0.8 and other parts of the landscape were assigned an LSF of 1.2 (Table 3). We examined two scenarios in which fire refugia occupied 25% of the landscape in evenly distributed squares that were 32 × 32 cells in size (scenario 10), and 64 × 64 cells in size (scenario 11). We also examined the effects of increasing the area of fire refugia to 50% of the landscape, distributed as squares that were 32 × 32 cells in size (scenario 12), and 64 × 64 cells in size (scenario 13).

The sensitivity analysis of fire spread was evaluated using the same approach as the sensitivity analysis of successional

Table 3
Parameters modified in the sensitivity analysis of fire spread

Scenario	VSF1	VSF2	VSF3	Number of landtypes	LSF1	LSF2	Fire refugia pattern
Baseline	1	1	1	1	1	NA	NA
7	0.8	0.8	1.2	1	1	NA	NA
8	0.8	1.2	0.8	1	1	NA	NA
9	1.2	0.8	0.8	1	1	NA	NA
10	1	1	1	2	1.2	0.8	25% of the landscape in 32 × 32 cell squares
11	1	1	1	2	1.2	0.8	25% of the landscape in 64 × 64 cell squares
12	1	1	1	2	1.2	0.8	50% of the landscape in 32 × 32 cell squares
13	1	1	1	2	1.2	0.8	50% of the landscape in 64 × 64 cell squares

VSF1: vegetation spread factor for early successional forests, VSF2: vegetation spread factor for open- and medium-canopy forests, VSF3: vegetation spread factor for closed-canopy forests, LSF1: landtype spread factor for non refugia, LSF2: landtype spread factor for fire refugia.

pathways, with two exceptions related to landscape and fire sizes. The landscape size was 256 × 256 cells, and the mean and standard deviation of fire size were each 3277 cells. Because we were specifically interested in the spatial interactions of fires, successional stages, and landtypes, we used larger fire sizes than in the successional pathway analysis to provide a more realistic representation of the interactions between fire spread and landscape pattern. The larger and more variable fire sizes resulted in a higher variance of the proportions of successional stages than in the preceding successional pathway analysis. Therefore, we used two-way analysis of variance (ANOVA) to determine whether the main

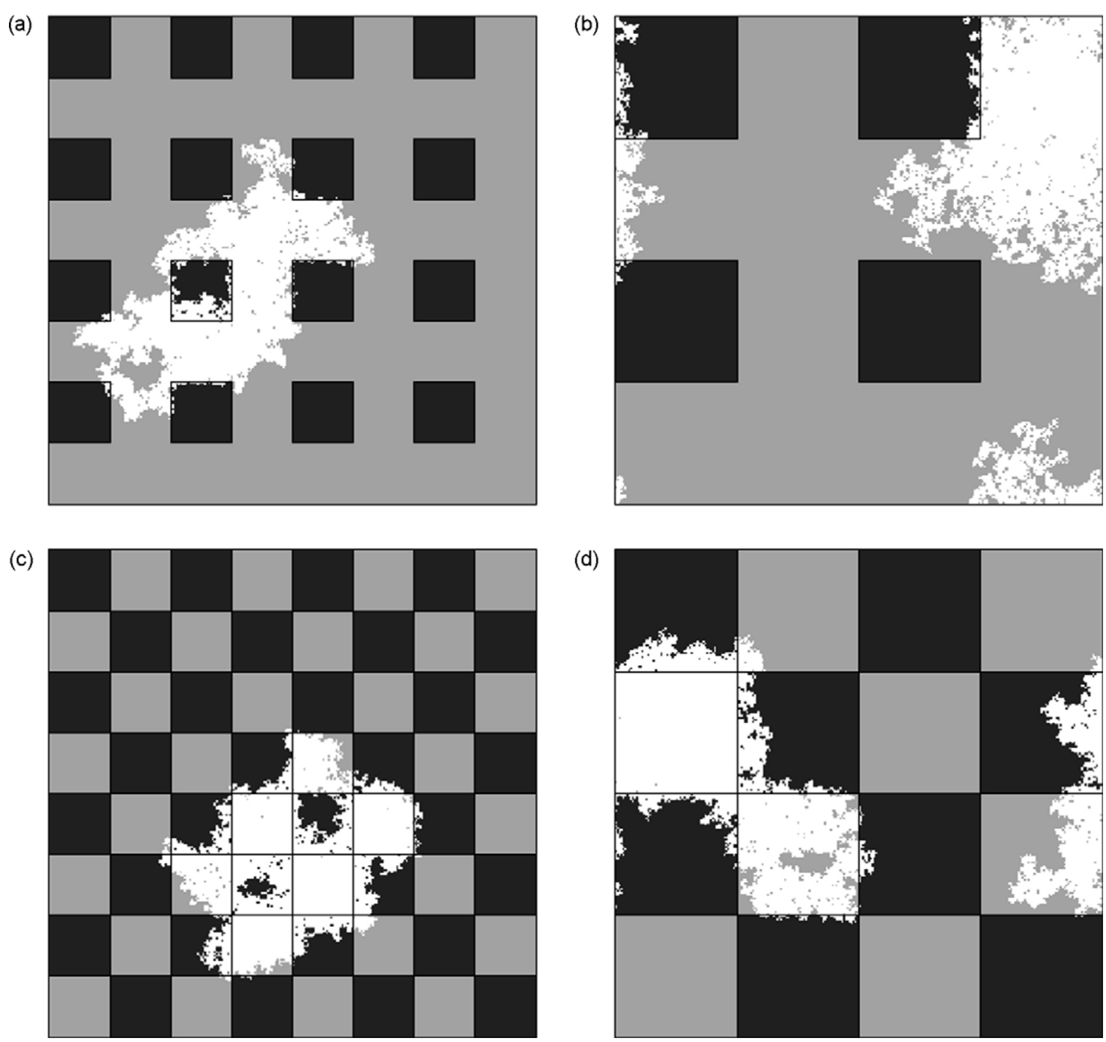

Fig. 2. Fire refugia patterns for the four fire refugia scenarios. (a) 25% of the landscape in 32 × 32 cell squares, (b) 25% of the landscape in 64 × 64 cell squares, (c) 50% of the landscape in 32 × 32 cell squares, (d) 50% of the landscape in 64 × 64 cell squares. Dark gray squares are refugia. Light gray squares are non refugia. White areas are examples of fires simulated in each landscape.

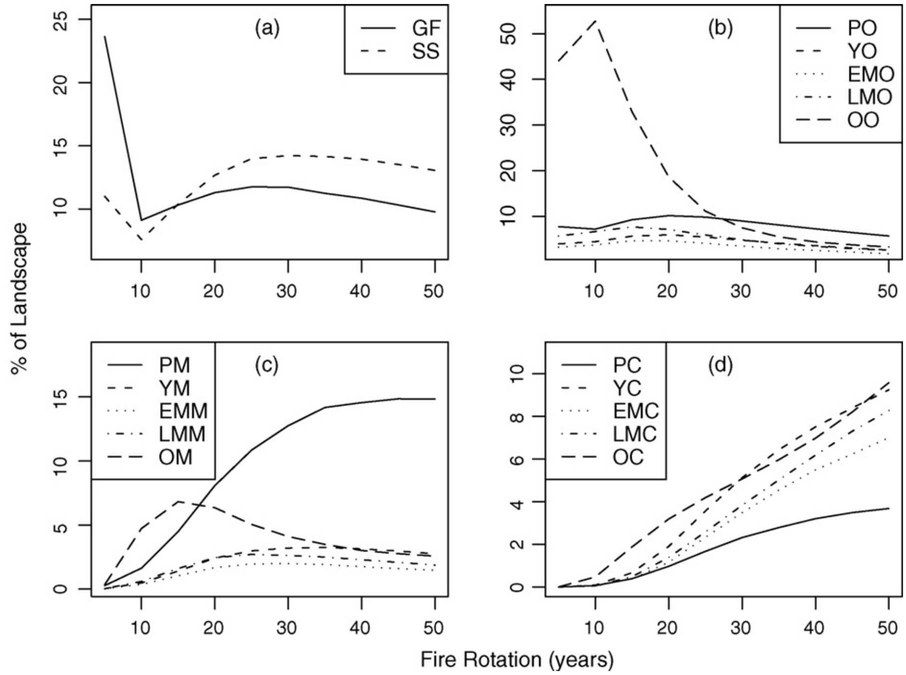

Fig. 3. Abundance of successional stages under the baseline runs with no spatial effects on fire spread. (a) Early-successional stages, (b) open-canopy stages, (c) medium-canopy stages, (d) closed-canopy stages. For definition of codes, see Table 1.

effects of fire rotation and scenario and the interaction between fire rotation and scenario had statistically significant effects on the proportions of successional stages.

4. Results

4.1. Sensitivity analysis of successional pathways

Under the baseline scenario, the abundance of closed-canopy forests increased monotonically with fire rotation (Fig. 3). In contrast, early-successional, open-canopy, and medium-canopy forests exhibited more complex unimodal and bimodal responses to fire rotation. The grass/forb and seedling/sapling stages had the highest abundance at a 5-year fire rotation, dropped precipitously when the fire rotation increased to 10 years, increased to a peak when the fire rotation reached 30 years, and decreased gradually with fire rotation length thereafter. The old open-canopy stage had the highest abundance at a 10-year fire rotation, and decreased in abundance with both shorter and longer fire rotations. Abundances of the other open-canopy stages remained relatively low at all fire rotation levels. The old medium-canopy stage had the highest abundance at a 15-year fire rotation, and decreased at both shorter and longer fire rotations. At fire rotations above 30 years, the pole stage became the most abundant size class for both open-canopy and medium-canopy forests.

The annual area burned by low-severity fires was highest at a 5-year fire rotation, and decreased with increasing fire rotation length (Fig. 4). The annual area burned by high-severity fires was also highest at a 5-year fire rotation, but remained relatively constant at fire rotations from 10 to 50 years. When computed as a percentage of the total area burned, high- and moderate-severity fires were most prevalent at a 50-year fire rotation, decreased with fire rotation lengths down to 10 years, and then increased again at a 5-year fire rotation. In contrast, the percentage of low-severity fire was lowest at a 50-year fire

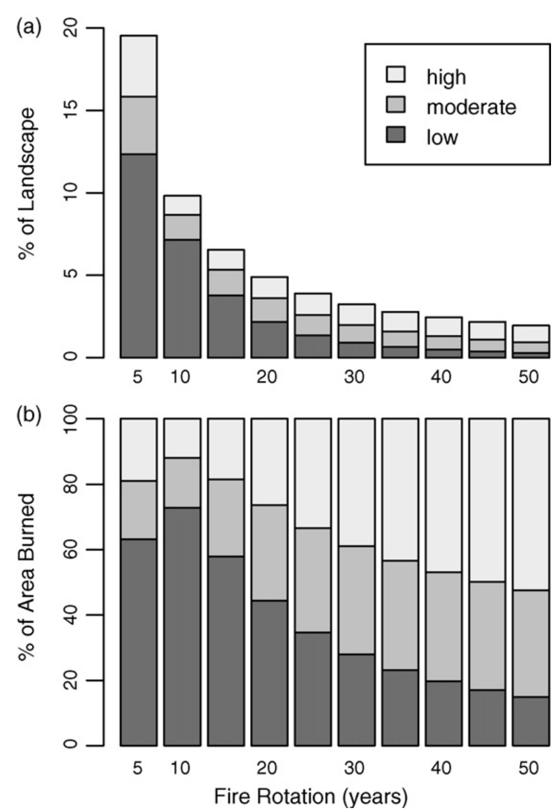

Fig. 4. Distribution of fire severities expressed as (a) percentage of the landscape burned per year and (b) percentage of total area burned.

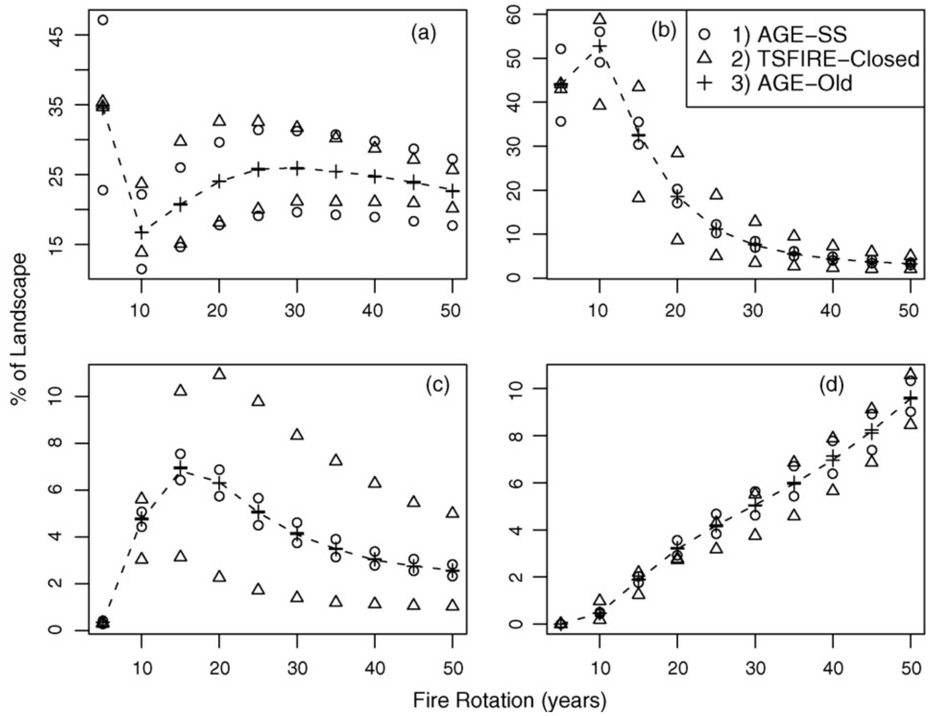

Fig. 5. Sensitivity to successional parameters for (a) early-successional stages, (b) old open-canopy stage, (c) old medium-canopy stage, and (d) old closed-canopy stage. Parameters are (1) the stand age at which patches transitioned from the grass/forb to the seedling/sapling stage, (2) the time since fire at which forests transitioned to the closed-canopy stage, (3) the stand age at which forests transitioned from late-mature age class to the old age class.

rotation, increased with decreasing fire rotation lengths down to 10 years, and then decreased again at a 5-year fire rotation.

Early-successional forests were sensitive to the TSFIRE value for transition to the closed-canopy stages and the AGE values for transition to the seedling/sapling stage (Fig. 5). In contrast, the old open-canopy and old medium-canopy stages were primarily sensitive to the TSFIRE value for transition to the closed forest stages. The old closed-canopy stage also responded to variation in the TSFIRE value for transition to the closed forest stages, but not as strongly as the old open-canopy and old medium canopy stages. The response of all stages to variation in the AGE parameter for transition to the old age class was minimal. The old open-canopy stage was sensitive to open-canopy fire severity modifiers when fire rotations were less than 15 years (Fig. 6). In contrast, the old closed-canopy stage was relatively insensitive to the fire severity modifiers at shorter rotations, but became increasingly sensitive to closed-canopy fire severity modifiers as fire rotation lengthened. The old medium-canopy stage was intermediate, exhibiting sensitivity to the open-canopy fire severity modifiers at shorter fire rotations, and becoming more sensitive to the closed-canopy fire severity modifiers at longer fire rotations. Early-successional forests were sensitive to fire severity modifiers of the grass/forb stage and of open-canopy forests at fire rotations less than 15 years, but were less sensitive at longer fire rotations.

4.2. Sensitivity analysis of fire spread

The relative amounts of successional stages were affected when spatial variability in fire spread was incorporated into the model (Fig. 7). The main effect of scenario and the interaction between fire spread scenario and fire rotation were statistically significant for all successional stages tested (Table 4). When fire spread more rapidly into open/medium-canopy forests, the abundances of old open-canopy and old medium canopy stages were slightly higher than the baseline. In contrast, faster fire spread into closed-canopy forests or early-successional forests reduced the abundance of old open-canopy and old medium-canopy stages. The old closed-canopy stages exhibited the strongest response to the fire spread scenarios, increasing when fire spread more rapidly into open/medium-canopy forests and decreasing when fire spread more rapidly into closed-canopy forests. At fire return intervals longer than 15 years, early-successional forests were more abundant than the baseline when fire spread more rapidly into closed-canopy forests and less abundant when fire spread more rapidly into open/medium-canopy forests. Increased rates of fire spread into early-successional forests had a weaker effect on the relative abundance of successional stages than increased rates of fire spread into closed-canopy or open/medium-canopy forests.

In the fire refugia analysis, the main effect of scenario was statistically significant for all successional stages except the old medium canopy stage, and the interaction between fire refugia scenario and fire rotation was statistically significant for all successional stages tested (Table 5). The relative area of successional stages was similar to the baseline in the scenarios where refugia occupied 25% of the landscape, and where refugia occupied 50% of the landscape distributed in small squares (Fig. 8). The proportions of successional stages differed

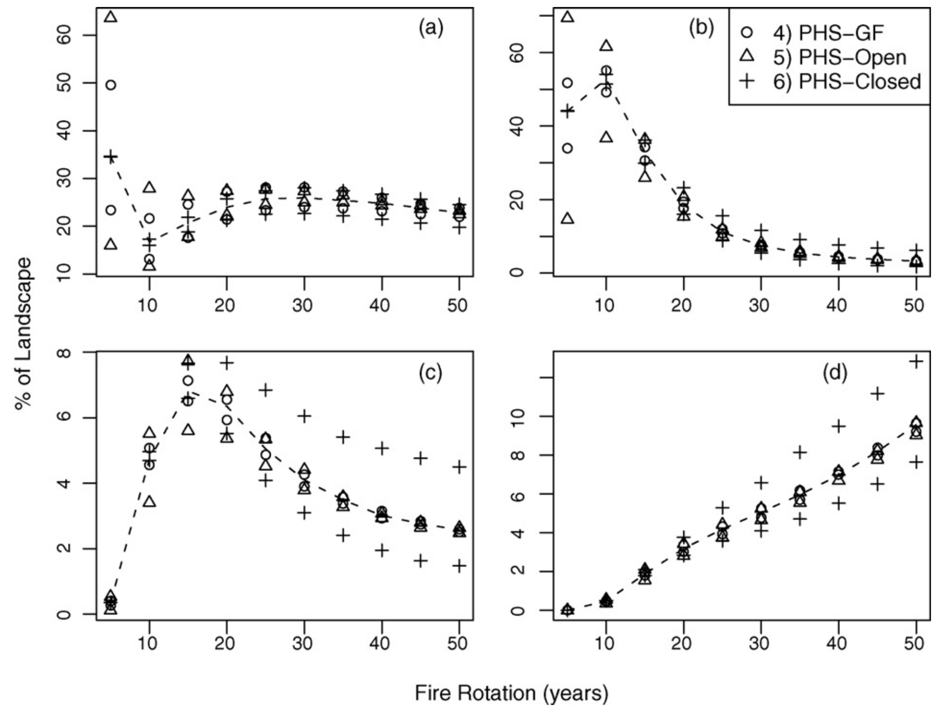

Fig. 6. Sensitivity to successional parameters for (a) early-successional stages, (b) old open-canopy stage, (c) old medium-canopy stage, and (d) old closed-canopy stage. Parameters are (4) the probability of high-severity fire for the grass/forb class, (5) the probability of high-severity fire for the open-canopy stages, and (6) the probability of high-severity fire for the closed-canopy stages.

from the baseline when refugia occupied 50% of the landscape and were distributed in large squares. At fire rotations shorter than 20 years, the amount of the old open-canopy stage decreased and the amount of early-successional forest increased relative to the baseline. The amount of the old closed-canopy stage increased relative to the baseline, and the amount of the old medium-canopy stage either increased or decreased depending on the fire rotation.

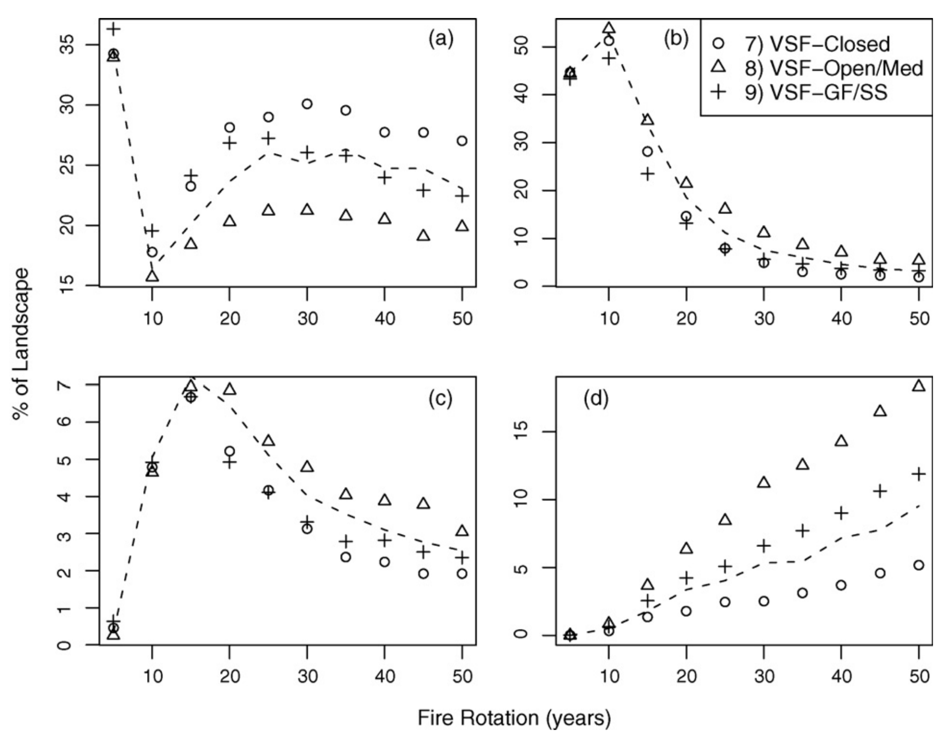

Fig. 7. Sensitivity to fire spread rates for (a) Early-successional stages, (b) old open-canopy stage, (c) old medium-canopy stage, and (d) old closed-canopy stage. Scenarios are (7) fire spreads more rapidly into closed-canopy forests, (8) fire spreads more rapidly into open- and medium-canopy forests, and (9) fire spreads more rapidly into early-successional forests.

Table 4
Two-way analysis of variance table for the effects of fire rotation and fire spread scenario on proportion of successional stages in the simulated landscapes

Response	Source of variation	SS	d.f.	MS	F-statistic	p-value
Early successional	Fire rotation	68980	9	7664	175.32	<0.0001
	Scenario	21397	3	7132	163.14	<0.0001
	Fire rotation × scenario	6239	27	231	5.29	<0.0001
	Residuals	173120	3960	44		
Open canopy very large	Fire rotation	1145197	9	127244	14011.17	<0.0001
	Scenario	17175	3	5725	630.40	<0.0001
	Fire rotation × scenario	8109	27	300	33.071	<0.0001
	Residuals	35963	3960	9		
Medium canopy very large	Fire rotation	12417	9	1380	285.89	<0.0001
	Scenario	719	3	240	49.69	<0.0001
	Fire rotation × scenario	443	27	16	3.40	<0.0001
	Residuals	19110	3960	5		
Closed canopy very large	Fire rotation	52704	9	5856	809.29	<0.0001
	Scenario	23809	3	7936	1096.77	<0.0001
	Fire rotation × scenario	10681	27	396	54.67	<0.0001
	Residuals	28654	3960	7		

Fire spread scenarios reflected different assumptions about the rates of fire spread in open- and closed-canopy forests.

5. Discussion

The hypothetical landscape and successional pathways used in this analysis are intended to provide a general model of forest dynamics in dry mixed-conifer forests of the interior Pacific Northwest rather than to characterize any particular site. Comparison with another recent modeling study suggests that our model provides a reasonable representation of the distribution of successional stages under natural disturbance regimes. Hemstrom et al. (2007) used VDDT to simulate landscape composition in the Blue Mountains of Oregon under a natural fire regime. They found that the mean percentage of forested land in the large single story class (roughly analogous to our old open- and medium-canopy stages) was just under 20%, whereas the mean percentage in the large multi-story class (roughly analogous to our old closed-canopy stage) was less than 5%. In comparison, our simulations with a fire rotation of 25 years, analogous to fire regimes on warm-dry sites in the Blue Mountains, resulted in 11% of the old open-canopy stage, 5% of the old medium-canopy stage, and 4% of the old closed-canopy stage. Despite the differences in successional stages, fire regimes, and spatial complexity of the two models, the general concordance of the results suggests that our characterization of successional pathways, fire regimes, and resulting landscapes in the baseline run is ecologically reasonable.

5.1. Successional feedbacks

Model predictions of landscape composition in disturbance-prone landscapes are sensitive to key parameters in the

Table 5
Two-way analysis of variance table for the effects of fire rotation and fire spread scenario on proportion of successional stages in the simulated landscapes

Response	Source of variation	SS	d.f.	MS	F-statistic	p-value
Early successional	Fire rotation	109799	9	12200	279.34	<0.0001
	Scenario	657	4	164	3.76	0.005
	Fire rotation × scenario	16975	36	472	10.80	<0.0001
	Residuals	216183	4950	44		
Open canopy very large	Fire rotation	1322087	9	146899	15552.86	<0.0001
	Scenario	1848	4	462	48.91	<0.0001
	Fire rotation × scenario	29034	36	806	85.39	<0.0001
	Residuals	46753	4950	9		
Medium canopy very large	Fire rotation	13429	9	1492	293.16	<0.0001
	Scenario	45	4	11	2.19	0.07
	Fire rotation × scenario	1143	36	32	6.24	<0.0001
	Residuals	25195	4950	5		
Closed canopy very large	Fire rotation	59421	9	6602	938.34	<0.0001
	Scenario	9007	4	2252	320.01	<0.0001
	Fire rotation × scenario	3971	36	110	15.68	<0.0001
	Residuals	24829	4950	7		

Fire spread scenarios reflected different sizes and distributions of fire refugia within the landscape.

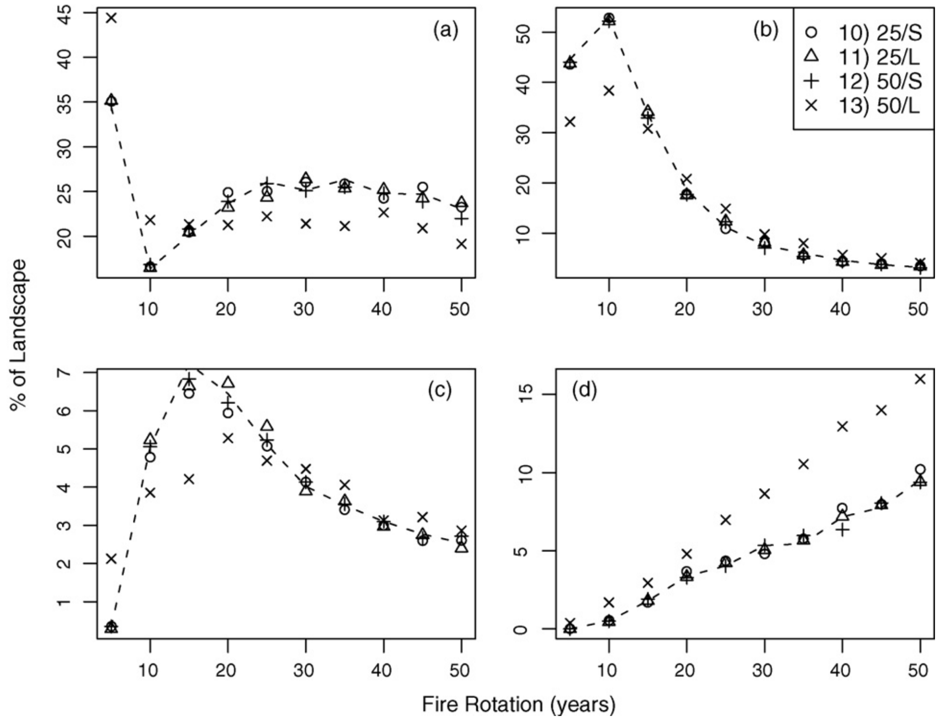

Fig. 8. Sensitivity to fire refugia size and abundance for (a) early-successional stages, (b) old open-canopy stage, (c) old medium-canopy stage, and (d) old closed-canopy stage. Fire refugia scenarios are (10) 25% of the landscape in 32 × 32 cell squares, (11) 25% of the landscape in 64 × 64 cell squares, (12) 50% of the landscape in 32 × 32 cell squares, and (13) 50% of the landscape in 64 × 64 cell squares.

successional pathway model, Specifically, the area of old forests is more sensitive to the length of the fire-free period required for a closed-canopy forest to develop than to the length of the early-successional stage or the time required for overstory trees to reach the old age class. For example, at a fire rotation of 15 years, the amount of forest in the old open-canopy stage varied from 18 to 43% of the landscape when the time required for transition to the closed-canopy stage was varied from 40 to 60 years. The probability of high-severity fire in open- and medium-canopy forests also has a strong influence on area of old forests, particularly at fire rotations of 20 years or shorter. Thus, understanding rates of ingrowth and the relationships between stand structure and probability of high-severity fire is critical for the accurate parameterization of successional pathways in mixed-severity fire regimes.

As the length of the fire rotation decreases, the fire regime changes from a predominance of high-severity fire to moderate- and low-severity fires. This trend occurs because the more frequent fires maintain the majority of the landscape in open canopy stages which have low probabilities of stand-replacement fire. However, when the fire rotation decreases below 10 years, a threshold is reached at which system behavior fundamentally changes as the landscape shifts from dominance by open forests to early-successional forests. This shift occurs because of increased area burned by stand-replacement fires that occur in the early-successional stages. A similar result was found in a previous study using the LANDIS model to simulate forest communities in the southeastern United States (Wimberly, 2004). Some species exhibited bimodal responses to the fire return interval, with high abundances in landscapes dominated by frequent, low-severity fires as well as in landscapes characterized by infrequent, stand-replacement fires. The results of the present study provide additional evidence that landscapes respond non-linearly to changing fire frequency when there are strong feedbacks between forest succession, fuel loads, and fire effects.

5.2. Spatial interactions

In addition to being sensitive to parameters characterizing successional pathways, landscape composition is sensitive to spatial variability in the rate of fire spread in different successional stages and landtypes. In particular, the coexistence of open-canopy and closed-canopy forests is enhanced when fires spread more rapidly into open- and medium-canopy forests. This scenario has a stabilizing effect on landscape composition, in which increased frequency of low-severity fires maintains old open-canopy forest, while decreased fire frequency in old closed-canopy forest reduces the rate at which this stage is lost to high-severity fires. In contrast, more rapid fire spread into closed-canopy forest increases the rate of stand replacing disturbance in these successional stages, while the decreased fire frequency in open- and medium-canopy forest allows more ingrowth and transition to the closed-canopy stages to occur. The combination of these effects reduces the total amount of both open-canopy and closed-canopy old forest in the landscape and increases the amount of early-successional forests.

Empirical evidence can be found to support all three of the fire spread scenarios that we simulated in this study. Most forest landscape models to date have assumed that fine fuel loads, and consequently fire susceptibility, increase monotonically with time since the most recent fire (Li et al., 1997; He and Mladenoff, 1999; Keane et al., 2006). This assumption of an increasing hazard of burning with time since fire is prevalent in the fire modeling literature. In their discussion of statistical models for fire history, Johnson and VanWagner (1985) did not consider formulations that imply a decreasing fire hazard with age because they make ''little fire ecology sense''. Schimmel and Granstrom (1997) similarly concluded that fire spread rates in boreal forests increase with stand age and total fuel loading. Changes in stand structure with time since fire also influence potential fire behavior. Regeneration and succession of shade-tolerant tree species in the absence of fire lead to the development of a dense, multilayered canopy structure that increases the chances of crown fire behavior such as torching, spotting, and active crowning (Agee and Skinner, 2005). If the fires occurring in closed-canopy forests are primarily crown fires, then spread rates may be faster by an order of magnitude or more than surface fire spread rates (Ryan, 2002).

In contrast, other research suggests that fuel loads and potential fire ignition and spread rates are highest immediately following a stand-replacement fire. Agee and Huff (1987) examined a chronosequence of western hemlock/Douglas-fir forests on the Olympic Peninsula and found that fuel loads and predicted spread rates were highest fewer than 20 years after fire, lowest at 100 years after fire, and increased gradually at ages greater than 100 years. Hall et al. (2006) found that dead surface fuel loads were low immediately following a stand-replacement fire, but increased rapidly thereafter to a peak at 10–20 years after fire. Surface fuels generally decreased with age after 20 years to a minimum at about 80 years post fire, and then increased gradually thereafter. In both of these studies, the post-disturbance pulse of fuels was attributed to gradual decomposition of trees killed in the stand-replacement fire.

In addition to fuel loads, canopy openness also constrains fire behavior through its effects on understory fuel moisture. Tanskanen et al. (2005) conducted a field experiment which showed that probabilities of ignition were highest in open stands less than 15 years old, and that probability of ignition decreased with increasing stand age and was lowest in closed-canopy forests that were 30–45 years old. These differences are attributable to an increase in the moisture content of surface fuels with canopy closure (Tanskanen et al., 2006). Although litterfall and the accumulation of dead surface fuels will be slower in stands with open canopies, understory productivity will be higher in these open stands leading to higher loadings of live herbaceous fuels that support rapid fire spread (Agee, 1993). Our simulations demonstrated that landscape composition in dynamic forest landscapes is particularly sensitive to assumptions about relative rates of fire spread in open- versus closed-canopy forests.

The presence of static landtypes with lower spread rates, or fire refugia (Camp et al., 1997), can also increase the amount of old closed-canopy forests in landscapes with frequent fire. However, this effect was manifested only when these fire refugia were relatively large and occupied 50% of the landscape. For these experiments, the landtype spread modifiers were selected such that fires could burn into the refugia, but at a slower rate than in the other portions of the landscape. Thus, the refugia affected landscape composition by altering the spatial pattern of fire frequencies on the landscape, with longer fire return intervals inside the refugia than outside. In this situation, it appears that the refugia must occupy a large proportion of the landscape and be large relative to the sizes of fires to have an effect on landscape composition. For smaller amounts or sizes of refugia to have an effect on the abundance of late-successional forests, they may need to either have a larger impact on fire spread rates or reduce fire severity in addition to fire spread.

6. Conclusions

Our baseline runs support the idea that closed-canopy, late-successional forests are relatively rare in dry mixed-conifer forests of the inland Pacific Northwest. However, model predictions are sensitive to assumptions about ingrowth rates and probabilities of high-severity fire in different successional stage. In addition, the abundance of late-successional forests may be higher than predicted by non-spatial models if fires preferentially burn in open-canopy forests, or if the presence of large fire refugia creates a heterogeneous distribution of fire frequencies across the landscape. In reality, fire behavior and effects depend on complex interactions between fuel quantity, fuel quality, fuel moisture, and weather conditions at the time of the burn. Simulation models of forest dynamics necessarily simplify these relationships to model landscape change over long temporal and large spatial scales. In forests with mixed-severity fire regimes, modelers should give careful consideration to assumptions about relative flammabilities of different successional stages and landtypes and the implications of these assumptions for predicted landscape dynamics.

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