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RESEARCH ARTICLE

Influence of fire regimes on lodgepole pine stand age and density across the Yellowstone National Park (USA) landscape

Tania Schoennagel · Monica G. Turner ·
Daniel M. Kashian · Andrew Fall

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Abstract A probabilistic spatial model was created based on empirical data to examine the influence of different fire regimes on stand structure of lodgepole pine (*Pinus contorta* var. *latifolia*) forests across a >500,000-ha landscape in Yellowstone National Park, Wyoming, USA. We asked how variation in the frequency of large fire events affects (1) the mean and annual variability of age and tree density (defined by postfire sapling density and subsequent stand density) of lodgepole pine stands and (2) the spatial pattern of stand age and density across the landscape. The model incorporates spatial and temporal variation in fire and serotiny in predicting postfire sapling densities of lodgepole pine. Empirical self-thinning and in-filling curves alter initital postfire sapling densities over decades to centuries. In response to a six-fold increase in the probability of large fires (0.003 to 0.018 year^{-1}), mean stand age declined from 291 to 121 years. Mean stand density did not increase appreciably at high elevations (1,029 to 1,249 stems ha^{-1}) where serotiny was low and postfire sapling density was relatively low (1,252 to 2,203 stems ha^{-1}). At low elevations, where prefire serotiny and postfire lodgepole pine density are high, mean stand densities increased from 2,807 to 7,664 stems ha^{-1}. Spatially, the patterns of stand age became more simplified across the landscape, yet patterns of stand density became more complex. In response to more frequent stand replacing fires, very high annual variability in postfire sapling density is expected, with higher means and greater variation in stand density across lodgepole pine landscapes, especially in the few decades following large fires.

Keywords Landscape modeling · *Pinus contorta* var. *latifolia* · Postfire regeneration · Stand density · Succession · Yellowstone National Park

Introduction

Fire regimes vary significantly over time in response to management, fuels and climate, yet our understanding of how variation in stand-replacing fire regimes affects stand and landscape structure is limited. Disturbance regimes interact with tree life-history traits to modify patterns of postfire

T. Schoennagel · M. G. Turner · D. M. Kashian
Department of Zoology, University of Wisconsin,
Madison, WI, USA

A. Fall
School of Resource and Environmental Management,
Simon Fraser University, Burnaby, BC, Canada

T. Schoennagel (✉)
Department of Geography, University of Colorado,
260 UCB, Boulder, CO 80309, USA
e-mail: tschoe@colorado.edu

regeneration and subsequent age-dependent changes in density and composition, thereby affecting the composition and structure of forested landscapes (Pickett and White 1985; Clark 1991a, b). It is well known that the size and frequency of stand-replacing fires affect the age structure of forested landscapes (Romme 1982; Turner et al. 1994; Weir et al. 2000), and spatiotemporal models have simulated the effect of different fire regimes on stand age distributions in subalpine forests (Baker et al. 1991; Gardner et al. 1996). However, the effect of fire frequency on variation in tree densities at both stand and landscape scales has not been previously considered for high-severity fire regimes, although stand-level responses to low-severity fire frequency have been well studied in low-elevation ponderosa pine forests in the southwestern US (Covington and Moore 1994).

In this study, we examine the influence of stand-replacing fire regimes on stand age and density in lodgepole pine-dominated (*Pinus contorta* var. *latifolia*) forests of Yellowstone National Park (YNP), at both stand and landscape scales, using an empirically based model. At the stand level, patterns of postfire stand density depend upon prefire legacies (Foster et al. 1998; Franklin et al. 2002), which can vary with prefire stand age (fire interval) and location (Schoennagel et al. 2003). The effect of variation in fire intervals on stand density has been relatively unexamined in stand-replacing fire regimes. As a consequence, debates about whether fire suppression (a decrease in fire intervals or area burned over time) can contribute to denser boreal and subalpine stands have ensued (Johnson et al. 2001). Furthermore, at the landscape level, it has been questioned whether large, stand-replacing fires homogenize forested landscapes (Weir et al. 2000). Although, high-severity fire regimes often produce large, even-aged stands, stand structure within these patches can vary widely (Turner et al. 2004; Kashian et al. 2005a). Although the effect of stand-replacing fire regimes on patterns of stand age and species composition has been considered (Romme 1982; Trabaud and Galtie 1996; Chuvieco 1999; Weir et al. 2000), effects on spatial patterns of stand structure have been relatively unexplored (except postfire sapling densities: Turner et al. 2004; Kashian et al. 2004). The response of stand and landscape structure to crown fire regimes is critical to basic understanding of pattern and process in subalpine forests, consideration of altered fire regimes associated with climate change (Dale et al. 2001), and application of ecosystem management approaches to emulating natural disturbance processes.

In lodgepole pine-dominated forests, which cover ~20,000,000 ha in western North America (Critchfield 1980), stand densities can vary orders of magnitude and represent a significant source of spatial heterogeneity across subalpine landscapes (Parker and Parker 1994; Kashian et al. 2004; Turner et al. 2004). Variation in stand age and density can affect susceptibility to subsequent disturbances, wildlife distributions and ecosystem processes. Insects such as mountain pine beetle (*Dendroctonus ponderosae*) respond to tree vigor that is in part a function of stand age and density, and large outbreaks are more likely in structurally homogenous, older landscapes (Anhold et al. 1996). Interactions among disturbance types often are a function of the legacies of stand age, composition and structure left by the previous disturbance (Veblen et al. 1994; Bebi et al. 2003). Abundance of wildlife, such as birds and elk, also responds to the age and density of lodgepole pine forests (Taylor 1972; Pearson et al. 1995; Smith et al. 2003). Lastly, stand age and density affect carbon and nitrogen dynamics across large landscapes (Pearson et al. 1984; Harmon et al. 1990; Smith and Resh 1999; Turner et al. 2004; Litton et al. 2004; Kashian et al. 2005b; Smithwick et al. 2005), providing important feedbacks to subsequent successional patterns.

In previous empirical studies, we evaluated how the time interval between stand-replacing fires influenced postfire lodgepole pine densities at the stand level (Schoennagel et al. 2003), and reconstructed how these initial postfire sapling densities changed via self-thinning and in-filling as stands mature (Kashian et al. 2005a). We also documented wide variation (six orders of magnitude) in postfire sapling density of lodgepole pine in response to the 1988 fires and varying pre-fire levels of serotiny (Turner et al. 1997; 2004; Schoennagel et al. 2003). In this study, we use these empirical analyses to create a landscape fire and succession model, YNPFIRE, that simulates the interaction between fire regimes and key processes that affect stand structure—namely initial postfire regeneration and subsequent self-thinning and in-filling in lodgepole pine forests.

Using the YNPFIRE model, we quantify the historical range of variability (HRV) of fire on the subalpine plateaus of Yellowstone National Park to evaluate how significant departures from HRV affect stand structure and spatial pattern of this subalpine landscape. Specifically, questions were addressed at two spatial scales: (1) How does variation in stand-replacing fire frequency and size influence the overall mean and annual variation in age and density of lodgepole pine-dominated stands in Yellowstone? (2) How do these different fire regimes affect spatial variation in age and density across the Yellowstone landscape?

Methods

Study area

Yellowstone National Park (YNP), in the northwest corner of Wyoming, is dominated by lodgepole pine forests on infertile subalpine plateaus that comprise the majority of the park (Despain 1990). Soils are relatively infertile across the rhyolitic plateaus, with slightly higher soil fertility on andesite and lacustrine substrates. The 1988 Yellowstone fires affected ~50% or >200,000 ha of the forested subalpine plateaus (Christensen et al. 1989; Turner et al. 1994). Large, stand-replacing fires have occurred historically, evidenced by fire scars and large patches of single-age cohorts of lodgepole pine on the recent landscape (Romme and Despain 1989; Tinker et al. 2003). The effects of fire suppression have been minimal in the park (Romme and Despain 1989). Mean fire intervals on the subalpine plateaus over the last half-century ranged between about 100 and 300 years (Schoennagel et al. 2003). Longer records of charcoal accumulations in lake sediments indicate that mean fire intervals ranged from 70 to 500 years during the Holocene (Millspaugh et al. 2000).

In high-elevation or high-latitude forests, fire regimes are tightly correlated with variation in climate, where large, stand-replacing fires are associated with extreme drought, which occurs infrequently (Romme and Despain 1989; Johnson and Wowchuk 1993; Millspaugh et al. 2000 Schoennagel et al. 2005). Although infrequent, large fires account for the majority of the area burned in lodgepole-dominated forests (Johnson et al. 2001; Schoennagel et al. 2004a). Summer drought is the primary cause of large stand-replacing fires on these high plateaus (Schoennagel et al. 2005) rather than fuel buildup (Bessie and Johnson 1995), and extreme weather rather than fuels was largely responsible for the extent and shape of the 1988 fires (Turner et al. 1994).

Lodgepole pine forests typically experience short-term regeneration phases following stand-replacing fire (Johnson and Fryer 1989; Turner et al. 1997). Postfire sapling densities of lodgepole pine are positively correlated with prefire serotiny (Turner et al. 1997; Schoennagel et al. 2003), where serotinous cones remain closed at maturity and release numerous seeds when heated by fire (Fowells 1965). Levels of serotiny vary across the park with higher serotiny at lower elevations (Tinker et al. 1994), apparently due to selection for this trait by more frequent fire on these drier sites (Schoennagel et al. 2003). Stand-level percent serotiny also varies as stands mature, peaking at intermediate stand ages (100 to 200 years; Schoennagel et al. 2003). On more fertile substrates at higher elevations, where cover by grass, forbs and shrubs is high, postfire sapling density can be sparse because lodgepole pine requires mineral soil and a high-light environment for successful seed establishment (Turner et al. 1997; Schoennagel et al. 2004b). Therefore, both the fire interval (the age of a stand when it burns) and fire location affect postfire lodgepole densities in YNP.

Dense postfire regeneration is followed by long periods of density-dependent mortality as shade-intolerant lodgepole pine mature (Johnson and Fryer 1989; Clark 1991a; Kashian et al. 2005a). Stands of low postfire sapling density, in contrast, gradually become denser as new individuals establish (Kashian et al. 2005a). In YNP, lodgepole pine stands converge to a mean density of ~1,200 stems ha^{-1} by ~200 years of age, after which mean stand densities do not change appreciably (Kashian et al. 2005a). Shade-tolerant Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) typically begin to replace lodgepole pine in the canopy after about 250 years, although this occurs less frequently in YNP where about 80% of the subalpine plateaus are dominated by relatively pure stands of lodgepole pine, regardless of age. Therefore, in the model we track the density of lodgepole-dominated stands (initial postfire sapling density and subsequent changes in stand density), rather than changes in overstory species composition.

Model overview

YNPFIRE is a probabilistic, cellular automata model of fire occurrence and forest stand succession created with the SELES (Spatially Explicit Landscape Event Simulator) modeling tool (Fall and Fall 2001). This model was designed to provide a parsimonious simulation of the spatio-temporal interactions between fire and regeneration processes affecting stand age and density attributes that were parameterized using available empirical data. YNPFIRE simulates changes in the age and density of lodgepole pine-dominated stands across the subalpine plateaus of Yellowstone in response to fire regimes (defined by the frequency of fires of different size). Lodgepole pine density is represented by ‘postfire sapling density’ (stems ha^{-1} established after fire) and ‘stand density’ (simply the stems ha^{-1} of older stands). Under different fire regime scenarios, the frequency of very large fires is altered from the historical frequency experienced over the last 100–500 years. All fires are stand replacing and return stand age to zero. Overall, fire regime scenarios affect the fire interval in each stand and the subsequent age to which it lives before burning again, thus modifying postfire sapling densities and subsequent stand densities. The simulated landscape has a spatial extent of ~580,000 ha of the subalpine plateaus of Yellowstone, and a cell size of 4 ha.

Because the model is stochastic and subject to infrequent fire events, scenario results are based on 10 replicates of 1,000-year simulations. Yearly means of dynamic output variables such as stand age, fire interval (the age at which a stand burns), area burned, serotiny and stand density are reported for the whole landscape and also separately for low- (<2,350 m) and high-elevation portions (≥2,350 m) of the study area. For variables that change only in burned cells each year (e.g., fire interval and postfire sapling density), area-weighted means are used. A scenario mean for each variable is calculated by averaging the 1,000 yearly means to produce replicate means, then averaging the 10 replicate means. For each scenario, coefficients of variation (CV), which capture annual variation, are calculated by dividing the standard deviation among the yearly means by the replicate mean (×100), then averaging the replicate CVs. Four fire scenarios were simulated to compare trends in the mean and annual variation of stand age, postfire sapling density and stand density.

Fire regime scenarios

Fire scenarios are defined by the probability of occurrence of different fire sizes. The nominal fire scenario, denoted as HRV to represent the historical range of variability in the fire regime over the last 500 years, is based on the frequency of small (<99 ha), medium (100–999 ha), large (1,000–9,999 ha) and very large (≥10,000 ha) fires observed historically in the park.

An 1895–1990 fire history dataset was used to estimate the frequency of fires in the smaller size classes (<10,000 ha). Estimating the average size and frequency of very large (>10,000 ha), infrequent fire events (e.g., 1988) from a century-long database is not possible, so we relied on a longer-term (500-year) fire history dataset for this estimate (Table 1; Romme and Despain 1989; Tinker et al. 2003). This dataset is a contiguous 130,000 ha map of stand ages recovering from historical stand-replacing fires, which is a standard method of characterizing fire history in subalpine forests (Romme and Despain 1989, Johnson and Gutsell 1994). Using this dataset,

Table 1 Summary statistics of historical fires (n=99) in Yellowstone National Park, Wyoming

Fire Size Class	Fire Size (ha)		Percentage of YNP Burned (%)	Frequency of Occurrence (year^{-1})
	Mean	SD		
Small (<99 ha)	6	14	0.0008	0.68
Medium (100–999 ha)	420	262	0.050	0.23
Large (1,000–9,999 ha)	5,422	3,408	0.61	0.084
Very large (>10,000 ha)	140,968	129,266	26.0	0.006

The historical fire size and frequency of occurrence depicted below defined the nominal fire regime (HRV) in the model (see *Fire regime scenarios* for details)

we identified at least 3 very large fire events during the last 500 years on the subalpine plateaus (1988, ~1740, ~1700). These very large fires occurred about every 167 years on average or with a 0.006 probability of occurrence each year (Table 1). The mean size of these three fires was calculated by taking the proportion of the study area where the ~1740 and ~1700 fire events were recorded and multiplying this by the extent of the subalpine plateaus. We then averaged these numbers with the size of the 1988 fires which occurred across the extent of the plateaus. From this calculation, the average size of 'very large fires' historically was 141,000 ha (Table 1).

Variation among fire scenarios is based on differences in the frequency of occurrence of very large fires (Table 1), which is the key determinant of area burned and therefore the age and spatial structure of subalpine forest landscapes. A scenario in which the frequency of very large fire occurrence is twice that of the nominal scenario (0.012) is referred to as '2HRV'. A fire scenario where the frequency of very large fire occurrence is half that of the nominal scenario (0.003) is denoted as 'HRV/2'. Scenarios ranged from HRV/2 to 3HRV, which represents a six-fold change in the occurrence of very large fires (0.003–0.018 year^{-1}). Wide variation in fire frequency has occurred over the Holocene, during which lodgepole pine continuously inhabited the plateaus (Millspaugh et al. 2000). Although fire regimes are much more complex than depicted by these scenarios, we focused on the key element affecting subalpine forests to configure the model experiments, namely, the frequency of very large fires.

Fire

Each simulation year, the number of fires in each fire-size class is selected based on defined probabilities of occurrence for the specified fire regime scenario (Table 1). For each fire, the area to burn is selected from a negative exponential distribution, where the mean reflects the average proportion of the subalpine plateaus burned in the historical record from the appropriate fire-size class (Table 1). Fires initiate on the landscape according to probabilities of burning calculated for each cell. For smaller fires, presumably burning under non-extreme weather conditions, the probability of burning increases with stand age, defined by the empirical hazard function below, to capture increases in fuel loading which increase with stand age (Eq. 1; Clark 1991a; Johnson and Gutsell 1994).

$$P(\text{burning}) = \frac{(c \times \text{StandAge})^{c-1}}{b^c} \qquad (1)$$

The parameter b is the age at which 63% of the stands are expected to be younger, while c is a unitless shape parameter which when greater than 1 defines a probability of burning that increases with stand age. Parameters for this equation were empirically derived from a large stand-age map from the subalpine plateaus of Yellowstone (Romme and Despain 1989; Tinker et al. 2003), where b=270 years and c=3. When very large fires burn during extremely dry and gusty weather conditions, however, all stands have an equal probability of burning, as observed in 1988 (Romme and Despain 1989). Fire spread is a stochastic process based on an algorithm developed by Fall, which creates complex fire perimeters and unburned islands typical of fires in YNP (Turner et al. 1994).

Succession

In each 4-ha cell, the succession module annually (1) updates stand age (years), (2) predicts postfire sapling densities of lodgepole pine (stems ha^{-1}) in stands burned the previous year, (3) updates stand densities of unburned cells based on stand age and previous year's density (stems ha^{-1}), and (4) recalculates serotiny (%) based on stand age and elevation. Predictions of postfire sapling density of lodgepole pine are based on empirically derived relationships to (1) soil substrate and serotiny, which is a function of prefire stand age, at low elevations, and (2) soil substrate and prefire stand age, at high elevations (Schoennagel et al. 2003). Where serotiny is relatively low (high elevations) it exerts little influence on postfire stand densities. The density of unburned stands is predicted annually according to self-thinning or in-filling curves for stands of different age and initial postfire sapling density (Kashian et al. 2005a). See *Study area* for detailed description of succession within the model.

Static maps depict elevation and soil substrate (YNP Spatial Analysis Center). Elevation (50 m DEM) ranges from 1,890 to 3,125 m, with the low-elevation portion of the landscape (<2,350 m) accounting for 23% of the model study area. Soil substrate is a binary map depicting infertile rhyolite substrates (76%) and slightly more fertile substrates (24%). For all simulations, the landscape is initialized with the same stand age and density base maps, where stand age varies positively with elevation, ranging from 50 to 450 years, with the majority of the landscape (65%) between 200 and 300 years old. Initial densities vary from 550 to 40,000 stems ha^{-1}, and the majority of the landscape (80%) has <1,200 stems ha^{-1}.

Three simplifying assumptions were adopted in the succession model. First, postfire sapling densities are based on data collected 12-years postfire, but they are predicted in the year directly following fire to permit model simulations with an annual time-step. Previous studies of succession following the 1988 fires showed peak recruitment of lodgepole pine seedlings occurred in 1990, and there have been no significant changes in lodgepole pine density through 2000 (Turner et al. 1997, 1999, 2003). Second, successful seed dispersal within each cell is assumed. Each cell represents 4 ha, which is greater than the range of typical lodgepole pine dispersal from open cones (Perry and Lotan 1977). Analysis of postfire densities following the 1988 Yellowstone fires suggests that seeds are effective in colonizing even very large fire patches, especially where prefire serotiny is high (Turner et al. 1997), so detailed dispersal was not characterized. Third, although we model variation in serotiny in response to stand age using different empirical equations for high and low elevations, these equations do not change dynamically throughout the simulation in response to fire frequency. Empirically, the degree of selection and inheritance of serotiny is poorly understood in response to particular fire events, and therefore adaptive changes are not parameterized.

Spatial analyses

Spatial patterns of stand age, postfire sapling density and stand density were examined in response to each fire regime. At 250-year intervals during each replicate simulation, maps representing the spatial distribution of stand age, postfire sapling density and stand density variables were output (n=4 for each variable per replicate run). In a GIS, maps of the continuous variables were classified in order to calculate spatial metrics using FRAGSTATS (McGarigal and Marks 1995). The landscape metrics Shannon's Evenness Index (range 0–1) and Contagion (range 0–100) were calculated to assess composition (dominance) and configuration (dispersion), respectively, of age and density classes across the landscape. Mean metrics for each scenario were calculated by averaging metrics for each variable across replicate maps. We performed spatial analyses on the full extent of the study area (579,568 ha) and on two large, square subsections (each 113,520 ha) that best represent high- and low-elevation portions of the subalpine plateaus.

Model evaluation

We verified (Rykiel 1996) the behavior of the fire module by comparing the area burned in the nominal fire scenario (HRV) to that observed in Yellowstone during the last century (Balling et al. 1992) and we compared the means and CVs of stand ages simulated under the nominal scenario to a 1985 stand-age map for a 130,000-ha section of the YNP subalpine plateaus (Romme and Despain 1989). To assess if the range of variability in stand age distributions following very large fires was represented in the model, the 1985 stand-age map was updated to 1988 by overlaying the extent of the 1988 fires, returning the age of stands burned in 1988 to zero and updating unburned stands by 3 years. Stand age statistics for years of very large fires during the nominal scenario were compared to the 1988 stand age map. For validation, the degree to which model output matches independent data (Rykiel 1996), we compared the mean and variation in serotiny and postfire sapling density under the nominal scenario to independent field data from YNP (Romme and Despain 1989; Tinker et al. 1994; Turner et al. 2004).

In model evaluations, overall scenario means were compared to means of independent data collected in YNP (Turner et al. 2004). Measures of annual variation calculated for each simulation (see *Model overview* above) are inappropriate for comparison with field data collected at one point in time. Hence, we compared coefficients of variation across the landscape (landscape CVs) from the simulations to CVs from the field data to depict the spatial variability of a parameter across simulated and real landscapes. Landscape CVs were calculated by dividing the standard deviation of a variable across the landscape each year by the yearly mean (×100). These yearly landscape CVs were then averaged across each 1,000-year simulation, and across replicates. This landscape CV calculation differs from the annual CV calculation described above and is necessary for comparing dynamic simulations to static field data collected during one year. Lastly, sensitivity analysis assessed the effects of a ±10% change in input parameters controlling probability of burning, fire size or the probability of large fire occurrence on output parameters (area burned, stand age, serotiny, postfire sapling density and stand density).

Results

Model evaluation

The nominal fire regime (HRV) agreed well with area burned in YNP during the last century. On average, 0.3% of the simulated landscape burned every year under the nominal fire regime, while 0.5% of the actual YNP landscape burned annually on average over the last century. The coefficient of variation for area burned per year was also similar between the model (1,005%) and the 1895–1990 fire record (887%).

The nominal fire regime produced a similar stand age distribution to that of a 1985 stand-age map derived from the YNP subalpine plateaus. Mean stand age (and landscape CV) under the nominal scenario was 252 years (65%), while for the 1985 YNP map from the park it was 257 years (52%). Under the nominal fire regime during very large fire years only, simulated mean stand age declined to 186 years while the landscape CV increased to 106%. The updated 1988 map had a mean stand age of 141 years and a CV of 90%.

The nominal fire scenario predicted mean postfire sapling density (and landscape CVs) of 13,868 stems ha^{-1} (116%) at low elevations and 1,441 stems ha^{-1} (127%) at high elevations within the study area. Independent field data from 0.25-ha plots (N=87) burned in 1988 indicate higher mean postfire sapling densities of 38,416 stems ha^{-1} (109%) and 7,472 stems ha^{-1} (186%) and median postfire sapling densities of 21,433 and 2,166 stems ha^{-1}, for low- and high-elevations respectively (Turner et al. 2004). Serotiny predictions by the model were similar to field observations. Mean serotiny (and landscape CV) was 28% (131%) for low elevation and 3% (98%) for high elevation. Field observations found 27% (102%) and 4% (226%) of the trees were serotinous in stands at low and high elevations, respectively (Tinker et al. 1994, unpublished). Model results were most sensitive to the frequency of large fires. Stand age and postfire sapling density varied ±11% and 14%, respectively, in response to a ±10% change in the frequency of large fires.

Effect of fire regimes on stand age and density

Variation in the frequency of large fires across the range of fire scenarios considered (HRV/2 to 3HRV) affected mean fire interval, stand age, postfire sapling density and stand density (Table 2). Mean stand age declined from 291 to 121 years and mean fire interval similarly declined as the frequency of large fires increased across the scenarios. Mean postfire sapling density responded to change in fire intervals, increasing from 1,252 to 2,203 stems ha^{-1} at high elevations and from 13,691 to 22,379 stems ha^{-1} at low elevations. Mean stand density increased from 1,466 to 2,826 stems ha^{-1} for the entire landscape and from 2,807 to 7,664 stems ha^{-1} at low elevations across scenarios (Table 2).

Overall, annual variability (measured as annual CVs) in mean postfire sapling density was high, especially at low elevations, and declined as the frequency of large fires increased (postfire sapling density CVs=242%–172% across scenarios) (Table 2, Fig. 1). In contrast, annual variability in stand age and stand density was relatively low as the frequency of very large fires increased (stand age CVs=24–40%, stand density CVs=40–53%) (Table 2, Fig. 2).

Effect of fire regimes on landscape pattern

The proportion of the landscape in each stand age class was more even at low fire frequency (HRV/2) and became dominated by younger age classes as fire frequency increased (3HRV) (Table 3a). These trends were accompanied by a more dissected spatial pattern of stand age classes with less frequent fires, and a more clumped stand-age pattern as fire frequency increased (Table 3b, Fig. 3). There were few differences in metrics based on stand-age class by elevation.

For density classes (postfire sapling density and stand density), spatial trends were the reverse of stand age (Table 3). At low fire frequency, the landscape was dominated by a few low-density classes, and as fire frequency increased the pro-

Table 2 Character of the fire regime, stand age, prefire serotiny, postfire sapling density, and stand density under less extreme (HRV/2), nominal (HRV) and more extreme (2HRV and 3HRV) fire regime scenarios. Means and annual variation (coefficients of variation: [(SD/mean) × 100]) are reported for different regions of the study area, where LS=whole landscape, Low =low elevation (<2,350 m), High=high elevation (≥2,350 m). Variables are averaged across 10 replicates of each scenario

		HRV/2		HRV		2HRV		3HRV	
		Mean	CV	Mean	CV	Mean	CV	Mean	CV
No. Very Large Fires/1,000 years	LS	3.0	50	5.9	33	11.8	23	18.6	20
Fire Interval[a] (years)	LS	317	38	282	41	186	53	138	59
Area Burned/year (ha)	LS	1,229	1,004	1,651	1,014	3,121	851	4,352	737
	Low	333	932	441	922	798	814	1,094	711
	High	896	1,045	1,210	1,057	2,324	870	3,258	750
Stand Age (years)	LS	291	24	252	29	172	43	121	40
	Low	264	27	227	30	158	39	110	37
	High	299	24	260	29	177	44	125	41
Prefire Serotiny (%)	LS	8	57	9	51	11	46	11	43
	Low	24	62	28	56	33	49	36	44
	High	3	50	3	46	3	42	3	39
Postfire Sapling Density (stems ha^{-1})[a]	LS	4,646	242	4,837	221	6,457	191	7,296	172
	Low	13,691	257	13,868	231	19,530	203	22,379	174
	High	1,252	153	1,441	144	1,972	123	2,203	118
Stand Density (stems ha^{-1})	LS	1,466	40	1,540	37	2,209	52	2,826	53
	Low	2,807	76	3,110	66	5,439	73	7,664	68
	High	1,029	11	1,028	13	1,156	23	1,249	27

[a] Area-weighted means

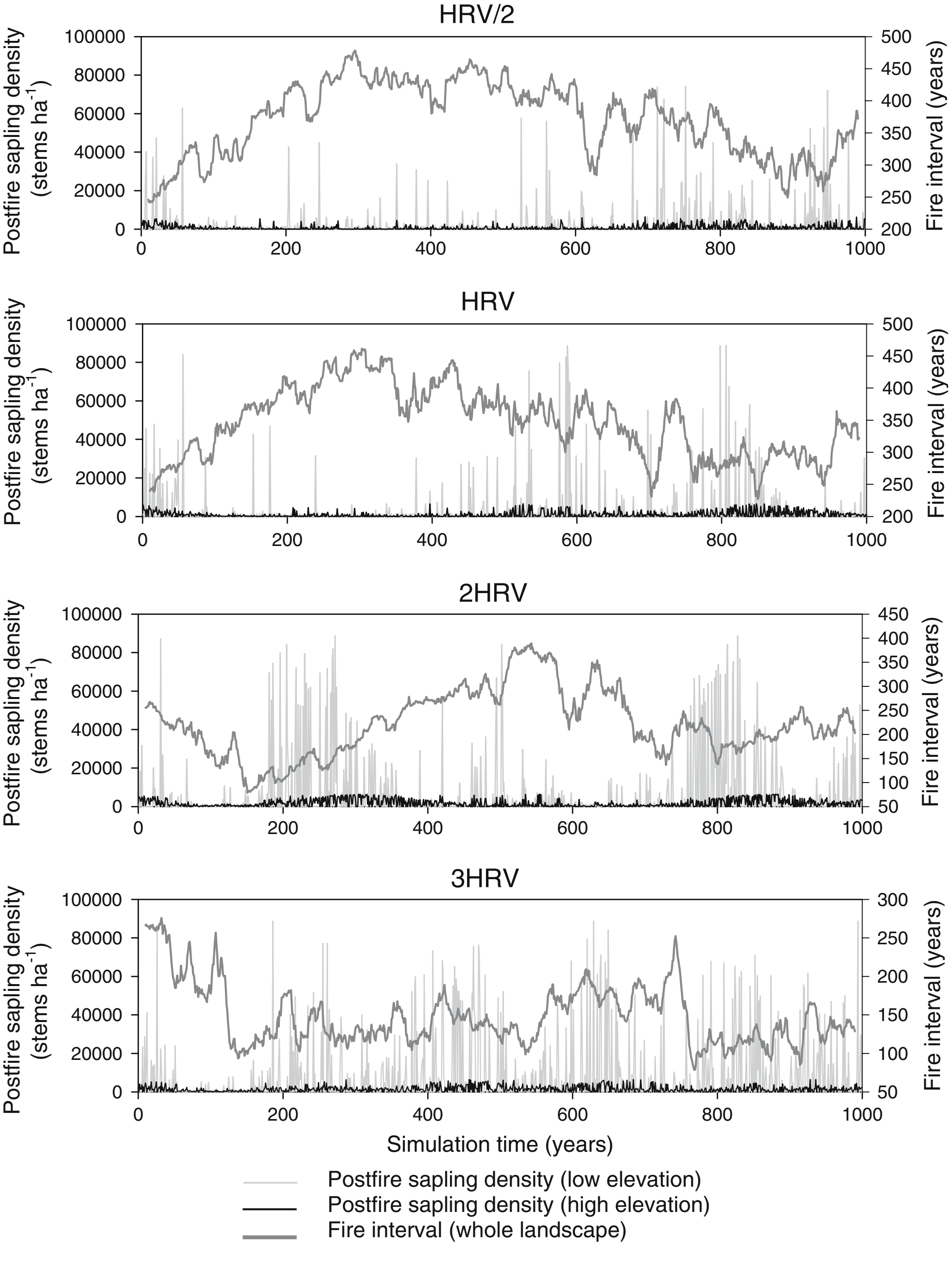

Fig. 1 Output from example model runs showing the response of mean postfire sapling density at low and high elevations over time to changes in mean fire intervals under different fire regimes (see *Fire regime scenarios* for details). Thin light grey lines represent mean postfire sapling density at low elevations; thin black lines represent mean postfire sapling density at high elevations. Thick dark grey lines represent a 20-year moving average of mean fire interval across the entire landscape

portion of the landscape in each density class became more even. With less frequent fire there was a more clumped spatial pattern of density classes, while more frequent fire produced more dissected or interspersed patterns of density classes across the landscape (Fig. 3). These density trends were more pronounced in the postfire landscapes and at low elevations.

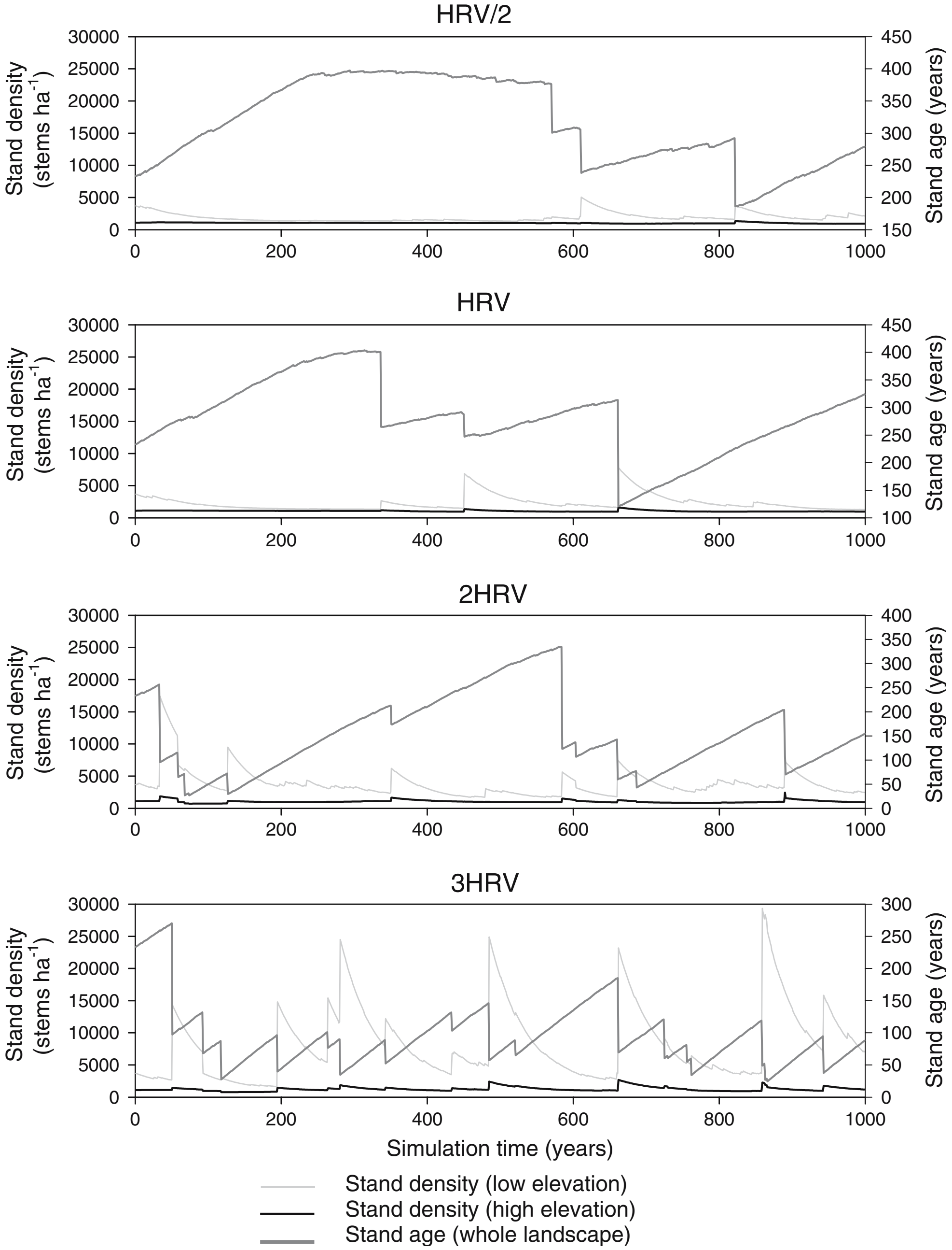

Fig. 2 Output from example model runs showing the response of mean stand density at low and high elevations over time to changes in mean stand age under different fire regimes (see *Fire regime scenarios* for details). Thin light grey lines represents mean stand density at low elevations; thin black lines represent mean stand density at high elevations. Thick dark gray lines represent mean stand age across the entire landscape

Discussion

Stand responses to altered fire regimes

Disturbance plays an important role in regulating species composition, stand structure and landscape heterogeneity (Pickett and White 1985). In lodgepole pine-dominated forests, variation in stand structure represents an important source of spatial heterogeneity (Parker and Parker 1994; Kashian et al. 2004, 2005a; Turner

Table 3 Results from spatial pattern analyses of stand-age class maps (7 classes) and density class maps (8 classes) from the HRV/2-3HRV scenarios using FRAGSTATS (McGarigal and Marks 1995)

	Stand age classes (years)		Postfire sapling density classes (stems ha^{-1})		Stand density classes (stems ha^{-1})	
	Low	High	Low	High	Low	High
(a) *Shannon Evenness Index (Composition)*						
HRV/2	0.63	0.62	0.69	0.54	0.44	0.38
HRV	0.54	0.60	0.72	0.54	0.44	0.43
2HRV	0.52	0.57	0.73	0.57	0.54	0.44
3HRV	0.44	0.46	0.78	0.58	0.62	0.46
(b) *Contagion (Configuration)*						
HRV/2	50.3	51.2	45.0	55.7	63.1	66.4
HRV	54.6	52.7	44.8	54.7	58.0	60.7
2HRV	56.7	54.4	38.2	49.7	53.9	58.4
3HRV	62.9	59.0	34.4	49.5	46.9	56.0

Landscape metrics shown are the mean (n = 40) of (a) the Shannon Evenness Index and (b) Contagion, for low- (Low) and high-elevation (High) portions of the Yellowstone Landscape across replicate maps (113,540 ha with 4 ha cells) from each fire regime scenario

et al. 2004). Our empirically based model simulations suggest that more frequent large fires (which result in shorter fire intervals and greater area burned over time) promote denser lodgepole pine stands and greater spatial variability across the landscape. This occurs as a consequence of three factors. First, postfire lodgepole pine densities are highest following fire intervals of 100–200 years, which occurred on average during the 2HRV and 3HRV scenarios, especially in areas of high prefire serotiny where postfire seed availability is abundant (Table 2; Turner et al. 1997). Other studies have shown that stands that burn at intermediate ages (when stands are highly productive, of relatively high density, and before significant loss of early successional species), are followed by relatively high postfire sapling densities (Clark 1991a; Lamont et al. 1991; Ne'eman et al. 1999; Schoennagel et al. 2003). Following relatively infrequent fire, postfire sapling densities tend to be lower, due to decreased productivity with age and increased senescence of early successional species from the prefire stand through density-dependent thinning or replacement by other species before fire recurs (Romme 1982), resulting in lower postfire recruitment (Clark 1991a; Ne'eman et al. 1999). Indeed, in the less frequent fire scenario (HRV/2) mean fire intervals of ~320 years resulted in relatively low postfire sapling densities (Table 2, Fig. 2). Overall, biotic legacies affecting postfire densities vary with prefire stand age, influencing responses to temporal variation in stand-replacing fire.

Second, the subsequent structure of stands comprised of predominantly shade-intolerant species such as lodgepole pine is highly dependent on initial postfire densities (Johnson and Fryer 1989; Kashian et al. 2005a). Postfire sapling densities affect subsequent stand densities, especially in the decades following fire, and can have a lasting imprint across forested landscapes (Turner et al.1997; Foster et al. 1998; Kashian et al. 2005a). Thus, postfire spatial patterns may be an important, predictive metric of subsequent landscape heterogeneity.

Lastly, stand density in lodgepole pine forests depends on the interaction of thinning rates and disturbance frequencies, where frequent disturbance promotes younger stands of higher densities and greater variability across the landscape (Clark 1991b). Younger stands (<200 years) more common across the landscape under the 2HRV and 3HRV fire regimes, experience shorter periods of self-thinning and therefore are denser than older stands of similar initial postfire sapling density. Less frequent fire (such as under the HRV/2 scenario) permits decades to centuries of self-thinning, resulting in convergence of initial variability in postfire sapling densities and relatively low stand densities (Kashian et al. 2005a). Therefore, for

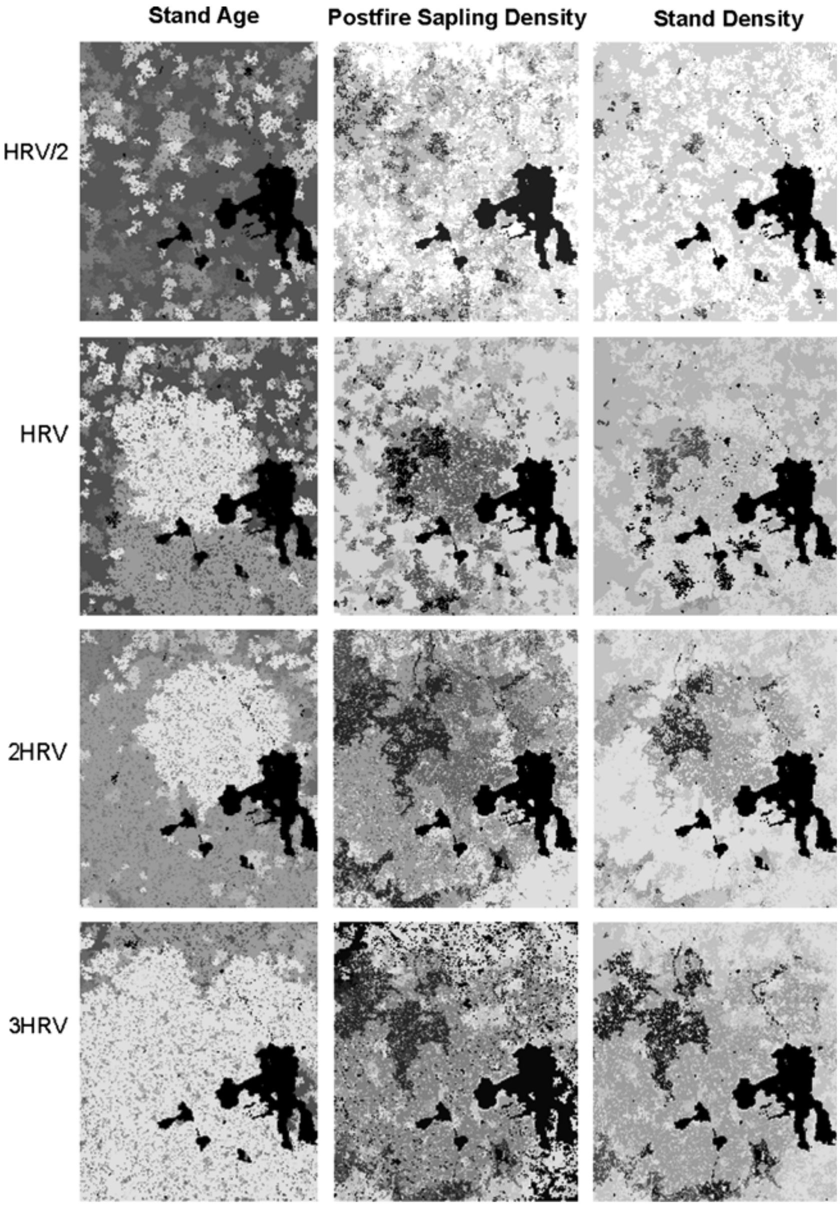

Fig. 3 Example maps depicting spatial variation in stand age, postfire sapling density and stand density across the Yellowstone landscape under fire regime scenarios to illustrate the spatial trends reported in Table 3. The variables depicted in each map correlate positively with image darkness. The four large solid black polygons are major lakes

example, suppression of fire would promote older, sparser lodgepole pine stands across the landscape in contrast to examples in southwestern ponderosa pine forests, where suppression generally has promoted denser stands (Covington and Moore 1994).

Self-thinning plays less of a role in stands of relatively low postfire sapling densities, which comprise much of the high-elevation plateaus in Yellowstone that burned in 1988 (Kashian et al. 2004; Turner et al. 2004). These stands showed low variability in stand density through time and across the simulated high-elevation landscape. Some very sparse stands may continue to recruit trees as they mature, becoming slightly denser with time since last fire, but are a very small component of the landscape in both our model and in Yellowstone (Kashian et al. 2005a).

Postfire sapling density is highly dependent on variation in serotiny across the landscape (Turner et al. 1997; Schoennagel et al. 2003). The spatial pattern of serotiny in the model was based on currently known relationships to elevation. High levels of serotiny, however, would expand spatially with moderate increases in fire frequency (Radeloff et al. 2004) where currently serotiny is low, resulting in potentially denser stands across a greater portion of the subalpine landscape (i.e., at higher elevations) than observed today. Results from more extreme scenarios not presented here (5HRV) indicate that relatively very short mean fire intervals (<80 years) could reduce serotiny in areas where serotiny currently is high. Lower postfire sapling densities following very short fire intervals in the model have been observed in other serotinous systems (Desponts and Payette 1992; Ne'eman et al. 1999), presumably due to lower serotiny in very young stands that burn (Schoennagel et al. 2003). Although mean serotiny and postfire sapling densities are expected to be lower under this extreme scenario, stand densities would be higher on average as younger stands experience less self-thinning. This serotiny response occurs under only relatively very extreme departure from the current fire regime, which we consider unlikely over the next century. In addition, this prediction does not accommodate adaptive responses in serotiny to very short fire intervals. Given the more likely expectation of increased serotiny across the landscape under the 2HRV and 3 HRV scenarios, in addition to the fact that our model underestimates postfire sapling densities relative to independent empirical data (Turner et al. 2004), suggests our simulations underestimate expected increases in stand density and spatial heterogeneity of lodgepole pine under these more frequent fire regimes, all else being equal.

Arguably, expected climate change during the next century may precipitate the most rapid and extensive changes in forest composition and structure due to altered disturbance regimes, such as fire, rather than slower physiological responses to changes in temperature, precipitation and CO_2 concentration (Dale et al. 2001). Nonetheless, climate change will undoubtedly affect competitive success during postfire establishment and self-thinning phases (Dale and Franklin 1989; Peterson 1994; Mooney et al. 1999). Although our modeling effort does not evaluate the direct influence of climate on density patterns in lodgepole pine forests, isolation of potential responses to variation in fire is an important step toward more comprehensive predictions of successional responses to climatically altered fire regimes.

Landscape responses to altered fire regimes

Although large stand-replacing fires in lodgepole-dominated landscapes create extensive even-aged stands, complex spatial heterogeneity in stand density does emerge, especially under more frequent fire regimes. Under the nominal fire scenario, the simulated YNP landscape was dominated by a matrix of relatively sparse postfire sapling density punctuated by patches of dense seedlings randomly distributed across the postfire landscape, predominantly at low-elevations. These spatial trends correlate well with the patterns of stand density following the 1988 fires (Kashian et al. 2004; Turner et al. 2004). Our simulations indicate that under more frequent fire regimes, the landscape becomes dominated by denser stands of high spatial variability, which promote a more disaggregated, dissected landscape. Greater spatial heterogeneity in stand density is expected when mean stand age is within the period of active self-thinning (Clark 1991b), which occurs <200 years under the 2HRV and 3HRV scenarios. Hence, successional changes at the stand level have important consequences for landscape structure.

Empirical studies support our modeling results that stand-replacing fire regimes can promote spatial heterogeneity across forested landscapes (Heinselman 1978; Romme 1982; Weir et al. 2000; Tinker et al. 2003; Turner et al. 1994, Turner et al. 2004, Kashian et al. 2004). Specifically, while more frequent stand-replacing fires simplify the spatial age mosaic, they appear to increase compositional and structural diversity across landscapes dominated by crown fire regimes (Romme 1982; Weir et al. 2000), with pre-fire biotic legacies playing an important role in promoting heterogeneous postfire landscapes (Foster et al. 1998; Turner et al.1994, 1999). These initial post-fire patterns can sustain lasting imprints across forested landscapes subject to recurrent fire (Kashian et al. 2005a).

Disturbance-generated successional patterns are an important process generating spatial and temporal variability of forested landscapes. Our stand- to landscape-scale study suggests that (1) prefire spatial heterogeneity (elevation, stand age and serotiny) affects postfire spatial patterns, (2) stand-level processes are an important factor affecting spatial heterogeneity and (3) overall, shorter stand-replacing fire intervals result in denser stands and a more spatially heterogeneous landscape. Lodgepole pine forests appear fairly resilient to wide variations in fire regimes (Millspaugh et al. 2000), but heretofore, an understanding of how stand densities respond to variation in disturbance regimes has been lacking. Our empirically based model simulations suggest that higher stand-replacing fire frequency or area burned relative to recent history will promote denser stands with greater variability across lodgepole-dominated landscapes (especially in the few decades following large fires), with very high annual variability in postfire sapling densities. Dense, rapidly thinning stands could become more dominant with more frequent stand-replacing fire as serotiny expands across subalpine landscapes. In contrast, less frequent stand-replacing fire should result in sparser, more homogenous lodgepole pine forests. In general, altered fire regimes (due to management or climate) are expected be an important catalyst of landscape change over the next century.

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