Spatial Ecology of Pre–Euro-American Fires in a Southern Rocky Mountain Subalpine Forest Landscape*

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Natural disturbances such as fires have been widely studied, but less is known about their spatial ecology than about other aspects of them. We reconstructed and mapped pre–Euro-American fire history in a subalpine forest landscape in southeastern Wyoming, and analyzed the fires using GIS. Mean fire interval varies little with topography (elevation, aspect, slope) and is spatially autocorrelated at distances of at least 2 km. Fires often spread downslope, and spread more than expected from the north and south and less than expected from the west, under the influence of particular synoptic climatic conditions. The landscape of 1868 A.D., at the time of Euro-American settlement, was strongly influenced by fires. However, it contained large patches of connected forest and few high-contrast edges, unlike the modern landscape, which is fragmented by industrial forestry and roads. The spatial ecology of the natural fire regime may be a useful guide for management. Key Words: fires, GIS, Rocky Mountains, spatial ecology, Wyoming.

Introduction

most of the world's ecosystems is now widely recognized, but spatial variation in natural disturbance is less appreciated. Spatial variation in disturbance intensity, size, and frequency may significantly influence the pattern and rate of postdisturbance recovery (Turner et al. 1998). However, relatively little is known about how topography affects disturbance intensity, severity, size, or frequency. In mountainous landscapes, topographic variation can be expected to influence many aspects of disturbance. Moreover, human land uses are increasingly a source of pattern on the landscape scale, and understanding spatial variation in natural disturbance might help guide management of these uses (see, e.g., Hunter 1993; DeLong and Tanner 1996; Wallin et al. 1996). For example, to what extent are the landscapes produced by natural disturbances similar to landscapes produced by timber harvesting? In this article, we examine the spatial ecology of pre-Euro-American fires in a mountainous landscape in the southern Rocky Mountains of Wyoming.

Topography is often considered an important influence on spatial variation in fire regimes in mountains, but fire regimes appear to have inconsistent relationships with topography. The higher incidence of solar radiation on south-facing slopes, relative to north-facing slopes, might lead to shorter mean fire intervals (MFIs) due to drier fuels. This is sometimes found (Taylor and Skinner 1998; Weisberg 1998), but other times is absent or is weak (Barrows, Sandberg, and Hart 1976; Ryan 1976; Engelmark 1987; Impara 1997). In the Rocky Mountains, absence of a strong north slope-south slope contrast in MFI (e.g., Barrows, Sandberg, and Hart 1976) could be due to dominant westerly storm tracks intersecting north-south-trending mountains (Fowler and Asleson 1984). The east side of north-south trending mountains, where air is dried by descending, may have shorter MFIs than the west side (Ryan 1976; Alington 1998).

Other expected trends include: (1) long MFIs at higher elevations, sometimes found (Ryan 1976; Morrison and Swanson 1990; Weisberg 1998)-note that shorter MFIs have also been found (Engelmark 1987); (2) long MFIs and lower intensity fires on less steep slopes, sometimes found (Barrows, Sandberg, and Hart 1976; Engelmark 1987), but sometimes not evident (Kushla and Ripple 1997); and (3) long MFIs on lower slopes and along streams or near lakes, sometimes found (Romme and Knight 1981; Larsen 1997) but absent in other cases (Barrows, Sandberg, and Hart 1976; Taylor and Skinner 1998). A potential explanation for low correlation of fires with topography may be the greater importance of the configuration of fire

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paths and fire breaks that more directly shape patterns of fire spread (Engelmark 1987; Andison 1996). Also, when fires are large relative to the grain of the landscape and are of high intensity, these fires may burn over many different topographic settings, diminishing the importance of topography in shaping the fire regime (Masters 1990; Turner et al. 1994; Andison 1996; Kushla and Ripple 1997). Fires in subalpine forests in the Rocky Mountains, the subject of our study, are predominantly stand-replacing crown fires; surface fires are comparatively rare in this area (Romme 1982; Kipfmueller and Baker 2000).

Fires may become large due to extreme fire weather, which-in the Rocky Mountains as elsewhere-is often associated with strong winds and dry weather. Winds in particular are shaped by topography, and fires may spread further when valleys are oriented toward sources of strong drying winds. Orientation to dry east winds may partly explain differences among fire regimes in watersheds of Oregon's Cascade Range (Weisberg 1998), and may explain the location of remnant forest patches in South Africa (Geldenhuys 1994). Reconstruction of fire-spread direction is possible using fire scars on trees (Bergeron and Brisson 1990), but has seldom been attempted. Do fires typically spread up valleys or up side-slopes, or is their direction of spread determined more by the direction of rare, strong, dry winds?

In the Rocky Mountains, most research on spatial variation in fires has used historical data collected over the last half century (Barrows, Sandberg, and Hart 1976; Ryan 1976). However, fire suppression since the turn of the century may have altered spatial variation in fires and the relationship of fires with topography. It is thus important to consider whether fire patterns over the last half-century parallel pre-Euro-American fire patterns. Alington (1998) analyzed spatial variation in pre-Euro-American fire sizes and mean fire intervals across the Sangre de Cristo Mountains in southern Colorado. In this study, we analyzed spatial variation in the fire regime in a subalpine landscape in the southern Rocky Mountains by reconstructing fires from the recent pre-Euro-American period prior to 1868 A.D. This is the approximate date on which Euro-American settlement began near the study area. After this date, use of the forest resource intensified through the extraction of timber for railroad and telegraph

construction and mining operations (Thybony, Rosenberg, and Rosenberg 1985).

Based on trends reviewed above, we hypothesized the following about the fire regime of this period in our study area:

- H₁: Fires had size, shape, and interval distributions typical of fires in other subalpine coniferous forests of the western United States.
- H₂: Area burned increased and MFI decreased as elevation and slope increased and toward drier, south-facing slopes.
- H₃: Fire spread was primarily in the direction of prevailing winds, but also upslope.
- H₄: The landscape produced by the fire regime had large patches with large percentages of interior relative to edge and much old forest, and was highly connected. This hypothesis is based on previous studies of crown-fire landscapes (e.g., Turner et al. 1994).

Methods

Study Area

The study area is in the Medicine Bow Mountains in southeastern Wyoming, about 50 km west of Laramie, primarily in the Rock Creek drainage of the Medicine Bow National Forest at the northern end of the Southern Rocky Mountains (Fig. 1). The study area of 3,241 ha was chosen because it contains one of the largest areas of old forests relatively free of timber harvesting on the Medicine Bow National Forest. The study area also was chosen to span a gradient from about 2700-3200 m in elevation. Forests in the study area are dominated by lodgepole pine (Pinus contorta Dougl. ex Loud var. latifolia Engelm. ex S. Wats.) at lower elevation and Engelmann spruce-subalpine fir (Picea engelmannii Parry ex Engelm.-Abies lasiocarpa [Hook.] Nutt.) at higher elevation.

Field Methods

Field and laboratory procedures to map past fire boundaries are summarized here from Kipfmueller and Baker (2000). Patches potentially created by fire were mapped initially using a stereoscope and 1:40,000-scale colorinfrared aerial photographs taken in 1989–90 as part of the U.S. Geological Survey's National



Figure 1 The study area and the five fires for which scar-direction data are available (a–e), and the reconstructed landscape in 1868 A.D. (f). The center of the study area is at approximately $41^{\circ}29'$ N and $106^{\circ}12'$ W. The study area includes parts of the watersheds of Cooper Creek and Rock Creek. Shown in each of a–e are the reconstructed fire boundary and the fire-spread direction (arrow) at the location of the scar, with an "N" indicating polygons within the study area that did not burn.

Aerial Photography Program. Boundaries were then refined in the field by observation from high viewpoints. Patches and patch boundaries were distinguished by visible changes in color, texture, and tree density. Each potential fire patch was visited, boundaries were adjusted as needed, and the patch was verified to be the result of fire. Additional patches identified during field sampling were mapped using a global positioning system (GPS), and GPS locations were differentially corrected using a base station.

We used fire scars supplemented by standorigin dating to determine the year of the fire that initiated each patch. Fire-scarred trees were systematically sought along patch boundaries and on surviving trees inside patches. A partial wedge was extracted from each visibly scarred tree using a chainsaw (Arno and Sneck 1977), and scar locations were mapped using the GPS. Stand-origin dates were estimated from tree ages obtained from increment cores, extracted from near the base of ten or more of the largest trees in a 20 m \times 50 m plot, following Kipfmueller and Baker (1998a). Plot locations were mapped using the GPS. In the laboratory, increment cores and fire wedges were processed following standard dendrochronological techniques (Stokes and Smiley 1968). Where possible, fire dates were cross-dated visually by comparing the pattern of wide and narrow annual rings to those in six master chronologies obtained from the International Tree-Ring Data Bank (ITRDB). If uncertain, cross-dating was verified by measuring tree rings and using a cross-dating program, COFECHA (Holmes 1983).

GIS Analysis

To produce computer maps of the fires in the GIS, GRASS 4.2 (USA-CERL 1997), we scanned and orthorectified the aerial photographs (see Kipfmueller and Baker 2000 for details). Firepatch boundaries, mapped in the laboratory and verified in the field, were digitized on screen using the orthorectified aerial photos as a backdrop. Digitized polygons were then converted to raster maps. The study area fits within a rectangle 8.6 km \times 11.0 km, represented in the GIS as a raster 2252 rows \times 2893 columns at 3.8 m resolution.

The estimated extent of all stand-replacing fires was reconstructed and digitized on screen using a variety of evidence, including, in order of importance: (1) the map of the patch from that year; (2) locations of fire scars dating from the fire; (3) locations of surviving trees dating within ten years of the fire year, found in plots in patches elsewhere in the study area; (4) natural fire breaks such as rock outcrops; and (5) the estimated fire-spread direction. Patchorigin dates were assigned based on dates from fire scars and increment cores. Fire dates not based on cross-dates from fire scars were assigned a five-year range. Our analysis is restricted to the period between 1680 and 1868 A.D., because a fire near 1680 A.D. burned much of the study area, erasing evidence of earlier fires, and Euro-American settlement began about 1868 A.D. (Thybony, Rosenberg, and Rosenberg 1985).

The r.le programs version 2.2 (Baker and Cai 1992), operating within GRASS, were used to measure patch size, fire size, and other landscape attributes. The depth-of-edge influence was assumed to be 100 m (see Baker 2000). Depth-of-edge influence is the distance, typically measured from the edge of a patch, over which a patch has a modified microenvironment or biota relative to the patch before edge creation (Baker 2000). A 100 m buffer was removed from the outside boundary of each patch to calculate the area of the patch interior. Also calculated were the compactness of the patch (a shape measure), using the corrected perimeter/area index and the length of patch perimeters (Baker and Cai 1992). Size-class distributions were developed for fires, fire patches, and patch interiors, and a shape-index distribution was calculated. The total area of a single fire may be distributed among several distinct patches.

A map of MFI for each pixel in the study area was developed (see, e.g., Wallin et al. 1996). MFI for a pixel was calculated for the 1680–1868 period as the year of the last stand-replacing fire, minus the year of the first fire divided by the number of fire intervals (one less than the number of fires). The total area burned (ha) after particular intervals during the 1680–1868 period was calculated using the GIS and reported in twenty-five-year classes. MFI and the standard deviation of fire interval for the landscape were calculated from the pixel-scale MFI values.

MFI at the pixel scale may be spatially autocorrelated, because MFI values are affected by a few fires of large extent. Spatial autocorrelation affects inferential statistics that assume independence of samples. However, it is also of interest to know whether the fire regime is spatially autocorrelated, and if so, over what distance. To analyze the spatial extent of autocorrelation in MFI, the MFI map was resampled to 10 m pixel resolution, then input into another GIS, Idrisi (Eastman 1997). We used the King's pattern (8-neighbor) AUTOCORR function in Idrisi, with increasing lag distances, to estimate the distance over which MFI values are spatially autocorrelated, measured by Moran's I with the normality assumption (Griffith 1987).

Elevation, slope, and aspect maps were derived from 30 m resolution U.S. Geological Survey digital elevation models (DEMs), using the GRASS GIS, to examine their influence on MFI. Elevation, slope, and aspect were divided into classes (e.g., 2801–2900 m) for analysis. The GIS was used to calculate how MFI and total area burned during the 1680–1868 interval vary across these classes of elevation, slope, and aspect, and in relation to the distribution of land area in these classes. The standard deviation of MFI was calculated, based on pixel-scale MFI, for all the pixels in a class. Because these are means and standard deviations for the entire population of pixels in a class within the study area, and this is a case study, samplebased statistical inference is not used.

The distribution of fire-spread directions was compared to the distribution of prevailing wind directions and upslope directions at the fire-scar locations. Fire scars typically form on the leeward side of trees, so the fire scar faces the approximate direction the fire was burning. We recorded this azimuth as the estimate of the direction of fire spread (Bergeron and Brisson 1990; Gutsell and Johnson 1996). We restricted this direction analysis to only the first scar on each tree, since subsequent scar directions are likely constrained by the direction of the first scar (Bergeron and Brisson 1990). We used the frequency of winds from eight cardinal directions, based on the summer average for 1978–1980 for Medicine Bow, Wyoming, ca. 40 km north of the study area (Martner 1986). Upslope direction was derived for each GPS-mapped fire scar location from 30 m U.S.

Geological Survey digital elevation models. Since this is a sample, chi-square analysis was used to test the hypotheses that the distribution of fire-spread directions (1) is random with respect to aspect and (2) does not differ from the distribution of wind directions. To examine whether fires generally burn upslope, we plotted the deviation of the fire-spread direction from the upslope direction for eight classes of deviation, each 22.5 degrees wide.

The age-class structure of the landscape in 1868 A.D., near the time of Euro-American settlement, was reconstructed from the fire-year maps. Beginning with the earliest fire, maps of fires to 1868 A.D. were overlain sequentially in the GIS, as would have occurred in the landscape. The age of each patch in 1868 was calculated for the resulting map of the 1868 landscape. The r.le programs (Baker and Cai 1992) were then used to calculate mean patch size, mean interior size (assuming 100 m depth-ofedge influence), and the corrected perimeter/ area shape index.

Results

There were eight stand-replacing fires in the study area between about 1680 and 1868 A.D. (Table 1). These fires burned 4,871 ha in total, or 1.5 times the land area of the study area, so the study period represents about 1.5 fire rotations. The land area of the study area is 1.22 times the size of the largest fire (Table 1). Some fires extended outside the study area boundary

| /ear(s) | Patch Number | Patch Area (ha) | Interior Area (ha)ª | Shape Index ^ь | Perimeter Length (km) ^o |
|----------|-----------------|--------------------|------------------------|-----------------------------|---------------------------------------|
| 676-1684 | 1 | 2651 | 2171 | 2 94 | 53.6 |
| 715-1720 | 1 | 61 | 20 | 2.20 | 6.1 |
| | 2 | 427 | 308 | 1.97 | 14.4 |
| 1743 | 1 | 818 | 460 | 4.32 | 43.9 |
| | 2 | 11 | 0 | 2.24 | 2.6 |
| | 3 | 408 | 265 | 2.58 | 18.5 |
| 1753 | 1 | 205 | 104 | 2.93 | 14.9 |
| 777 | 1 | 9 | 0 | 1.68 | 1.7 |
| 1809 | 1 | 50 | 7 | 2.60 | 6.5 |
| 827 | 1 | 22 | 0 | 2.79 | 4.6 |
| 1844 | 1 | 209 | 109 | 2.96 | 15.2 |
| | | Total = 4871 | Total = 3444 | Mean = 2.66 | |

Table 1 The Eight Fires in the 3,241 ha Study Area between about 1680 and 1868 A.D.

^a Interior area is the total area of the fire patch minus the area of the edge, assuming a 100 m depth-of-edge influence.

^b The shape index is the corrected perimeter/area index (Baker and Cai 1992), which varies from 1.0 to infinity, with a square having the value 1.13.

° Perimeter length is the length of the boundary around each patch.

(Fig. 1). Thus, the study area is small and the study period short relative to the potential size and frequency of fires; this was unavoidable, because adjoining areas are extensively harvested, and further work was beyond the scope of this study.

Fires, patches, and interiors have roughly inverse-J-shaped size distributions, with numerous small fires, patches, and interiors and two larger ones (Fig. 2). Most fires are single patches, but



Figure 2 Size-class distribution of (a) fires (n = 8), (b) patches (n = 11), and (c) patch interiors (n = 11), assuming a 100 m depth-of-edge influence, and (d) shape index distribution for the eleven patches. The corrected perimeter/area index varies from 1.0 for a circle to infinity for an infinitely complex shape. A square has the value 1.13.

one fire had three patches (Table 1). Mean patch size is large (about 600 ha) relative to median patch size and fire size, which are a little more than 200 ha. Mean interior size is about 71 percent of patch size, but the four patches \leq 50 ha in area have little or no interior area, so the median patch has about 51 percent interior. In contrast, the largest patch has about 82 percent interior. Shapes are moderately complex, but vary over a relatively narrow range of index values, with the exception of patch 1 of the 1743 fire (Fig. 1b, Fig. 2d, Table 1). Patch size and shape are not significantly correlated (r = 0.348, p = 0.295).

MFIs vary little with topography, but are quite variable among pixels within a particular class of each topographic variable. The areabased fire-interval distribution varies widely and reflects discrete fire events, and thus appears multimodal (Fig. 3). MFI is 137 years, which is also approximately equal to the fire rotation (Kipfmueller and Baker 2000). There are no clear trends in MFI with elevation, since the standard deviation of MFI is large within each elevation class (Fig. 4a). Similarly, there appears to be a decline in MFI as slope increases, but the trend is swamped by the large standard deviation within a slope class (Fig. 4b). MFI appears to be shorter on west-northwest-facing slopes and longer on northeast-facing slopes, but the large standard deviation again obscures any trends (Fig. 4c).

Moran's I values can vary between -1.0, indicating strong negative autocorrelation (dissimilar values clustering), and +1.0, indicating



Figure 3 Total area burned versus the length of interval between fires, for the 1680–1868 A.D. study period.



Fire Interval (mean in years, s.d.) Versus Aspect

Figure 4 Mean and standard deviation (error bars) of fire intervals for the study area for classes of: (a) elevation, (b) slope, and (c) aspect. Labels on the X-axis in (a) are the midpoint of the elevation classes, which are 50 m wide. The dashed horizontal line in (a) and (b) is the MFI for the whole study area. In (c), the dark shading in the pie chart is used to emphasize the shortest MFIs and the light shading the longest MFIs.

strong positive autocorrelation (similar values clustering). Since they are between +0.5 and +1.0 in this sample, they indicate significant positive autocorrelation in MFI over distances of at least 2 km (Table 2), meaning that pixels within at least 2 km of each other have similar

| Table 2 | Spatial | Autocorr | elation | in N | lean F | ire |
|-----------|---------|----------|-----------|-------|--------|------|
| Interval, | Measure | ed by Mc | oran's I, | for I | ncrea | sing |
| Lag Dist | ances | | | | | |

| Lag (<i>m</i>) | Moran's <i>I</i> | Z statistic ^a | Sample size (<i>n</i>) |
|------------------|------------------|--------------------------|-----------------------------|
| 100 | 0.966 | 439.6 | 53652 |
| 200 | 0.936 | 222.0 | 14659 |
| 300 | 0.908 | 145.2 | 6696 |
| 400 | 0.881 | 105.6 | 3780 |
| 500 | 0.854 | 82.5 | 2464 |
| 1000 | 0.748 | 35.8 | 616 |
| 2000 | 0.542 | 12.9 | 154 |
| | | | |

^a Z is the standard normal deviate; all Z statistics in the table are highly significant ($\alpha < 0.00001$).

MFI values. Sample size declines rapidly as lag distance increases, so the estimated value of Moran's I is less reliable at large lag distances. Beyond 2 km lag distance, sample size is too small for adequate analysis.

Total area burned (4,871 ha) during the study period is spread across elevation, slope, and aspect classes in approximately the proportions that these classes occur in the landscape, but with some slight deviations (Fig. 5). There is a little more area burned than expected in the 3001-3100 m elevation class (Fig. 5a) and on westerly-facing slopes (Fig. 5c), and a little less burned than expected in the 3101-3200 m elevation class (Fig. 5a) and on northeasterly-facing slopes (Fig. 5c). These results mirror the trends in MFI with aspect (Fig. 4c). So, the hypothesis that area burned increases and MFI decreases as slope and elevation increase (H₂) is rejected.

Of seventy-three fire-scarred trees, only the twenty-seven that have first scars incurred prior to 1868 A.D. were used to indicate firespread direction (Fig. 6). Fire-scar directions do appear to indicate fire-spread directions. This is supported by the tendency of these directions to be congruent with the shifting directions of spread suggested by the shape and boundary of the fire (e.g., Fig. 1a).

The distribution of fire-spread directions differs from the distribution of wind directions. The hypothesis that fire-spread directions are randomly distributed among the eight aspects used in the analysis (Fig. 6a) cannot be rejected ($\chi^2 = 11.6, p = 0.113$). The hypothesis that the distribution of fire-spread directions is the same as the distribution of wind directions (Fig. 6a) can be rejected ($\chi^2 = 34.1, p = 0.000$). Large deviations from expected fire spread directions directions from the spread direction of the spread direction of the spread direction of the spread directions (Fig. 6a) can be rejected ($\chi^2 = 34.1, p = 0.000$).



Figure 5 The percentage of the total area burned between 1680 and 1868 A.D. (observed) that burned in each class of (a) elevation, (b) slope, and (c) aspect. The expected percentage is the percentage of the land area in the study area that is found in each class. The null hypothesis is that the distribution of observed percentages does not differ significantly from the distribution of expected percentages.

rections, if winds were strongly controlling, are seen in (1) the low frequency of fire-spread from westerly directions, even though this is the most frequent wind direction, and (2) the high frequency of fire-spread from both northerly and southerly directions relative to the frequency of winds from those directions (Fig. 6a). These tendencies are visible in the map of fire-spread directions for five fires (Fig. 1).

Fires often spread downslope. If fires generally spread upslope, then deviations from the upslope direction would be small (arbitrarily defined as <22.5 degrees). The null hypothesis that the direction of fire spread is no different from the upslope direction can be rejected (χ^2 = 43.2, *p* = 0.000). Fires in our study area, in fact, spread downslope (deviations exceeding 112.6 degrees) more often than upslope (deviations less than 67.5 degrees; see Fig. 6b). There were no scars indicating spread across the slope, reflected in the absence of deviations between 67.6 and 112.5 degrees (Fig. 6b). The hypothesis that fire spread was primarily in the direction of prevailing winds but also upslope (H₃) is rejected.

The landscape in 1868 A.D. (Fig. 1f) had a total of 20 patches differing in age, with a mean patch size of 158.9 ha and a mean interior size of 90.8 ha. Median patch size was 44.9 ha. The size-class distribution was dominated by patches <200 ha in area (Fig. 7a), but the land area was dominated by large patches (Fig. 1f). The mean shape index was 2.433, and shape index values for individual patches ranged from 1.13 to 3.75. Total unique edge (shared boundaries between patches were counted only once) for the study area was 70.52 km, which led to an edge density of 2.1 km/km². The age-class structure of the landscape was dominated by old forest (Fig. 7b), with a mean patch age of 150.3 years. The landscape contained a matrix of connected old forest, much of it interior forest, perforated by a few younger patches (Fig. 1f). The hypothesis that the landscape produced by the fire regime had large patches with large percentages of interior relative to edge and much old forest and was highly connected (H₄) is supported.

Discussion

Fire Size, Shape, and Edge

The inverse-J-shaped fire-size distribution (Fig. 2a) appears typical of many ecosystems (see, e.g., Minnich 1983; Baker 1989). Historical records of fires in Rocky Mountain National Forests since 1946 A.D. reveal that about 97 percent of lightning fires in subalpine forests remain smaller than 2 ha, and only about 0.6–0.7 percent of fires exceed 40 ha (Ryan 1976; Barrows, Sandberg, and Hart 1976). Our reconstruction did not identify fires smaller than 9 ha in the pre–Euro-American period (Table 1), but we probably could not detect fires smaller than a few hectares in area. About



Figure 6 (a) The distribution of fire-spread direction compared to the distribution of wind directions. Fire-spread direction is the field-recorded azimuth perpendicular to the scar face. The pie chart highlights where fire-spread direction is more frequent than expected based on wind direction (solid black), is less frequent than expected (light shading), or is about as frequent as expected (intermediate shading). (b) The deviation of fire-spread direction from upslope direction at the scar.

90 percent of the area burned in our study area was from the three largest fires (Table 1), consistent with the post-Euro-American record for nearby areas and many other areas (e.g., Ryan 1976; Strauss, Bednar, and Mees 1989). Average fire sizes similar to ours, in the hundreds of hectares, have been reported for montane and subalpine forests in Colorado (Alington 1998) and other parts of the western United States (e.g., Morrison and Swanson 1990; Rasmussen and Ripple 1998; Taylor and Skinner 1998), but much larger mean fire sizes may be typical of other ecosystems (Eberhart and Woodard 1987; Hunter 1993; Impara 1997; Knapp 1998).

The largest fire in our study area, the 2,651ha fire of about 1680 A.D., is not particularly large for a maximum fire size but may be large for the southern Rockies. The size of this fire is underestimated here because it appears to extend outside our study area. Much larger fires occurred in the central Rockies during the 1988 Yellowstone fires (Turner et al. 1994), and four fires exceeding 8,000 ha occurred in the northern Rocky Mountains between 1946 and 1973 A.D. (Barrows, Sandberg, and Hart 1976). However, the three largest subalpine fires in Colorado during this same period averaged only 520 ha each (Ryan 1976). The largest recent subalpine fire in the Colorado Front Range was about 1280 ha (Alington 1998). While these data suggest maximum fire sizes may be smaller in the southern than in the northern Rockies, due to insufficient data it remains unclear whether this was also true in the pre-Euro-American period. Moreover, the heterogeneity of maximum fire sizes over time makes inferences about maximum fire sizes tenuous (Strauss, Bednar, and Mees 1989).

Fire shapes and boundaries are often complex, due to varying fuel conditions, wind directions, and terrain (Anderson 1983). Patch shapes in our study area (Fig. 2d) are more complex than in Oregon, where shapes vary in area from 1.32 to 1.52 (Morrison and Swanson 1990), but in British Columbia and Alberta fire shapes vary more widely, spanning values similar to ours (Eberhart and Woodard 1987; Andison 1996). We found patch size and shape index to be uncorrelated in our study area, in contrast to the significant positive correlation between these two attributes observed in Can-



Figure 7 The 1868 A.D. (a) size-class structure and (b) age-class structure.

ada (Eberhart and Woodard 1987; Andison 1996; DeLong and Tanner 1996). However, the second largest fire in our study area has the most complex shape (Table 1). Reflecting the rather complex boundaries of fire patches in our study area is the length of perimeter, which is as much as 53.6 km for a single large fire (Table 1). However, it is important to note that fire boundaries from stand-replacing fires are relatively low contrast, since dead trees in the Rocky Mountains may remain standing for decades (Brown et al. 1998), suggesting a low depth-of-edge influence and a high percentage of interior-forest conditions. Even assuming a 100 m depth-of-edge influence, fire patches are 71 percent interior. Some Rocky Mountain plants and animals are positively associated with interior forest and negatively affected by the high-contrast edges produced by clear-cut logging and roads (Dillon 1998; Ruefenacht and Knight 2000).

Fire Intervals and Area Burned Versus Topography

Fires occur in the study area after varied intervals (Fig. 3). Although there were few fires in the study period, the distribution suggests that burned areas can be reburned within a few decades. Thus, insufficient fuel buildup does not prevent fire recurrence, and weather conditions suitable for fire must play a significant role in the fire-interval distribution. However, fuel buildup does appear to play some role, as area burned is larger after intervals exceeding 50 years (Fig. 3). During less extreme conditions, fires in Yellowstone National Park also burn preferentially in old-growth lodgepole pine and spruce-fir forests (Renkin and Despain 1992), while during more extreme fire weather this preference breaks down (Turner et al. 1994). Thus, the effects of climate and fuels on the fire-interval distribution are not simple.

Our findings suggest a relatively homogeneous fire regime insensitive to topography. The finding that fire frequency may be shorter on uplands than in valley bottoms (Romme and Knight 1981) is not supported in our study area. The high variation within a class swamps any potential trend in MFI across classes of elevation, slope, or aspect (Fig. 4). Area burned is not differentially distributed across elevation, slope, and aspect relative to expectation (Fig. 5), and there is significant spatial autocorrelation in MFI over distances of at least 2 km (Table 2). Since most of the area burned and most of the contribution to MFI comes from a few large fires, and these fires appear insensitive to topography, the fire regime is also insensitive to topography. Our study area is sufficiently topographically diverse that even smaller fires may exceed the extent of topographically homogeneous areas.

As in previous empirical studies, a shiftingmosaic steady state was not evident (Romme 1982; Baker 1989), although our study area is too small to test whether this occurs on a larger land area, where it is more expected. The shifting-mosaic-steady-state theory postulates that small land areas may be in perpetual disequilibrium due to large disturbances relative to land area, but on some larger land area the overall mosaic may remain relatively constant while individual disturbances shift (Bormann and Likens 1979). In our study area, as in the Boundary Waters Canoe Area, the size of disturbances is large relative to the size of homogeneous land area and disturbances vary considerably in size and timing, both of which preclude a stable mosaic (Baker 1989). Instead, our study area experienced temporal variability in the structure of the mosaic, as episodes of large fire were followed at irregular intervals by smaller fires. The absence of topographic effects and absence of a stable mosaic are thus both linked to the same cause: the irregular occurrence of fires that are large relative to the scale of the topography.

Fire-Spread Directions

Deviation of fire-spread directions from prevailing wind directions (Fig. 6a) may suggest weather conditions that discourage or promote fire spread. Fires spread less than expected from west to east, probably because westerly winds often bring somewhat moist, cool Pacific air. Winds from the south, leading to higher than expected fire spread, are associated with (1) the northward flow of moist tropical air of the North American monsoon (Carleton 1985), which brings thunderstorms that are a primary source of lightning ignitions (Watson, Holle, and López 1994), and (2) jet streams and rapidly moving cold fronts that are sources of strong southerly-to-southwesterly winds (Baker in press a). Major fire runs to the northnortheast in Yellowstone National Park during 1988 were aligned with winds from cold fronts (Thomas 1991). A large fire adjoining our study area in 1955 was associated with dry, northeast-trending jetstream winds (Schaefer 1957). Winds from the north, also leading to higher-than-expected fire spread, are commonly the result of high pressure over the northern Great Plains, a synoptic climatic pattern associated with drying conditions and strong hot winds that promote fires in the Rockies (Heilman, Eenigenburg, and Main 1994). Fires in our study area spread downslope more than upslope (Fig. 6b). Downslope fire spread is not unusual when driven by winds (see, e.g., Kushla and Ripple 1997), but its prevalence in our study area may reflect the greater importance of winds, relative to terrain variables such as slope direction and valley orientation, in shaping fire spread. Another possible explanation for downslope spread may be nocturnal downslope winds associated with cold-air drainage (Sturman 1987).

Fire Severity and Spatial Complexity Inside Single Burns

Fire severity in Rocky Mountain subalpine forests and other forests may vary within a single fire or fire episode and often includes a combination of severe stand-replacing burns, severe surface burns, light surface burns, and unburned areas (Turner et al. 1994; Kushla and Ripple 1997). This spatial complexity is evident from studies done a few years after the fires, but we did not find a similar complexity in our landscape. In retrospective studies done long after the fires, it may be impossible to distinguish severe surface burns from stand-replacing fires, both of which lead to high mortality of over-story dominants and leave similar firescar and cohort evidence. While we specifically sought evidence of surface fires, only one, of 9 ha, was found (Kipfmueller and Baker 2000). We did find surviving trees and small groups of unburned trees too small to map as unburned area on our fire maps (Kipfmueller and Baker 1998b), but larger islands were not found. However, it is uncertain whether islands can be adequately detected long after a fire. Such detection would likely require intensive searching and sampling. Thus, our fire boundaries could include undetected islands, and could have resulted in part from severe surface burns. However, we believe there are no large areas of undetected light surface burns.

The Landscape in 1868 A.D.

Some authors have suggested that southern Rocky Mountain landscapes are unlikely to be significantly affected by forest fragmentation from timber harvesting (Buskirk et al. 2000). These authors argue that this is so because these landscapes (1) were naturally patchy, (2) were affected by disturbances (e.g., fire) that were strongly influenced by Indians, and (3) are subjected to timber cutting in the form of small clearcuts that influence very little land area (Buskirk et al. 2000).

Our results and previous research do not support these conclusions. First, in our study area, forests were patchy prior to Euro-American settlement, but patch sizes were large (mean = 158.9 ha, median = 44.9 ha) relative to the size of clearcut patches (mean = 6.2 ha; Tinker and Baker 2000). The landscape in 1868 A.D. was dominated by large connected patches of old forest, with some smaller, younger patches (Figs. 1f, 7b). While the landscape in 1868 A.D. comprises only one snapshot of a variable pre-Euro-American landscape, large patches of connected forest would nearly always have dominated, because patterns from infrequent large fires retain dominance in the landscape during periods when small fires occur. Moreover, the road system, which was not present in the pre-Euro-American landscape, may reduce average patch size in the landscape as a whole to about 8 ha (Reed, Johnson-Barnard, and Baker 1996). Most important, the pre-Euro-American landscape contained little highcontrast edge, since trees typically remain standing after a fire, while large amounts of high-contrast edge adjoining roads and harvest units are a central impact of industrial forestry in western landscapes (Baker 2000). Highcontrast edge has significant adverse effects on native biodiversity, including trees, orchids, and birds (Vaillancourt 1995; Dillon 1998; Ruefenacht and Knight 2000).

Second, evidence suggests that Indians had little or no influence on fires in subalpine forests in the Rockies (Baker in press b). Finally, in contrast to the findings of Buskirk et al. (2000), because the high-contrast edges of industrial forestry lead to edge effects that extend 100 m or more into adjoining forests, the small land areas occupied by harvest units and roads have effects that extend over a large part of the landscape (see also Reed, Johnson-Barnard, and Baker 1996). The fragmented industrial-forest landscape of today is quite different from the pre–Euro-American landscape, because these land uses do not mimic natural disturbances.

Mimicking the structure of landscapes produced by natural disturbances could help perpetuate native biodiversity in landscapes subject to timber harvesting and other land uses (Hunter 1993; DeLong and Tanner 1996; Wallin et al. 1996). The landscape of 1868 A.D. and the spatial pattern of past fires suggest that some adverse effects of timber harvesting and roads could be offset by avoiding the creation of high-contrast edges, maintaining large patches of old forest well connected with other patches of old forest, and mimicking pre-Euro-American variation in patch size, shape, and other patch attributes. Landscapes near our study area are fragmented by past timber harvesting and roads (Reed, Johnson-Barnard, and Baker 1996). A period of restoration (e.g., road closures), rather than continued harvesting and road construction, is needed if the goal is to achieve a landscape within the range of variability of the pre-Euro-American landscape.

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