Ecological Applications, 21(6), 2011, pp. 2210–2222

Fire history and tree recruitment in the Colorado Front Range upper montane zone: implications for forest restoration

Tania Schoennagel,[1,3] Rosemary L. Sherriff,[2] and Thomas T. Veblen[1]

[1]*Department of Geography, University of Colorado, Boulder, Colorado 80304 USA*
[2]*Department of Geography, Humboldt State University, Arcata, California 95521 USA*

Abstract. Forests experiencing moderate- or mixed-severity fire regimes are presumed to be widespread across the western United States, but few studies have characterized these complex disturbance regimes and their effects on contemporary forest structure. Restoration of pre-fire-suppression open-forest structure to reduce the risk of uncharacteristic stand-replacing fires is a guiding principle in forest management policy, but identifying which forests are clear candidates for restoration remains a challenge. We conducted dendroecological reconstructions of fire history and stand structure at 40 sites in the upper montane zone of the Colorado Front Range (2400–2800 m), sampled in proportion to the distribution of forest types in that zone (50% dominated by ponderosa pine, 28% by lodgepole pine, 12% by aspen, 10% by Douglas-fir). We characterized past fire severity based on remnant criteria at each site in order to assess the effect of fire history on tree establishment patterns, and we also evaluated the influence of fire suppression and climate. We found that 62% of the sites experienced predominantly moderate-severity fire, 38% burned at high severity, and no sites burned exclusively at low severity. The proportion of total tree and sapling establishment was significantly different among equal time periods based on a chi-square test, with highest tree and sapling establishment during the pre-fire-suppression period (1835–1919). Superposed epoch analysis revealed that fires burned during years of extreme drought (95% CI). The major pulse of tree establishment in the upper montane zone occurred during a multidecadal period of extreme drought conditions in the Colorado Front Range (1850–1889), during which 53% of the fires from the 1750–1989 period burned. In the upper montane zone of the Colorado Front Range, historical evidence suggests that these forests are resilient to prolonged periods of severe drought and associated severe fires.

Key words: climate; Colorado Front Range; dendroecology; fire regimes; fire suppression; forest restoration; resilience.

Introduction

In the western United States, restoration of forests altered by suppression of frequent low-severity fire regimes is a significant management priority in order to reduce the risk of uncharacteristic stand-replacing fires (e.g., National Fire Plan, Healthy Forest Restoration Act, and Collaborative Forest Landscape Restoration Act), given expected increases in fire severity in some forest types (Miller et al. 2009) and with climate warming (Fried et al. 2004). While restoration is a high management priority, identifying which forests are clear candidates remains a challenge (Schoennagel and Nelson, *in press*). For example, while many forests have been appropriately targeted for restoration of pre-fire-suppression forest structure, in many other forest types, the need for restoration is less obvious. This is especially true in upper montane or mixed-conifer forests, where ponderosa pine, the poster child for restoration, may compose a significant portion of the overstory or forest landscape, yet the effects of past fire regimes and land use on fuel build-up is either complex or unknown, making restoration need less clear (Kaufmann et al. 2006, Baker et al. 2007, Klenner et al. 2008, Naficy et al. 2010).

Forests experiencing mixed- or moderate-severity fire are widespread across the western United States, but these regimes are some of the most complex and least-studied (hereafter we refer to mixed- or moderate-severity fire regimes simply as mixed severity, which is the most common term in the literature, unless otherwise noted; Agee 1993, Schoennagel et al. 2004). In contrast to predominantly low- or high-severity fire regimes, mixed-severity regimes require complex field techniques to characterize often high spatial and temporal variation in fire frequency and severity present within sites, study areas, and across geographic regions (Baker et al. 2007, Hessburg et al. 2007). Although empirical studies of mixed-severity fire regimes are mounting, geographic representation and standard approaches are still lacking. Given the widespread distribution of mixed-severity fire regimes across the western United States, understanding

Manuscript received 18 June 2010; revised 29 October 2010; accepted 21 December 2010. Corresponding Editor: D. McKenzie.
[3] E-mail: tschoe@colorado.edu

the ecological implications of past fire regimes and fire suppression remains an important priority for future forest management.

Mixed-severity fire regimes are intermediate on the fire frequency–severity spectrum (Agee 1993, Schoennagel et al. 2004). At one end of the spectrum, frequent low-severity fire regimes represent surface fires recurring (about <35 yr) within a stand (~100 ha) that kill young seedlings and saplings and maintain open low-density stands of large fire-resistant trees. Such fire regimes were common prior to fire suppression and grazing in ponderosa-pine-dominated forests in the Southwest and California, where reduction in the frequency of fires has contributed to a dramatic increase in fuels and subsequent fire severity (Covington and Moore 1994, Swetnam 2009). At the other end of the spectrum, infrequent high-severity fire regimes are characterized by stand-replacing, often crown, fires that recur ~100+ years within a stand (Romme and Despain 1989, Sibold et al. 2006). Such fire regimes have had minimal alteration due to past land use activities, yet fires are expected to increase in area and frequency in response to predicted warming and earlier snowmelt, especially in northern latitudes (Westerling et al. 2006). Mixed-severity fire regimes, in contrast, represent mosaics of low- to high-severity fire both within stands and across landscapes, often in relation to topography (Agee 1993, Baker et al. 2007, Hessburg et al. 2007). Such variation in severity may occur within a single fire event and across successive fires, which tend to recur at intermediate frequencies (35–100+ yr; Rollins and Frame 2006).

Although direct empirical information is lacking across a wide geographical range, it is expected that a large proportion of forests in the western United States likely experienced mixed-severity fire regimes historically, in roughly equal proportion to the distribution of historical low-severity fire regimes (Schoennagel and Nelson, *in press*). These intermediate regimes likely occurred in forests of the Rocky Mountain and Pacific Northwest states at intermediate elevations often defined as the upper montane zone. According to Landfire (Rollins and Frame 2006), Douglas-fir-dominated forests and mixed-conifer forests each compose ~20% of this fire regime across the West, while subalpine, ponderosa-pine-dominated woodlands and aspen forests each compose <10%. Twenty percent of the mixed-severity fire regime according to Landfire is predicted to have occurred in pinyon–juniper woodlands, which may in fact be more appropriately classified as having experienced predominantly high-severity fires (Romme et al. 2009).

In the Colorado Front Range, the upper montane zone poses a significant management challenge due to complexity of both the landscape and historical fire regime (Veblen et al. 2000, Sherriff and Veblen 2006, Sherriff and Veblen 2007). Prior studies have shown the relative importance of low- and high-severity fires across the gradient of ponderosa pine in the central Colorado Front Range, where fire regime complexity was largely observed in the upper montane zone (Sherriff and Veblen 2006, 2007). Despite such complexity, this zone is often targeted for restoration management (e.g., Front Range Fuels Treatment Partnership Roundtable 2007) due to the relatively high tree densities, the occurrence of ponderosa pine with other species (e.g., Douglas-fir, lodgepole pine, and aspen), and motivation to reduce fire risk in areas of high residential development. For example, a relatively small (<2800 ha) high-severity fire in this zone recently burned 168 homes, making it the costliest wildfire in Colorado. Therefore, in the central Colorado Front Range upper montane zone, we asked: (1) What was the predominant historical fire severity? (2) How do patterns of tree establishment correspond with past fire history (e.g., periods of high fire activity and fire suppression)? (3) What is the influence of climate on patterns of tree establishment and historical fire? Lastly, we discuss the implications for restoration management in this zone, especially under expected climate change.

Methods

Study area

The central Colorado Front Range (CFR) rises from the plains to the continental divide spanning Gilpin, Boulder, and southern Larimer counties (approximate latitude, longitude: 39.89° N, 40.38° W), where increasing moisture availability with elevation, due to increasing precipitation and decreasing temperatures, influences the dominant vegetation patterns (Peet 1981). Below the high-elevation subalpine zone, the upper montane zone extends from ~2400 to 2800 m and is composed of dense stands of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) on north-facing slopes with pure, less-dense stands of *Pinus ponderosa* on south-facing slopes at lower elevations. Aspen (*Populus tremuloides*), limber pine (*Pinus flexilis*), and lodgepole pine (*Pinus contorta* var. *latifolia*) co-occur with ponderosa pine and Douglas-fir at higher elevations. In contrast, the lower montane zone (~1800–2400 m) is dominated by ponderosa pine, ranging from open park-like stands at the plains–grassland ecotone to denser stands mixed with Douglas-fir at mid-elevation, north-facing slopes. Soils in the montane zone are shallow, poorly developed, and coarsely textured, derived primarily from Precambrian granitic rocks (Peet 1981). In the upper montane zone, mean annual precipitation is ~53 cm and mean annual maximum temperature is 11.7°C compared to 48 cm and 18.2°C, respectively, in the lower montane zone.

Field sampling

We conducted a stratified random sample with proportional allocation, where we sampled forest types in proportion to their representation in the study area, which typically provides more precise estimation than simple stratified random sampling and permits summary inferences from the global data set to reflect trends across the study area. First we classified the study area, defined

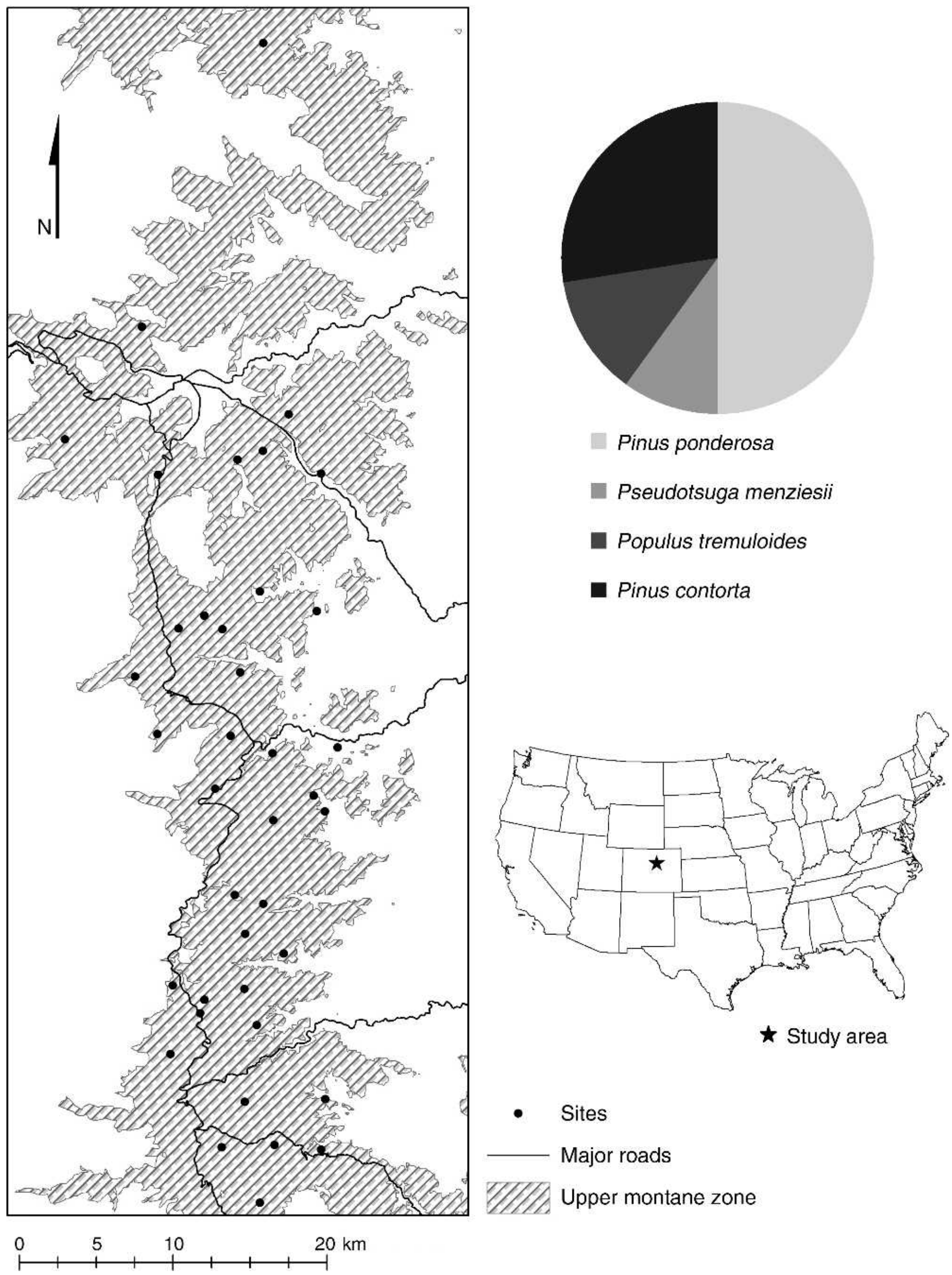

FIG. 1. Location of 40 sites sampled in the upper montane zone of the Colorado Front Range, USA, with the pie chart depicting the proportion of sites by forest type.

by an elevation zone of 2400–2800 m, into five subpopulations represented by dominant forest types characteristic of the upper montane zone using the US Forest Service Integrated Resource Inventory (IRI) layer (USDA Forest Service 2010). The IRI layer characterizes homogeneous polygons of dominant and subdominant tree species from aerial photo interpretation and field sampling. We excluded polygons listing subalpine species such as subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and limber pine as dominant or subdominant species, which captured 72% of this elevation zone. We grouped these polygons by forest type based on the dominant species, then sampled proportionally to their areal representation: (1) ponderosa pine (50% of the selected area), (2) lodgepole pine (28%), (3) aspen (12%), and (4) Douglas-fir (10%) (Fig. 1).

This study took advantage of previous sampling efforts in the region (Veblen et al. 2000, Sherriff 2004) by incorporating fire history and stand structure data from 10 ponderosa-pine-dominated sites previously sampled that fell within the elevation range of the upper montane zone (Sherriff and Veblen 2006). In a stratified-random design, we selected 30 additional polygons from the IRI layer in relative proportion to forest types in the upper montane zone that were also easily accessible to permit efficient sampling. We rejected sites that had evidence of past logging or if no fire scars were found within ~1 km of the polygon. This is a conservative measure to ensure we were sampling fire-affected sites. We acknowledge that this procedure may bias the sampling toward less evidence of high-severity fires, which provide fewer scarring opportunities compared to low-severity fire. For sampling fire dates, we targeted searches in or near the target polygons where fire scars are more commonly found: on older remnant trees, at junctures in slope or aspect (ridges, valleys), on south-facing slopes (where stands were more open and surface fires were more common), at the boundary between two polygons in the IRI database (which often reflected differences in age or species composition). We removed partial cross-sections from fire-scarred trees opportunistically found either within or surrounding the target polygon (see Plate 1 and Appendix B).

For the analysis, we only considered fires where at least two trees at a site recorded fire in the same year (min2). At 13 sites we were either unable to satisfy the min2 criterion (six sites) or min2 fire dates post-dated a clear pulse of establishment (seven sites), and we incorporated fire scar data from the nearest site (mean = 1.4 km, range = 0.1–5.0 km) either within this study or from a previous study where no age structure data had been collected (Veblen et al. 2000) in order to satisfy the min2 criterion. At these sites, burned at high to moderate severity, fire scar samples were relatively scarce, indicating either undersampling or low availability of scarred trees. We compared this nearest neighbor approach to considering fires where only one tree at the focal site recorded a fire date; the nearest neighbor approach did not alter classification of fire severity at the focal sites, suggesting a lack of significant error or bias with this nearest neighbor approach, while satisfying the min2 criterion. In terms of min2 fire dates, nearest neighbor sites provided 67 recorder trees that contributed 13 of the total of 51 unique fire dates.

We employed a stratified-random sampling approach to establish four 120-m transects oriented downslope >100 m apart, where one transect was randomly located within each of four quadrants of the focal polygon. We used closest-individual sampling (Mueller-Dombois and Ellenberg 1974), in which at each 10-m point along the transect we cored the closest standing tree (live or dead) 20 cm above the ground on the contour and perpendicular to the tree and recorded the tree species, diameter at breast height (dbh), status (live or dead), and distance to transect point. If the closest tree was a stump we recorded the diameter at the base and identified the species, if possible, yet cored the next closest standing live tree. Previous sampling in ponderosa pine sites in this zone resulted in very few (4.5% per site on average) of the total tree ages from dead-standing trees and downed remnant wood (Sherriff and Veblen 2006). Given this low return on sampling effort in this zone, the paucity of remnant wood at our sites, and variation in decay rates of downed wood across species that would introduce bias, we concentrated our sampling efforts on standing (live or dead) trees. In addition to the closest-individual sampling above, along each 120-m transect we established two belt transects: (1) within a 20-m wide belt transect we selectively cored five of the largest live or dead trees that appeared to represent the most recent post-fire cohort to ensure large trees important for dating cohort establishment were adequately sampled, and (2) within a 10-m belt transect we counted all saplings and seedlings by species, where saplings were ≤4 cm dbh and established seedlings were between 20 cm and 1.4 m tall.

Laboratory techniques

In the laboratory, annual rings of tree core samples ($n = 3114$) were counted and visually cross-dated by comparison with a master chronology developed from drought-sensitive sites in the Colorado Front Range (Veblen et al. 2000) in order to estimate dates of tree establishment and mortality. When core samples did not include the pith, a geometric model of annual tree growth estimated the number of missing rings to the pith (Duncan 1989). Cores missing the pith by more than 20 years were excluded ($n = 13$). To date establishment and mortality of dead trees ($n = 89$), samples were quantitatively cross-dated using the COFECHA program; 72% were successfully cross-dated (Grissino-Mayer 2001*a*). To determine the date of tree establishment, we added the median number of rings to 20-cm core height, based on previously harvested seedlings in open-grown upper montane sites (>2400 m; aspen, 1 yr; ponderosa pine, 3 yr; Rocky Mountain juniper (*Juniperus scopulorum*), 4 yr; Douglas-fir, 8 yr; lodgepole pine, 8 yr; limber pine, 9 yr; mean = 5.5 yr; R. L. Sherriff, M. H. Gartner, and T. T. Veblen, *unpublished manuscript*). Saplings (stems <4 cm dbh, $n = 6630$) were not cored, but we estimated the upper limit of sapling ages based on the age of trees with 4 cm dbh, as follows: Rocky Mountain juniper, ponderosa pine, and Engelmann spruce, <80 yr old; lodgepole pine, <70 yr old; Douglas-fir, <55 yr old; aspen, <40 yr old; subalpine fir, <25 yr old. Assuming the age distribution of saplings is positively skewed, mean and median ages of saplings would be significantly lower than these upper age estimates. Partial cross-sections from fire-scarred trees ($n = 409$) were visually cross-dated using marker rings, and when necessary, rings were measured and cross-dated with COFECHA, in order to date fire scar years.

Quantitative analysis

Historical fire regime.—Our goal was to identify the predominant structural impact of historical fires at each site, termed the fire severity regime, which refers to the

TABLE 1. Two metrics for characterizing fire severity at the site scale (~100 ha): (1) remnant, based on calculating the proportion of the stand older than (i.e., survived) a fire, and (2) establishment, based on the proportion of the stand that established within 40 yr after a fire.

Severity	Remnant (%)	Establishment (%)
High	≤20	≥80
Moderate	21–79	79–21
Low	≥80	≤20

principal ecological impact of fire on vegetation across space and time. Fires were too infrequent to calculate fire frequency statistics at each site (Grissino-Mayer 2001*b*). We calculated two metrics of fire severity based on the date of each fire in relation to the dates of tree establishment at each site. The main metric (remnant) calculates the proportion of live trees sampled that established prior to (i.e., survived) the fire. The second metric (establishment) calculates the proportion of the live trees that established within a 40-yr window following a fire, where a high proportion of trees established in this window after fire is assumed to reflect high fire severity and a low proportion is assumed to reflect a low fire severity (Table 1). The latter metric provides corroborative but not diagnostic information about fire severity; post-fire tree establishment is not a direct measure of fire severity and can vary significantly among species due to differences in regeneration niche (sensu Grubb 1977) and within species according to seed availability and climate. The remnant metric is the most direct measure of fire severity as the proportion of trees that predate (i.e., survive) the fire reflects the lethality or severity of the fire. These metrics for defining fire severity are generally consistent with previous studies of fire history and effects across the range of ponderosa pine in the study area (Sherriff and Veblen 2006), but the current study differs in giving the mortality criterion priority over other criteria such as fire frequency, establishment pulse, and tree ring release.

Using the metrics above, we calculated the average (or predominant) fire severity at each site, then classified the severity at each site based on the criteria from Agee (1993) and Hessburg et al. (2007) (Table 1). In calculating the average fire severity at each site, we excluded fires where no tree establishment followed within 40 yr (there were only three instances of this), as it is assumed the fire had no structural impact or perhaps did not burn the stand. Individual fires classed as high severity by the remnant criterion that occurred prior to another high- or moderate-severity fire and were not associated with a pulse in establishment (>20% of trees in a stand within 40 yr of the fire) did not enter into the fire severity calculation at each site. There is a higher probability of individual fires being classed as high or moderate severity by the remnant criterion due to the subsequent mortality of older trees with time, especially if they predate a lethal fire that may have subsequently killed them; therefore proportion of remnants may be especially low for older fire events. If fires of different severities occurred within a site over time, the fire regime was categorized as "mixed severity through time," which is functionally different from "moderate severity across space" and is highlighted with a star in Fig. 2C and in Appendix A. We created a confusion matrix of the remnant and establishment metrics to compare the two

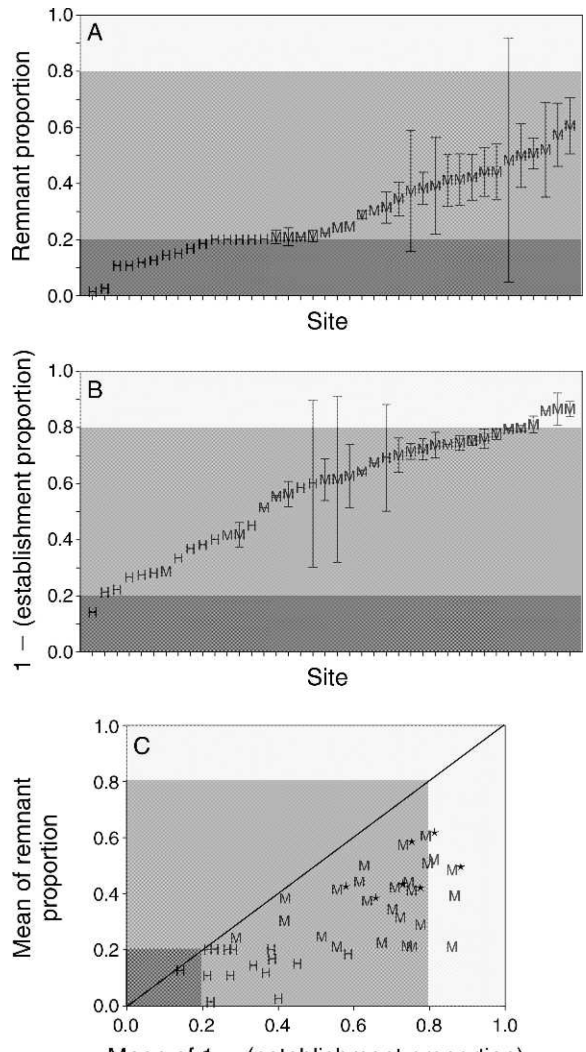

FIG. 2. Ranked distribution of (A) remnant proportion at each site (mean ± SE) and (B) 1 – (establishment proportion) (the complement of establishment proportion, so that criteria in both graphs indicate high severity on the left; mean ± SE). (C) The mean remnant proportion and 1 – (mean establishment proportion value) for each site, which reveals that the establishment metric tends to register lower fire severity, on average. Dark gray shading corresponds to the high-severity fire classification, light gray shading to moderate-severity fire, and white to low-severity fire based on the criteria in Table 1. H and M represent those sites classified as high and moderate fire severity, respectively, based on the remnant criteria. Sites in which fire severity classes are mixed through time are delineated with stars in panel C.

TABLE 2. Topographic characteristics of the forest types sampled in the upper montane zone: the average and range of elevation and slope and percentage of sites by aspect.

	Area (ha)		Elevation (m)		Slope (°)		Aspect (percent of sites)			
Forest type	Mean	Range	Mean	Range	Mean	Range	North	East	South	West
POTR	34	10–49	2708	2618–2782	12	7–18	33	33	17	0
PICO	56	12–209	2581	2409–2773	14	5–32	80	20	0	0
PIPO	60	21–138	2552	2318–2724	21	10–32	5	32	63	0
PSME	48	31–61	2444	2313–2644	21	9–33	50	25	0	25
Overall mean	54	12–209	2573	2313–2782	18	5–33	33	30	35	3

Note: Sites were sampled in the upper montane zone of the Colorado Front Range, USA. Species abbreviations are: ABLA, *Abies lasiocarpa*; JUSC, *Juniperus scopulorum*; PICO, *Pinus contorta*; PIEN, *Picea engelmannii*; PIFL, *Pinus flexilis*; PIPO, *Pinus ponderosa*; POTR, *Populus tremuloides*; PSME, *Pseudotsuga menziesii*.

approaches to classifying severity of each fire and the predominant fire severity experienced at a site. We also plotted average fire severity per site to assess remnant and establishment metrics on a continuous spectrum.

Tree establishment.—We examined how the relative frequency of tree ($n = 2963$) and sapling establishment within the 1750–2004 period varied across the modern fire suppression period (1920–2004), an equal length period (1835–1919) including Euro-American settlement activities, and a previous period (1750–1834) that predates any known Euro-American settlement (Veblen and Donnegan 2006). Using chi-square tests, we evaluated whether tree and sapling establishment were significantly different among the three 84-yr periods. Using a chi-square test, we also assessed whether age structure was significantly different between sites experiencing different predominant fire severities.

Climate influences.—To test whether regional drought was significantly different during fire events (year 0) compared to 1–4 yr prior and up to 2 yr after fire events, we used superposed epoch analysis (SEA; Grissino-Mayer 2001*b*). Statistical significance was evaluated using 95%, 99%, and 99.9% confidence intervals derived from 1000 Monte Carlo simulations with block resampling. Regional drought was reconstructed using a master chronology derived from drought-sensitive trees sampled within the Colorado Front Range (Veblen et al. [2000] and updated by collecting additional tree cores). To assess the influence of climate and fire on patterns of tree establishment we graphically examined the temporal association between periods of tree establishment pulses, regional drought, and high fire activity.

RESULTS

Site summary

We sampled sites in proportion to the distribution of those forest types in the study area, where 50% of the sites were primarily ponderosa pine (10% were pure ponderosa, where >90% of the overstory trees sampled were ponderosa pine), 28% were lodgepole pine (13% was pure), 12% were aspen (8% was pure), and 10% were Douglas-fir (0% was pure, with all Douglas-fir sites having a high proportion of ponderosa pine in the overstory) (Fig. 1). On average, stumps from previous logging were 22 stumps/ha or 2% of total live tree density. Overall, there was considerable variation among forest types in the upper montane in terms of topography, fire severity, cover, and tree and sapling density (Tables 2–4).

Fire severity

A total of 406 fire-scarred trees were sampled; 85% recorded only one fire scar per tree, 11% recorded two

TABLE 3. Fire severity and cover of the forest types sampled in the upper montane zone: the percentage of sites by predominant fire severity determined in this study and percent overstory cover by trees and percent understory cover by shrubs, grasses, and forbs (mean, with range in parentheses), as determined by spatial overlays with the USFS Integrated Resource Inventory data layer.

	Fire severity (percentage of sites)			Cover (%)			
Forest type	High	Moderate	Low	Tree	Shrub	Grass	Forb
POTR	50	50	0	50 (30–67)	7 (5–10)	16 (10–27)	7 (3–11)
PICO	64	56	0	58 (48–66)	11 (3–19)	6 (3–10)	3 (0–7)
PIPO	21	79	0	44 (32–68)	16 (7–27)	10 (2–17)	5 (1–8)
PSME	25	75	0	50 (41–57)	14 (13–17)	7 (4–11)	4 (2–6)
Overall mean	38	62	0	49 (30–68)	13 (3–27)	10 (2–27)	4 (0–11)

Note: See Table 2 for species abbreviations.

TABLE 4. Tree density (no. live trees/ha), sapling density (no. saplings/ha), and basal area (m^2/ha) by species (mean, with range in parentheses) for the forest types sampled in the upper montane zone.

Forest type	ABLA	JUSC	PICO	PIEN	PIFL	PIPO	POTR	PSME	All species
Tree density									
POTR	9 (0–49)	0 (0–0)	63 (0–198)	21 (0–76)	1 (0–8)	27 (0–110)	2168 (331–4309)	100 (0–534)	2389 (543–4309)
PICO	0 (1–0)	0 (0–0)	1676 (610–2610)	5 (0–54)	59 (0–387)	93 (0–195)	37 (0–198)	284 (0–1054)	2172 (1050–2899)
PIPO	1 (0–12)	17 (0–123)	60 (0–538)	0 (0–0)	19 (0–75)	500 (85–1301)	12 (0–50)	142 (0–781)	755 (123–2238)
PSME	0 (0–0)	4 (0–16)	32 (0–91)	0 (0–0)	19 (0–60)	390 (228–715)	34 (0–67)	747 (372–1485)	1273 (760–2365)
Overall mean	2 (0–49)	8 (0–123)	502 (0–2610)	5 (0–76)	28 (0–387)	306 (0–1301)	345 (0–4309)	236 (0–1485)	1442 (123–4309)
Sapling density									
POTR	47 (0–253)	0 (0–0)	44 (3–223)	29 (0–68)	5 (0–10)	8 (0–21)	554 (128–1085)	43 (0–190)	728 (443–1593)
PICO	0 (0–0)	1 (0–8)	87 (15–192)	4 (0–25)	15 (0–68)	12 (0–78)	68 (3–278)	68 (0–165)	254 (20–573)
PIPO	0 (0–0)	14 (0–125)	6 (0–30)	0 (0–3)	8 (0–65)	44 (3–153)	41 (0–148)	80 (0–770)	193 (4–1040)
PSME	0 (0–0)	21 (0–58)	0 (0–0)	11 (0–33)	7 (0–28)	52 (30–72)	152 (25–338)	182 (130–278)	424 (308–558)
Overall mean	7 (0–253)	9 (0–125)	33 (0–223)	6 (0–68)	9 (0–68)	30 (0–153)	136 (0–1085)	81 (0–278)	313 (4–1593)
Basal area									
POTR	0 (0–0)	0 (0–0)	2 (0–7)	1 (0–4)	0 (0–0)	10 (0–57)	51 (6–101)	3 (0–15)	67 (35–107)
PICO	0 (0–0)	0 (0–0)	55 (23–80)	0 (0–1)	1 (0–7)	4 (0–17)	0 (0–1)	11 (0–44)	71 (36–90)
PIPO	0 (0–0)	0 (0–1)	2 (0–18)	0 (0–0)	1 (0–4)	38 (12–101)	0 (0–1)	4 (0–26)	45 (13–106)
PSME	0 (0–0)	0 (0–0)	1 (0–4)	0 (0–0)	0 (0–0)	28 (9–84)	1 (0–1)	30 (12–51)	60 (27–135)
Overall mean	0 (0–0)	0 (0–1)	15 (0–180)	0 (0–4)	0 (0–7)	18 (0–101)	3 (0–101)	5 (0–51)	77 (13–135)

Note: See Table 2 for species abbreviations.

successive fire scars per tree, and 4% recorded three successive fire scars or more per tree. There were 114 fire events that were recorded on two or more trees at a site (min2), but only 51 dates were unique among these, which spanned 1601–1953. Of the 114 individual fires used in the site classifications, 44% were classed as high severity, 45% were moderate, and 11% were low severity. Twenty percent of all fires occurred in 1859 or 1860, and 45% of all sites recorded these fires, which were classed evenly among sites as either high or moderate severity. On average, sites recorded one high-severity fire (range, 0–5), one moderate-severity fire (range, 0–4), and less than one low-severity fire (range, 0–2).

The classification of fire severity based on the remnant criteria at each site revealed that 38% of the sites sampled in the upper montane zone experienced predominantly high-severity fire, 62% were moderate severity (7 of these 25 sites were mixed severity through time, whereby both moderate-severity and low-severity fires occurred), and no sites were burned exclusively by low-severity fires (Appendix A). The majority (64%) of lodgepole-pine-dominated sites was classed as high severity, and the majority of ponderosa-pine- and Douglas-fir-dominated sites was classed as moderate severity (79% and 75%, respectively; Table 3). High-severity sites, compared to moderate-severity sites, had similar elevations (2591 m compared to 2561 m), but the majority of high-severity sites were north-facing (compared to south-facing) and had higher tree cover (54% compared to 46%) and lower shrub cover (11% compared to 14%), as determined by spatial overlays with the IRI data layer. High-severity sites had higher densities of live and dead trees overall, particularly of lodgepole and aspen, while moderate-severity sites had higher ponderosa pine, limber pine, and Rocky Mountain juniper tree densities (Table 5). Sapling densities were higher in high-severity sites (Table 6).

There was an overall agreement of 60% between remnant and establishment classifications of fire severity at the site level. The probability of commission (chance of remnant classification being the same as establishment classification) was 92% for moderate severity yet only 7% for high severity. The probabilities of omission (chance of the establishment classification being the same as remnant classification) were 100% and 62% for the high- and moderate-severity classes, respectively. The low probability of commission for the high-severity class is due to the fact that many fires classed as high

TABLE 5. Live and dead stem density (no. stems/ha) and tree density (no. live trees/ha) by species (mean, with range in parentheses) for high- and moderate-severity fire sites that compose the upper montane zone.

Fire severity	Live stems	Dead stems	ABLA	JUSC	PICO	PIEN	PIFL	PIPO	POTR	PSME
High	1924 (345–4309)	140 (0–990)	0 (0–0)	4 (0–40)	793 (0–2100)	8 (0–76)	8 (0–33)	188 (0–577)	615 (0–4309)	295 (0–1054)
Moderate	1152 (123–2892)	68 (0–494)	3 (0–49)	11 (0–122)	327 (0–1916)	2 (0–49)	41 (0–386)	376 (0–1301)	181 (0–2284)	199 (0–1484)

Note: See Table 2 for species abbreviations.

severity based on the <20% remnant criteria were classed as moderate severity by the establishment metric because they could not meet the very strict criteria of >80% of tree establishment within 40 yr of the fire occurrence.

Considering fire severity metrics on a continuum, the average proportion of remnants surviving fires at each site varied from 0.01 to 0.61, with an overall average of 0.28 across all sites (Fig. 2A). The average proportion of tree establishment 40 yr after fire at each site varied from 0.13 to 0.86, with an overall average of 0.46 across all sites (Fig. 2B). The variation in remnant proportion per site increased as fire severity decreased and generally was higher than the variation in post-fire establishment. The Pearson correlation coefficient between average remnant and establishment metrics at each site was moderate (–0.64). Plotting average remnant and establishment metrics per site shows that very few sites fall on the 1:1 line (Fig. 2C); where the complement of the establishment metric (1 – establishment; see Table 1) is consistently higher than remnant proportion. This trend is due in part simply to the calculation of the two metrics, which would be perfect complements of one another if establishment proportion included the full period from fire to present, but in fact is based only on the 40-yr period after fire. Therefore, by definition (remnant + establishment + proportion of trees established >40 years after fire = 1), establishment registers slightly lower fire severity on average.

Tree establishment

The frequency of tree and sapling establishment was significantly different among the three time periods based on a Pearson's chi-squared test ($\chi^2 = 29.3581$, df = 6, $P < 0.001$), with the 1835–1919 time period having the highest proportion of total tree and sapling establishment during 1750–2004 (Fig. 3). Douglas-fir establishment was not pronounced during the 1920–2004 period, accounting for only 7% of the total tree and sapling establishment during 1750–2004, which is the same proportion as in the preceding period of equal length.

The distribution of tree establishment in 20-yr bins was also significantly different between high- and moderate-severity sites (chi-squared test: $\chi^2 = 246.47$, df = 11, $P < 0.001$) with tree establishment in the high-severity sites being more peaked than the distribution in the moderate-severity fire sites, which was more broadly spread across the 1750–1989 period (Fig. 4). For example, 58% of the total tree establishment occurred during 1870–1909 in the high-severity sites, whereas only 30% occurred during this period in the moderate-severity sites. Both high- and moderate-severity sites are characterized by low tree establishment rates during the post-1920 fire suppression period.

Climate influences

Superposed epoch analysis confirmed that in the Colorado Front Range upper montane zone over the 1600–1959 period, fires burned during years of negative departures in radial growth of ponderosa pine, indicating extreme drought ($n = 51$; 95% CI). There were no significant departures of the drought index 1–4 years prior or two years after fire events. The major pulse of tree establishment in the upper montane zone initiated during a multidecadal period of extreme drought conditions in the Colorado Front Range (1850–1889), during which 53% of the fires from the 1750–1989 period burned; establishment declined over the subsequent 20–30 years (Fig. 5).

Discussion

Fire severity

In the central Colorado Front Range upper montane zone (2400–2800 m), where ponderosa pine is the dominant forest type across half of the forested area, we found that moderate-severity fires predominantly

TABLE 6. Sapling density (no. saplings/ha), the ratio of sapling density to tree density, and sapling density (no. saplings/ha) by species (mean, with range in parentheses) for high- and moderate-severity fire sites that compose the upper montane zone.

Fire severity	Saplings	Saplings/trees	ABLA	JUSC	PICO	PIEN	PIFL	PIPO	POTR	PSME
High	382 (65–1592)	0.20 (0.04–0.53)	18 (0–252)	3 (0–22)	41 (0–115)	11 (0–67)	7 (0–45)	10 (0–30)	214 (3–1085)	80 (0–190)
Moderate	269 (4–1040)	0.29 (0.01–1.03)	0.7 (0–17)	12 (0–125)	28 (0–222)	4 (0–50)	10 (0–67)	43 (0–153)	90 (0–513)	82 (0–770)

Note: See Table 2 for species abbreviations.

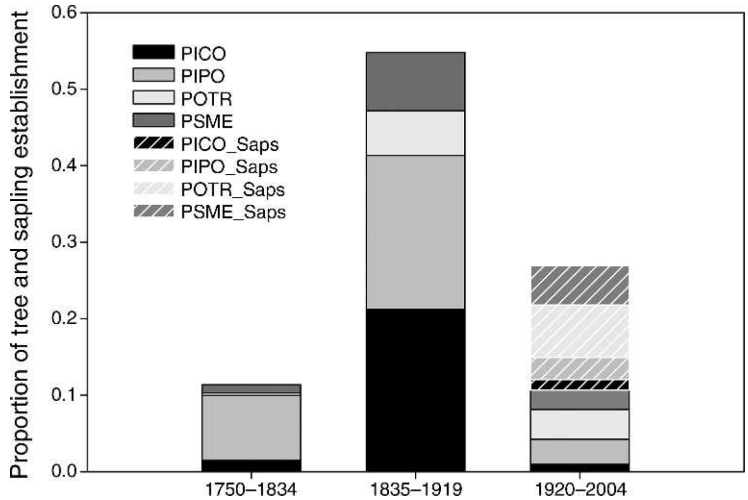

Fig. 3. The proportion of tree and sapling establishment by species in three equal time periods. The majority of the trees in this upper montane zone established during the 1835–1919 period, with relatively little recent tree establishment during the 1920–2004 fire suppression period. Species abbreviations are: PICO, *Pinus contorta*; PIPO, *Pinus ponderosa*; POTR, *Populus tremuloides*; PSME, *Pseudotsuga menziesii*. Minor species (*Abies lasiocarpa*, *Picea engelmannii*, *Pinus flexilis*, and *Juniperus communis*), which account for 5% of the total establishment, are not shown. "Saps" indicates saplings.

burned this landscape historically. While ~10% of individual fires were classed as low severity, no sites sampled burned predominantly by low-severity fire during the period of analysis, based on the remnant metric (four sites were classed as predominantly low severity according to the establishment metric). The majority of the fire-scarred trees sampled recorded only single fire scars (85%), suggesting long fire intervals and providing little evidence of frequent low-severity burning. These results for the compositionally diverse upper montane zone are consistent with previous findings for the complete elevation range of ponderosa pine in the Front Range, in which only the lower 20% of the zone was characterized by low-severity fires (Sherriff and Veblen 2007). Given the broad range of mixed- or moderate-severity fire regimes, other regions may include a more significant portion of low-severity fire, however.

Existing studies characterizing mixed- or moderate-severity fire regimes are relatively few compared to predominantly low- or high-severity fire regimes. Geographically, mixed- or moderate-severity fires have been documented in mid-elevation, ponderosa pine, or mixed-conifer forests in the Colorado Front Range (Brown et al. 1999, Ehle and Baker 2003, Sherriff and Veblen 2006), the Black Hills (Brown et al. 2008), Arizona (Fulé et al. 2003, Iniguez et al. 2009), California (Taylor and Skinner 2003, Stephens et al. 2004, Bekker and Taylor 2010), eastern Cascades (Hessburg et al. 2007, Everett et al. 2008), and interior British Columbia (Klenner et al. 2008). Methodologies for characterizing variation in fire severity through space and time vary considerably across these studies, however. Many of these studies rely on dendrochronological reconstructions of fire history or stand age structure, but only a few directly combine age structure and fire history information at the stand scale in developing inferences about fire severity (e.g., Ehle and Baker 2003, Sherriff and Veblen 2006).

In addition, while contemporary studies of fire severity emphasize tree mortality, most retrospective studies tend to rely on tree establishment patterns, instead of more direct evidence of mortality from fire. Post-fire tree establishment is only an indirect proxy for fire severity that can vary significantly with climate, species, seed availability, and time since fire (Krannitz and Duralia 2004). For example, little regeneration occurred following several severe fires in the Front Range in the late 1980s and early 2000s, suggesting

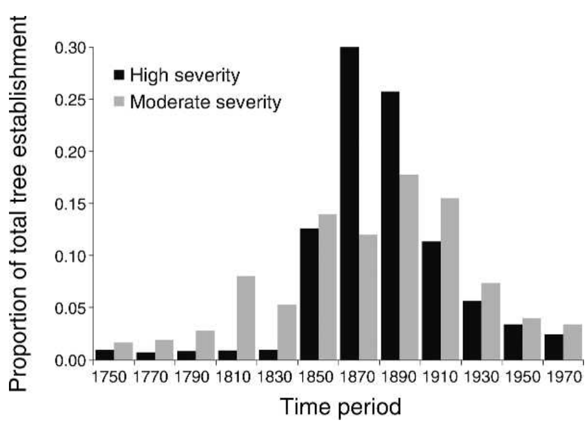

Fig. 4. Proportion of tree establishment in 20-yr bins within high- (dark gray) and moderate- (light gray) severity sites during the 1750–1989 period.

Plate 1. Panoramic photograph showing the juxtaposition of a dense ponderosa pine stand that regenerated after a lethal canopy fire (left) and a sparse stand where the same fire burned at low severity, scarring many of the trees without killing them (right). Dating of fire scars on trees surviving a fire within (left) and adjacent to (right) target polygons, can provide dendrochronological evidence of the timing of the fire event, when fire-scar dates and post-fire tree establishment dates correspond. Calculating the proportion of living trees in the target stand that predate the fire event (percentage remnants) provides an index of the fire severity. A color version of this panorama is available in Appendix B. Photo credits: T. Schoennagel.

caution in relying solely on post-fire establishment metrics of fire severity. Post-fire remnant, in contrast, is a more direct measure of mortality from fire; however, it still remains a proxy for absolute survivorship from fire. The absolute proportion of the stand that survived fire is equivalent to the proportion of remnants in the current stand, only if the pre-fire and current tree densities are similar. Although not a perfect index of fire lethality, in systems where fire intervals are relatively long and tend to burn older, mature stands and sampled stands are also mature, as was the case in this study, this assumption remains relatively robust. In systems in which stand densities have significantly increased during periods of fire suppression, caution should be used in

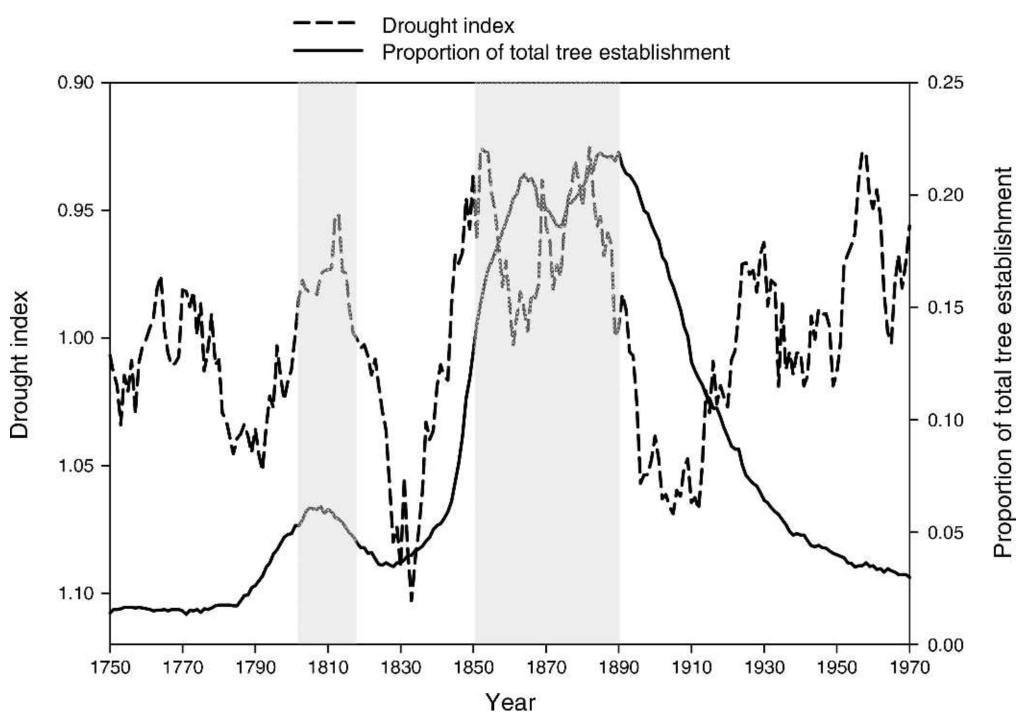

Fig. 5. Graph showing 20-yr smoothing of a regional drought index (dotted line, where smaller values are drier [note inverted axis]) and the proportion of total tree establishment (solid line) during the 1750–1989 period. The area shaded in gray highlights a multidecadal period of drought associated with high fire activity and subsequent tree establishment. During the 1850–1890 period, 53% of the fires from the 1750–1989 period burned.

interpreting the remnant criteria as an absolute index of survivorship from fire. In these cases, if stands have experienced similar changes in stand density since before the last fire, then the remnant criteria is still a useful index of relative fire severity. With both metrics, evidence of remnants and establishment is destroyed by subsequent severe fire. As such, fires prior to moderate- or high-severity fires will more likely register as high severity based on the remnant metric and as low severity based on the establishment metric; approaches and interpretations need to address this potential bias. Lastly, remnant and establishment are not perfect complements of one another, so severity classifications based on these metrics need to take this into account, otherwise establishment metrics will consistently record lower severity.

In general, to improve methodologies for characterizing a range of fire severities and effects on stand structure we recommend that: (1) fire dates and stand age structure be directly integrated at the stand level in developing metrics of fire severity; (2) post-fire establishment be used cautiously as a metric of fire severity, especially with ensuing climate change; (3) post-fire remnants be considered as a more direct index of fire severity, which could be used in conjunction with establishment criteria as in Fig. 2C; and (4) consideration be given to characterizing fire severity along a continuous spectrum rather than discrete classes of fire behavior, although this may not be easily adopted by managers due to complexity and convention.

Tree establishment

The vast majority of the trees sampled in the current study of the upper montane zone and in a companion study encompassing both the lower and upper montane (Sherriff and Veblen 2006) established during 1850–1910, before the advent of fire suppression. This contrasts with patterns in mixed-conifer forests in California (Scholl and Taylor 2010) and the Southwest (Fulé et al. 2003), where significant tree establishment has occurred during the fire suppression era. It is generally expected that more shade-tolerant trees, such as Douglas-fir or white fir (*Abies concolor*), have invaded during the fire suppression period, contributing to high tree densities, but we found relatively low Douglas-fir establishment during the 1920–present period, perhaps due to relatively high tree densities already in place following earlier high-severity fires. In addition to the tree age data presented here and for ponderosa-pine-dominated sites in Sherriff and Veblen (2006), aerial photo comparisons reveal relatively stable tree densities across the upper montane zone between 1938 and 1999 (Platt and Schoennagel 2009). Therefore, while forests in the upper montane zone of the CFR are relatively dense, this condition is not a consequence of fire suppression, yet suppression has been a common justification for creation of open stand structures in this zone in the CFR (e.g., Front Range Fuels Treatment Partnership Roundtable 2007).

Climate influences

During a regional multi-decadal period of drought (1850–1890) (Gray et al. 2004) and mining activity (Veblen and Lorenz 1986, Veblen and Donnegan 2006), over half of the fires recorded in the 1750–1989 period burned. Rapid colonization followed this period of drought and high-to-moderate severity burns. A similar but less-pronounced pattern occurred in the 1800–1820 period during a relatively short drought period that coincided with elevated fire activity. Such pulses of establishment of ponderosa pine following high- and moderate-severity burning during periods of extreme drought are observed in numerous studies (Ehle and Baker 2003, Sherriff and Veblen 2006, Klenner et al. 2008). In contrast, in the Black Hills and southwest Colorado, major pulses of establishment, although closely following fires in time, have been attributed primarily to episodic recruitment opportunities associated with pluvials, not fires (Brown and Wu 2005, Brown 2006). While recruitment at ecotones with grasslands and in open-canopy ponderosa pine forests may be aided by moister conditions (League and Veblen 2006), opportunities for pulsed, episodic recruitment of shade-intolerant species in closed forests have been shown to be directly linked to overstory mortality events and reduction of understory competition facilitated by severe fire (Lentile et al. 2005, Shepperd et al. 2006).

Restoration implications

Ecological restoration concepts have shifted considerably recently, due to recognition of climate change impacts on disturbance processes. Recreating historic conditions for which there may be no future analogs (Williams and Jackson 2007) is being replaced by efforts to promote ecosystem resilience: the capacity of ecosystems to return to desired conditions after disturbance (Millar et al. 2007, Hobbs and Cramer 2008). Information on past conditions, including historic fire regimes and the effects of past management, however, still plays a critical role in understanding potential ecological resilience in fire-adapted forests. In the upper montane zone of the Colorado Front Range, historical evidence suggests that these forests are resilient to prolonged periods of severe drought and associated severe fires. Given that these upper montane forests appear resilient to moderate- to high-severity fires, they are not high priorities for restoration and may show resilience to prolonged drought and high fire activity expected in the near term. With high levels of exurban development in this zone, we recommend that management focus on fuels reduction directly adjacent to residential communities and curtailing further residential expansion to reduce wildfire risks to people in fire-prone landscapes.

Acknowledgments

Support was provided by the National Science Foundation (DEB BCS-0540928, 0541480, and 0802667) and a David H. Smith Postdoctoral Fellowship. We thank our field and lab crew, Juan Paritsis, Andres Holz, Larissa Meyers, and Dan Jarvis, for their hard and careful work. For helpful comments on an earlier version we thank two anonymous reviewers.

Literature Cited

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Baker, W. L., T. T. Veblen, and R. L. Sherriff. 2007. Fire, fuels and restoration of ponderosa pine-Douglas-fir forests in the Rocky Mountains, USA. Journal of Biogeography 34:251–269.

Bekker, M. F., and A. H. Taylor. 2010. Fire disturbance, forest structure, and stand dynamics in montane forests of the southern Cascades, Thousand Lakes Wilderness, California, USA. Ecoscience 17:59–72.

Brown, P. 2006. Climate effects on fire regimes and tree recruitment in Black Hills ponderosa pine forests. Ecology 87:2500–2510.

Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. 1999. Long-term landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology 14:513–532.

Brown, P. M., C. L. Wienk, and A. J. Symstad. 2008. Fire and forest history at Mount Rushmore. Ecological Applications 18:1984–1999.

Brown, P. M., and R. Wu. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. Ecology 86:3030–3038.

Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. Journal of Forestry 92:39–47.

Duncan, R. P. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). New Zealand Natural Sciences 16:31–37.

Ehle, D. S., and W. H. Baker. 2003. Disturbance and stand dynamics in ponderosa pine forests in Rocky Mountain National Park, USA. Ecological Monographs 73:543–566.

Everett, R., D. Baumgartner, P. Ohlson, and R. Schellhaas. 2008. Structural classes and age structure in 1860 and 1940 reconstructed fir-pine stands of eastern Washington. Western North American Naturalist 68:278–290.

Fried, J. S., M. S. Torn, and E. Mills. 2004. The impact of climate change on wildfire severity: a regional forecast for northern California. Climatic Change 64:169–191.

Front Range Fuels Treatment Partnership Roundtable. 2007. Living with fire: protecting communities and restoring forests. 2006–2007 Annual Report. ⟨http://www.frftp.org/docs/frftp06rtanrpt.pdf⟩

Fulé, P. Z., J. E. Crouse, T. A. Heinlein, M. M. Moore, W. W. Covington, and G. Verkamp. 2003. Mixed-severity fire regime in a high-elevation forest of Grand Canyon, Arizona, USA. Landscape Ecology 18:465–486.

Gray, S., C. Fastie, S. Jackson, and J. Betancourt. 2004. Tree-ring-based reconstruction of precipitation in the Bighorn Basin, Wyoming, since 1260 A.D. Journal of Climate 17:3855–3865.

Grissino-Mayer, H. D. 2001*a*. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research 57:205–221.

Grissino-Mayer, H. D. 2001*b*. FHX2—software for analyzing temporal and spatial patterns in fire regimes from tree rings. Tree-Ring Research 57:113–122.

Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Review 52:107–145.

Hessburg, P. F., R. B. Salter, and K. M. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landscape Ecology 22:5–24.

Hobbs, R. J., and V. A. Cramer. 2008. Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. Annual Review of Environmental Resources 33:39–61.

Iniguez, J. M., T. W. Swetnam, and C. H. Baisan. 2009. Spatially and temporally variable fire regime on Rincon Mountain, Arizona, USA. Fire Ecology 5:3–21.

Kaufmann, M. R., T. T. Veblen, and W. H. Romme. 2006. Historical fire regimes in ponderosa pine forests of the Colorado Front Range, and recommendations for ecological restoration and fuels management. Ecology Workgroup, Front Range Fuels Treatment Partnership Roundtable. ⟨www.frftp.org/roundtable/pipo.pdf⟩

Klenner, W., R. Walton, A. Arsenault, and L. Kremsater. 2008. Dry forests in the Southern Interior of British Columbia: historic disturbances and implications for restoration and management. Forest Ecology and Management 256:1711–1722.

Krannitz, P. G., and T. E. Duralia. 2004. Cone and seed production in *Pinus ponderosa*: a review. Western North American Naturalist 64:208–218.

League, K., and T. T. Veblen. 2006. Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado. Forest Ecology and Management 228:98–107.

Lentile, L. B., F. W. Smith, and W. D. Shepperd. 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. Canadian Journal of Forest Research 35:2875–2885.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145–2151.

Miller, J., H. Safford, M. Crimmins, and A. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. Ecosystems 12:16–32.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, New York, USA.

Naficy, C., A. Sala, E. G. Keeling, J. Graham, and T. H. DeLuca. 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. Ecological Applications 20:1851–1864.

Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. Vegetatio 45:3–75.

Platt, R. V., and T. Schoennagel. 2009. An object-oriented approach to assessing changes in tree cover in the Colorado Front Range 1938–1999. Forest Ecology and Management 258:1342–1349.

Rollins, M. G., and C. K. Frame, editors. 2006. The LANDFIRE Prototype Project: nationally consistent and locally relevant geospatial data for wildland fire management, General Technical Report RMRS-GTR-175. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Romme, W. H., and D. G. Despain. 1989. The long history of fire in the Greater Yellowstone Ecosystem. Western Wildlands 15:10–17.

Romme, W. H., et al. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in pinyon–juniper vegetation of the western United States. Rangeland Ecology and Management 62:203–222.

Schoennagel, T., and C. R. Nelson. *In press.* Restoration relevance of recent National Fire Plan treatments in forests of the Western United States. Frontiers in Ecology and the Environment. [doi: 10.1890/090199]

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels and climate across Rocky Mountain forests. BioScience 54:661–676.

Scholl, A. E., and A. H. Taylor. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecological Applications 20:362–380.

Shepperd, W. D., C. B. Edminster, and S. A. Mata. 2006. Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado Front Range. Western Journal of Applied Forestry 21:19–26.

Sherriff, R. 2004. The historic range of variability of ponderosa pine in the Northern Colorado Front Range: past fire types and fire effects. Dissertation. University of Colorado, Boulder, Colorado, USA.

Sherriff, R. L., and T. T. Veblen. 2006. Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range. Journal of Vegetation Science 17:705–718.

Sherriff, R. L., and T. T. Veblen. 2007. A spatially explicit reconstruction of historical fire occurrence in the ponderosa pine zone of the Colorado Front Range. Ecosystems 9:1342–1347.

Sibold, J. S., T. T. Veblen, and M. E. Gonzales. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. Journal of Biogeography 32:631–647.

Stephens, S. L., D. D. Piirto, and D. F. Caramagno. 2004. Fire regimes and resultant forest structure in the Native Ano Nuevo Monterey Pine (*Pinus radiata*) Forests, California. American Midland Naturalist 152:25–36.

Swetnam, T. W. 2009. Special issue: fire history in California. Fire Ecology 5:1–3.

Taylor, A. H., and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications 13:704–719.

USDA Forest Service. 2010. Arapaho-Roosevelt National Forest Integrated Resource Inventory. ⟨http://www.mpcer.nau.edu/sage/SJPLC/r2veg.htm⟩

Veblen, T. T., and J. A. Donnegan. 2006. Historical range of variability of forest vegetation of the National Forests of the Colorado Front Range. USDA Forest Service, Rocky Mountain Region and the Colorado Forest Restoration Institute, Fort Collins, Colorado, USA.

Veblen, T. T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecological Applications 10:1178–1195.

Veblen, T. T., and D. C. Lorenz. 1986. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. Physical Geography 7:1–24.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943.

Williams, J., and S. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5:475–482.

APPENDIX A

Graphs showing the total proportion of tree and sapling establishment in 20-yr bins and the proportion of fires in 20-yr bins at each site, with associated remnant and establishment metrics (*Ecological Archives* A021-100-A1).

APPENDIX B

A color version of Plate 1, showing the juxtaposition of a dense ponderosa pine stand that regenerated after a lethal canopy fire and a sparse stand where the same fire burned at low severity (*Ecological Archives* A021-100-A2).