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Variability in fire regimes of high-elevation whitebark pine communities, western Montana, USA[1]

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Abstract: We investigated the stand history of whitebark pine forests on 3 mountains in the Lolo National Forest, Montana, USA to characterize the fire regimes and other disturbance agents that historically operated at these sites and to explore the potential influences of modern fire suppression on these forests. We used historical fire atlas data and dendroecological data to reconstruct the distinct history of each stand. The fire regimes of each site fit within the general definition of mixed-severity fire regimes, but distinct differences in fire frequency and severity existed between them. All 3 stands contained at least 1 post-disturbance cohort and had experienced at least 1 widespread fire over their histories. We found no consistent fire–climate relationship at these sites. Mountain pine beetles were the primary mortality agent in the current stands at all 3 sites. Subalpine fir began establishing at each site within 2 decades of the most recent widespread fire and well before fire suppression was effective in this region. Fire suppression may have reduced the occurrence of fire during the late 20th century at all 3 sites, but only the forest on Point Six has exceeded the mean interval between widespread fires. The differences in fire activity and effects of fire suppression that we observed at these sites are likely the result of different biophysical site characteristics and disturbance legacies and hold important implications for the development of site-specific management strategies for whitebark pine restoration.
Keywords: fire history, fire suppression, mixed-severity fire regime, Montana, *Pinus albicaulis*, whitebark pine.

Résumé : Nous avons examiné l'historique de peuplements forestiers de pin albicaule sur 3 montagnes dans la Forêt nationale Lolo, Montana, États-Unis, afin de caractériser les régimes de feu et d'autres agents de perturbation qui ont historiquement influencé la dynamique de ces sites et aussi d'explorer les influences potentielles sur ces forêts de la présente suppression de feu. Nous avons utilisé des données historiques d'atlas de feu et des données dendroécologiques pour reconstruire l'historique distinct de chaque peuplement. Le régime de feu de chacun des sites suivait la définition générale des régimes de feu de sévérité variable, mais des différences existaient entre les sites dans la fréquence et la sévérité des feux. Les 3 peuplements avaient tous au moins une cohorte d'arbres établis après perturbation et avaient tous subi au moins 1 feu de grande étendue au cours de leur histoire. Nous n'avons trouvé aucune relation climat-feu cohérente entre les sites. Le dendroctone du pin ponderosa constituait la cause de mortalité principale dans les peuplements actuels des 3 sites. Le sapin subalpin a commencé à s'établir dans chacun des sites moins de 2 décennies après le feu de grande étendue le plus récent et bien avant que la suppression de feu ait été en vigueur dans cette région. La suppression de feu peut avoir réduit la fréquence des feux à la fin du 20e siècle aux 3 sites, mais l'intervalle moyen entre les feux de grande étendue a été dépassé seulement dans le cas de la forêt de Point Six. Les différences observées entre les sites dans l'activité de feu et les effets de la suppression sont probablement le résultat de caractéristiques biophysiques différentes et de legs des perturbations passées; elles comportent des implications importantes pour le développement de stratégies d'aménagement spécifiques à chacun des sites pour la restauration du pin albicaule.
Mots-clés : historique de feu, Montana, pin albicaule, *Pinus albicaulis*, régime de feu de sévérité variable, suppression de feu.

Nomenclature: ITIS, 2008.

Introduction

Fire is a fundamental component of the disturbance regimes of nearly all forests of North America. Fire regimes, or general descriptions of the role of fire in a particular system (Romme, 1980), are most often defined in terms of the historical frequency and severity of fires, ranging from relatively frequent low-severity surface fires to relatively infrequent high-severity, stand-replacing fires (Agee, 1993). In between these extremes, the spectrum of fire activity includes what are referred to as mixed-severity fire regimes. Mixed-severity fire regimes include both surface and crown fire components, often spatially distributed over a single fire event, that result in patchy, post-burn mosaics of mortality and reductions in fuels (Arno, Parsons & Keane, 2000). Historically, a large proportion of fire history research has focused on characterizing the fire regimes on the extreme ends of this spectrum, namely the frequent, low-severity fire regimes of many dry conifer forests (*e.g.*, Swetnam, Allen & Betancourt, 1999; Grissino-Mayer & Swetnam, 2000; Heyerdahl, Brubaker & Agee, 2001) and

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the infrequent, high-severity fires of many subalpine and boreal forests (*e.g.*, Heinselman, 1973; Romme, 1982; Veblen, Hadley & Reid, 1991; Kipfmueller & Baker, 2000; Weir, Johnson & Miyanishi, 2000). Less common have been investigations into the fire dynamics of forests that are characterized by mixed-severity fire regimes (but see Barrett, Arno & Key, 1991; Fulé *et al.*, 2003; Buechling & Baker, 2004), even though a considerable proportion of North American forests experienced this type of fire regime in the past (Schoennagel, Veblen & Romme, 2004). The resulting gaps in our understanding of mixed-severity fire regimes are particularly important when considering forest systems maintained by these rather broadly defined fire regimes that are also the subject of intensive management and restoration activities. One such forest is the whitebark pine (*Pinus albicaulis*) ecosystem.

Whitebark pine is a high-elevation conifer found throughout western North America (Arno & Hoff, 1990). It is long lived (1000+ y, Perkins & Swetnam, 1996; Luckman & Youngblut, 1999; Kipfmueller, 2003), moderately shade tolerant, and an important component of many subalpine forest types (Arno, 2001). Whitebark pine often survive low- to moderate-severity surface fires and persist on productive sites where it is otherwise limited to an early successional role in the absence of disturbance (Arno, 1980; Keane *et al.*, 1990; Morgan *et al.*, 1994). Fire history reconstructions for whitebark pine forests in the northern Rocky Mountains have identified a range of fire return intervals from 13 to 400+ y at the stand scale (Arno, 1976; Romme, 1982; Arno & Petersen, 1983; Morgan & Bunting, 1990; Barrett, 1994; Murray, Bunting & Morgan, 1998; Kipfmueller, 2003). This wide range of fire return intervals is likely the product of differences in topography and microsite conditions (Arno, 2001), yet few studies have offered detailed comparisons of fire history date from whitebark pine forests in differing biophysical settings. Additionally, with the exception of a few (*e.g.*, Morgan & Bunting, 1990; Kipfmueller, 2003), these studies have relied on age-structure data and non-crossdated fire scars. While these data provide valuable descriptions of the general patterns of fire activity in whitebark pine forests, they are limited in their temporal resolution (Weisberg & Swanson, 2001) and ability to examine relationships between fire and inter-annual climate variability.

The lack of temporally precise, site-specific data is particularly important in light of recent management efforts that attempt to counter declines observed in many whitebark pine communities. Mountain pine beetle (*Dendroctonus ponderosae*) outbreaks and white pine blister rust (*Cronartium ribicola*) infections have caused extensive mortality in many whitebark pine forests (Keane, Morgan & Menakis, 1994; Campbell & Antos, 2000; McDonald & Hoff, 2001; Zeglen, 2002), and fire suppression has been implicated as an agent accelerating the loss of whitebark pine dominance in forests throughout the Pacific Northwest and Rocky Mountains (Keane, Morgan & Menakis, 1994; Murray, Bunting & Morgan, 2000; Keane, 2001). In response, a number of management initiatives have been developed to restore whitebark pine communities to their former structure and health (Tomback, Arno & Keane, 2001b), with prescribed fire being an important component to counter the effects of fire suppression (Keane & Arno, 2001). Yet, recent research suggests that many high-elevation forests are still operating within their historical range of variability and have not been affected by modern fire suppression (Sherriff, Veblen & Sibold, 2001; Buechling & Baker, 2004). The potential uncertainty that surrounds past fire regimes and the effects of fire suppression in whitebark pine forests creates a need for site-specific data to inform management efforts.

Our research investigated the role of fire in whitebark pine forests on 3 mountains in the Lolo National Forest, western Montana. Each site falls within the relatively coarse-scale Fire Regime Condition Classification mixed-severity fire regime type (Type III, mean fire return interval 35–100+ y) (Schmidt *et al.*, 2002; Hann & Strohm, 2003), but the biophysical characteristics of the sites differ. This enabled us to examine the disturbance regimes of whitebark pine forests in different settings for both similarities and differences. Specifically, we sought answers to the following questions: 1) What were the historical fire regimes in these whitebark pine forests and how did they vary among sites with different biophysical characteristics? 2) Did any consistent fire–climate relationships exist at either the scales of these sites individually or collectively? 3) What disturbance processes other than fire affected the forests at these sites? 4) Has fire suppression affected these sites? We then explored the implications of our findings for fire management and restoration activities in whitebark pine forests.

Methods

Study site descriptions

Study sites were located in whitebark pine forests covering 3 peaks in the northern Rocky Mountains, near Missoula, Montana, in the Lolo National Forest: Morrell Mountain, Mineral Peak, and Point Six (Figure 1). These sites were subjectively chosen due to the presence of abundant fire-scarred material. We recognize that this subjectivity limits our ability to generalize our results across the range of whitebark pine forests, but that was not the intent of this study. Rather, these sites were selected to provide data on the variability that exists in whitebark pine forests.

The stands included in our study were relatively small for this region, ranging from 51 to 84 ha, and varied in elevation from 2200 m to 2350 m, with slopes ranging from 25% to 45% (Table I). Mean annual temperature ranges are similar, but a gradient of decreasing precipitation exists from west to east among the 3 sites (mean annual precipitation = 1051 mm at Point Six, 776 mm at Mineral Peak, and 623 mm at Morrell Mountain) (Daly *et al.*, 2000). Soils are poorly developed at all 3 sites, and the underlying geology is composed of a mix of Quaternary and Cenozoic glacial deposits, Precambrian shales and siltstones, and Precambrian argillites and quartzites (Ross, Andres & Witkind, 1955; Raines & Johnson, 1996). Subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) were both present in the stands we examined, although not always within our plots. At lower elevations the forests on all 3 mountains transitioned into stands dominated by

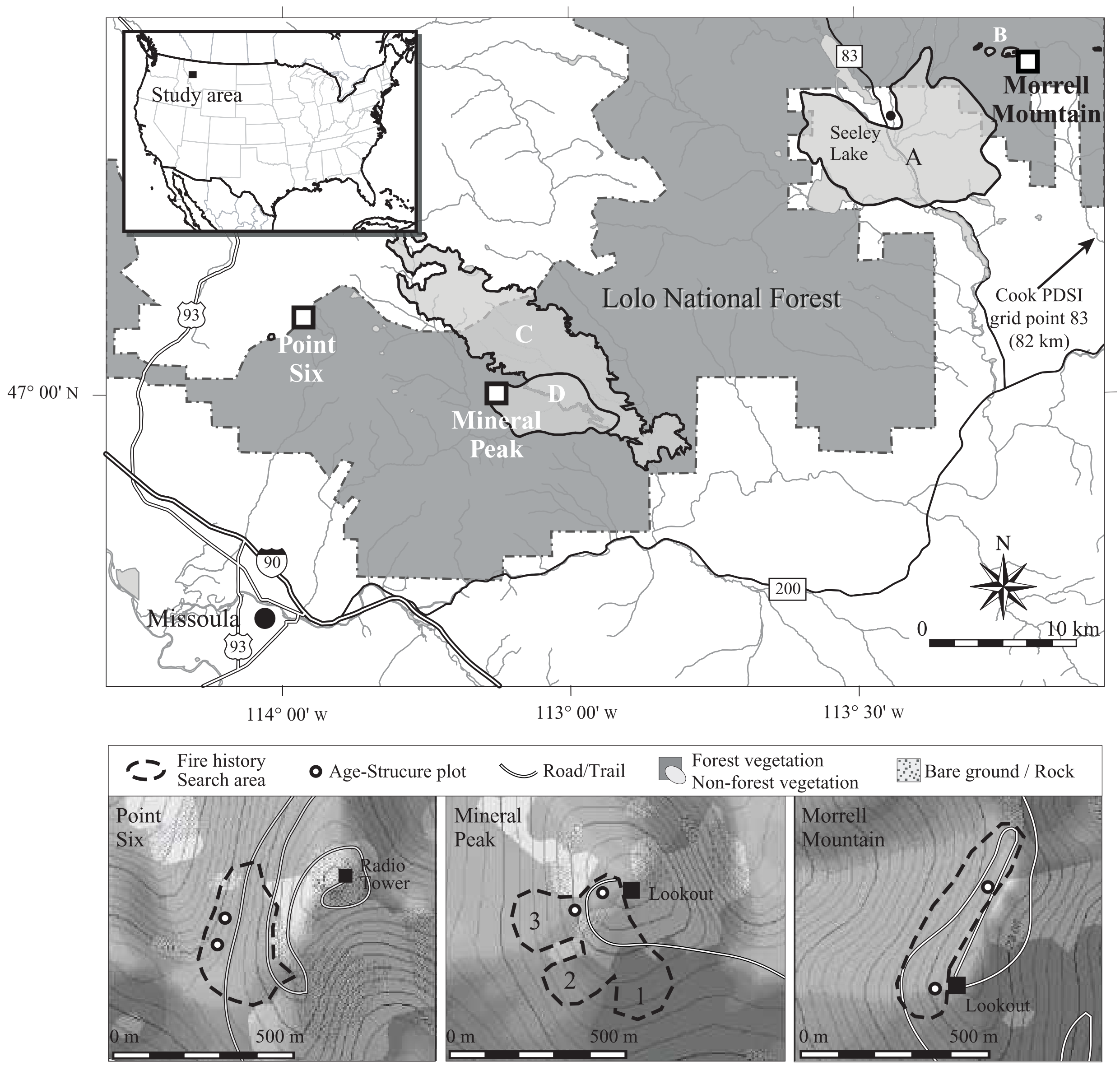

Figure 1. Locations of the 3 study sites in the Lolo National Forest, western Montana. Light grey areas indicate large historic fires that burned near the study sites: A: An area of the 1910 fires; B: Four fires on Morrell Mountain, including 1 that burned 60 ha in 1935 and 3 fires that burned a combined 13 ha in 2000; C: The 8400-ha Mineral-Primm Fire complex of 2003; D: Part of the 1919 fires (USDA Lolo National Forest, 2003b,c,a). Individual site maps are at the bottom of the figure. The numbers shown inside of the fire history search area for Mineral Peak indicate clusters of trees that were relatively isolated from each other on the lower slopes by open talus fields.

Rocky Mountain lodgepole pine (*Pinus contorta*). Forest cover on Point Six was relatively continuous, the forest on Morrell Mountain was broken by a few alpine meadows, and the forest on Mineral Peak was dissected by open talus that created 3 distinct forest clusters (Figure 1). Herbaceous cover at Morrell Mountain and Point Six was dominated by grouse whortleberry (*Vaccinium scoparium*), red mountain-heath (*Phyllodoce empetriformis*), smooth woodrush (*Luzula glabrata*), bear grass (*Xerophyllum tenax*), and elk sedge (*Carex garberi*), while similar species were present at Mineral Peak but in lower abundances.

Evidence of past disturbances was common at each site. Whitebark pine had experienced high rates of mortality in each stand (approximately 80%), predominantly from mountain pine beetles that we identified by the presence of j-shaped galleries on the boles of dead trees (Kipfmueller, Swetnam & Morgan, 2002) and blue stain fungus in the sapwood (Solheim, 1995). Evidence of past fires was common, with many whitebark pine trees displaying multiple fire scars. We did not observe any fire-scarred fir or spruce. Blister rust was ubiquitous. Evidence included open cankers and flagging of the upper canopy of many whitebark pines (*i.e.*, red needles due to the recent mortality of a branch or stem).

Land use has varied among the 3 sites. Fire lookouts were constructed on Morrell Mountain and Mineral Peak in 1921 and 1920, respectively (USFS, 1986), and staffed until the 1970s (NHLR, 2005). The Snowbowl Ski Area was established on Point Six in 1961, and several ski runs

TABLE I. General setting of the study sites in the Lolo National Forest, Montana.

Site	Latitude Longitude	Elevation (m)	Slope (%)	Area (ha)
Morrell Mountain	47° 11' N 113° 21' W	2350–2370	30–40	84
Mineral Peak	47° 00' N 113° 49' W	2200–2250	30–40	51
Point Six	47° 02' N 114° 00' W	2250–2350	25–45	63

dissect the subalpine forest zone of the peak. A utility road that accesses a radio facility on the peak of the mountain cuts through our study area. Timber extraction has occurred near all 3 peaks since the early 1900s, with some harvesting on the southern slopes of Morrell Mountain as recently as the 1960s (B. Oelig, Seeley Lake Ranger District, pers. comm.), but our study sites have not been directly affected by logging. Some gold prospecting occurred on the lower slopes of Mineral Peak in the 1950s (USBM, 1992), but due to the area's value as a municipal watershed for Missoula, the Rattlesnake National Recreation and Wilderness area was established in 1980 and no further mineral explorations were conducted. The Bureau of Land Management has issued resource exploration leases for the area including Morrell Mountain, but no mining or extraction has occurred near our study site (BLM, 2001).

FIELD METHODS

We conducted a thorough search for fire-scarred material within the boundaries of each of the 3 forest stands. A variety of disturbances can injure trees in the subalpine environment (*e.g.*, Burrows & Burrows, 1976; Stuart *et al.*, 1983; Butler, Oelfke & Oelfke, 1986; Morgan & Bunting, 1990). We therefore only collected samples from trees that displayed classic characteristics of fire injury (Gutsell & Johnson, 1996), including at least 2 of the following: 1) the presence of charcoal on the scar face or on the bark of the tree; 2) an inverted V-shaped scarred surface that extended to ground level; 3) injuries located on the upslope side of the bole; and 4) a smooth surface beneath the healing lobe of the scar. We used a chainsaw to cut partial and/or full cross-sections from fire-scarred whitebark pine trees (Arno & Sneck, 1977), with all but 2 of our samples coming from the abundant snags, stumps, and logs at each site. We sampled almost all fire-scarred material we encountered within each stand, thereby avoiding the potential bias that may result from sampling only trees that displayed multiple fire scars (Baker & Ehle, 2001).

Stand age-structure data were collected in two 0.05-ha fixed-radius (r = 12.66 m) plots placed randomly at each site, for a total of 6 plots. We recorded the species and diameter at breast height (dbh; height = 1.47 m) of all trees ≥ 5.0 cm dbh within each plot. We then collected increment cores from 2 radii of each tree. All cores were taken at or below 30 cm above the root collar and along the contour of the slope to minimize the effects of reaction wood on the growth patterns in each sample (Fritts, 1976). We also cut 5–12 non-whitebark pine saplings (trees > 1.2 cm diameter at ground level and < 5 cm dbh) in each plot to include in the age-structure data.

SAMPLE PREPARATION

We glued all increment cores to wooden core mounts and used a band saw to remove the rough surface of the chainsaw cuts on the cross-sections before sanding each sample with progressively finer grits until there was clear cellular resolution under 7–40× magnification (Stokes & Smiley, 1996; Orvis & Grissino-Mayer, 2002). We visually and graphically crossdated each sample based on ring-width patterns (Stokes & Smiley, 1996) and frost rings (LaMarche & Hirschboeck, 1984) common to all 3 sites. Samples that we could not crossdate were excluded from all additional analyses. The ring widths of all of the crossdated fire-scar samples were measured to the nearest 0.001 mm along 2 to 4 radii using a Velmex measuring system interfaced with Measure J2X software (Voortech Consulting, 2005). The number of radii per sample depended on the shape and condition of the sample, with more radii used when visible breaks in the tree-ring series were evident. We used the computer program COFECHA (Holmes, 1983; Grissino-Mayer, 2001a) to assess the accuracy of the assigned ring dates among our samples and against a whitebark pine tree-ring chronology developed on Carlton Ridge in the northeast corner of the nearby Selway–Bitterroot Wilderness Area (Kipfmueller, 2003).

FOREST HISTORY

We reconstructed the forest history of each of our sites using both historical fire records and dendroecological data. We used digitized fire atlas data from the USDA Forest Service (USDA Lolo National Forest, 2003a,b,c) to determine the occurrence of ignitions and wildfires at our sites during the 20th century. Forest history prior to the written records was reconstructed using cambial scarring and trauma rings in the samples collected from each site and from the age-structure data. Most samples collected for fire history data included multiple scars, and even after careful identification in the field, many scars were difficult to distinguish between fire scars and strip-kill scars from mountain pine beetles (Mitchell, Martin & Stuart, 1983). We therefore used morphological characteristics to describe each scar as highly probable (classic scar morphology including consistent intra-ring position, smooth scar boundary, healing lobes, and occasionally the presence of charcoal within the healing lobe), likely (consistent intra-ring position, smooth scar boundary, relatively small scar and/or scars at multiple locations around the circumference of a single sample), or unlikely to represent a fire event (the presence of blue stain at the scar face, an uneven scar boundary that included multiple growth rings) (Lafon, 2005). We included scars that were highly probable and likely to represent fires in our fire history analyses, while the remaining scars were considered to represent other disturbance events.

The intra-ring position of each fire scar and injury was identified where possible and assigned a date and season (Baisan & Swetnam, 1990) relative to the growing season of whitebark pine, which ranges from late May through September (Weaver, 2001). Initial analyses found that the majority of scars occurred along the boundary between 2 rings representing fires that burned during the dormant season, and we therefore labelled each disturbance event as a growing season event, a dormant season event, or an unknown seasonality event. The fire season in the northern Rocky Mountains typically begins in the late summer or early fall (Brown, 1994), which is near the end of the growing season for high-elevation forests (Schmidt & Lotan, 1980). Dormant season fire scars were therefore assigned to the preceding year. The presence of blue stain fungus in the sapwood of any fire-scarred sample was noted as evidence of mountain pine beetle-related mortality. To describe fire frequency at each site, we used the program FHX2 (Grissino-Mayer, 2001b) to calculate 1) the mean number of years between all fires and 2) the mean number of years between likely stand-initiating and widespread fires for each site (*sensu* Ehle & Baker, 2003). For this study, we defined stand-initiating events as disturbances that likely preceded the establishment of the oldest trees or cohort of trees in each stand (*sensu* Taylor & Skinner, 1998) and widespread fires as those that scarred ≥ 5 trees in a stand. The relatively small number of fires at each site limited the utility of additional statistical descriptions of each fire regime. Instead, we progressively interpreted each fire with respect to its size, severity, and climatic context to illustrate the site-specific disturbance histories of each stand.

The age structure for each stand was determined by obtaining or estimating the innermost dates for the living and dead trees within each age-structure plot. We added a correction to the innermost date of cores that did not contain pith, based on the curvature of the innermost rings and a pith estimator made of concentric circles that represented different growth rates (Applequist, 1958). For solid cores that contained neither pith nor the curvature necessary to use pith estimators but were determined to be within 2 cm of the centre of the tree by comparing the length of the core to the dbh of the tree (*sensu* Frelich & Graumlich, 1994), the innermost ring was used to represent the minimum age of the tree (Soulé & Knapp, 2000). If the inner date of any samples could not be determined due to rot, narrow growth rings, erratic ring structure, or lack of ring curvature, the sample was excluded from the age-structure data. Due to the variability in growth rates for seedlings and saplings at these sites, we did not apply a correction for the age at coring height, and thus these data should be considered the minimum age of trees within the stand rather than the absolute establishment date for these trees. To further accommodate the uncertainty prevalent in increment core-based tree establishment dates (Villalba & Veblen, 1997) and the implications of this uncertainty in assessing stand dynamics (Wong & Lertzman, 2000), the data were grouped into 20-y age classes for construction of age-structure charts.

Fire–climate relationships

We examined the drought conditions surrounding each individual widespread fire recorded at our sites and used superposed epoch analysis (SEA) to assess the overarching fire–climate relationships at our sites and to highlight important limitations when using SEA in studies that include only a small number of fire events. SEA has been widely employed to identify annually resolved fire–climate relationships and has consistently identified drought conditions during the year of a fire event as the primary relationship between climate and fire for forests growing in a variety of environmental settings (*e.g.*, Swetnam & Betancourt, 1990; Grissino-Mayer & Swetnam, 2000; Heyerdahl, Brubaker & Agee, 2002; Schoennagel *et al.*, 2005). However, the power of SEA is limited when only a low number of events are considered due to the increased potential for extreme conditions surrounding a single event to bias the results of the analysis. Due to the relatively low number of fires typically recorded within individual stands of high-elevation forests, we decided to first examine drought conditions for an 11-y window surrounding each individual fire event that scarred more than 2 trees at each site. This approach allowed us to examine the data for single events that could influence the results of a SEA. Keeping these results in mind, we then combined the dates of all fires that scarred more than 2 trees into a master fire chronology and conducted a SEA to explore the data for consistent fire–climate relationships. As summer drought is linked to fire activity (Westerling *et al.*, 2006), we used the reconstructed mean summer (June through August) Palmer's Drought Severity Index (PDSI), which is a measure of available soil moisture, for grid point 83 (47.5° N, 112.5° W) developed by Cook *et al.* (2004) as our climate parameter in these analyses. While this grid point is 80 km from our study area, it is the nearest point available, and the spatial autocorrelation of drought (Karl & Koscielny, 1982) suggests it is a reasonable data source. We interpreted PDSI values as indicating relatively wet (positive values) or relatively dry conditions (negative values) based on the qualitative scale suggested by Palmer and described in Alley (1984).

Results

Fire history

The fire atlases provided fire history data from 1870 to 2005 and included 4 large fires in the general vicinity of our sites (Figure 1) and several smaller fires that burned small areas on or near our study sites. Small fires were ignited on Morrell Mountain in 1987 (area burned = 0.05 ha), 1988 (0.01 ha), 2000 (0.4 ha), and 2003 (0.6 ha); on Mineral Peak in 2000 (0.1 ha); and on Point Six in 2003 (0.4 ha). All of these fires were successfully suppressed (USDA Lolo National Forest, 2003a,b). Our sites were not within the digitized burn perimeter of any of the large fires.

We collected fire-scarred samples from 115 whitebark pine trees among the 3 sites. We crossdated 110 of these, with a frost injury in 1601 CE that provided a clear marker ring in 33 of the 47 fire-scarred samples that extended before the year 1600. We identified 153 injuries recorded in the rings of the fire-scarred samples, representing 68 unique disturbance events between the 3 sites over the past 506 y. Of the total number of scars, 112 were considered to be highly likely or likely to represent a fire-caused injury, resulting in a total of 33 fires identified across the 3 sites (Table II). We inferred seasonality for 79% (n = 90) of the

TABLE II. Description of the fire history data.

	Morrell Mountain	Mineral Peak	Point Six
No. trees	30	38	42
Time span	1467–1999	1087–2000	1581–2003
No. fire scars/events	36/19	28/9	48/5
Earliest fire	1531	1488	1661
Mean no. years between all fires	19	45	54
Mean no. years between widespread fires	*ca* 250	*ca* 350+	*ca* 100

fire scars, with the vast majority of those occurring in the dormant season (89%, n = 80). Indications of mortality related to mountain pine beetle were present on 86% (n = 95) of the samples that we collected. Most disturbance events were recorded by only 1–3 trees within a site, but each fire chronology included at least 1 fire that scarred multiple trees across the site. The mean number of years between all fires was 19 y on Morrell Mountain, 45 y on Mineral Peak, and 54 y on Point Six. The mean number of years between stand-initiating and widespread fires at each site was longer: *ca* 250 y on Morrell Mountain, *ca* 350+ y on Mineral Peak, and *ca* 100 y on Point Six. In no single year did fire scar trees at more than 1 site, and none of the tree-ring–based fires corresponded with fires recorded in the fire atlas data.

AGE STRUCTURE

We collected core samples from 372 trees and 39 saplings in our plots, for a total sample size of 411 in our age-structure data. For trees ≥ 0.05 cm dbh, subalpine fir was most abundant at Morrell Mountain, while whitebark pines were more numerous than subalpine firs at Mineral Peak and Point Six. Subalpine fir saplings were more abundant than whitebark pine saplings at all sites. No Engelmann spruce occurred within our age-structure plots. We were able to crossdate 302 of the cores and cross-sections collected for age-structure analyses. The average correction for cores that did not contain pith was 6–7 y, with a maximum correction of 12 y on 1 sample. Inner-ring dates varied by site and species, but the oldest trees at all 3 sites were whitebark pines, with a general increase in the representation of subalpine fir in the age-structure data during the 19th and 20th centuries. The subalpine fir saplings that we sampled ranged widely in age, with a pith date of 1 sapling on Morrell Mountain of 1769 and saplings at all 3 sites with inner dates in the late 1800s.

FOREST HISTORY AT MORRELL MOUNTAIN

The majority of whitebark pine trees sampled at Morrell Mountain established *ca* 1500 CE, although a few individual trees have persisted on the site for nearly 700 y (Figure 2). The latter decades of the 1400s were relatively droughty for the region (mean PDSI from 1460 to 1499 is –0.60) and were punctuated by several years of extreme summer drought (*e.g.*, PDSI for 1489 and 1492 were –4.8 and –5.3, respectively) (Cook *et al.*, 2004). Drought is an important driver of fires in subalpine forests (Kipfmueller & Swetnam, 2000; Sherriff, Veblen & Sibold, 2001; Buechling & Baker, 2004; Schoennagel *et al.*, 2005). While we lack fire-scar evidence in this case, the relatively severe drought conditions of the late 1400s would have been conducive to a widespread fire, which is supported by the clear cohort establishment of whitebark pine *ca* 1500 that is suggestive of a post-canopy disturbance episode of establishment. The earliest fire scar recorded on the site dated to 1531, indicating that at least a small fire burned on the site within a relatively short time following the initiation of the stand. Another small cohort of trees established following a fire that was recorded in 1564, as indicated by a short but steep incline in the fire history sample depth (Figure 2b).

Several fires were recorded by trees on Morrell Mountain in the 1600s, but no single event scarred more than 1 tree, suggesting that these were small, patchy fires. Relatively few trees that were present at the time of our sampling established during this period. The earliest establishment dates of subalpine fir that were sampled in the age-structure plots occurred in the 1690s. Subalpine fir abundance increased in the age-structure data throughout the 1700s, 1800s, and 1900s, with a distinct period of lower establishment or low survival rates in the 1920s and 1930s (Figure 2c) that coincided with a period of mild drought (mean PDSI from 1917 to 1940 = –1.2) (Cook *et al.*, 2004). Fires became more common at this site in the mid-1700s. One tree recorded a fire event in 1748, a widespread fire year across the western United States (Swetnam & Betancourt, 1998), and the most widespread fire recorded at the site burned in 1754. Although 1754 is identified as a year of above average summer moisture (reconstructed summer PDSI = 0.7) (Cook *et al.*, 2004), this was a time of transition into a severe 3-y drought (mean PDSI 1755–1757 = –2.9, Figure 3a). It is after this date that the majority of subalpine fir present on the site today established. The second half of the 1700s experienced only 1 fire event, a 1796 fire that burned during a year of mild drought conditions (PDSI = –1.0, Figure 3a) and scarred 3 trees. Several fires burned on Morrell Mountain in the 1800s that scarred only a few trees each, and no obvious post-fire cohorts appear in the age-structure of the stand during this time, suggesting that these fires were patchy and of relatively low severity. Only 1 fire event was recorded in our data in the 1900s, and that event took place in 1901 and scarred only 1 tree.

The earliest evidence of mountain pine beetle–related mortality in whitebark pine at Morrell Mountain occurred in 1820. Two episodes of beetle-related mortality followed: one from the late 1800s into the early 1900s and the other in the 1970s and 1980s, both of which are evident as declines in the fire history sample depth (Figure 2b). The 1970s and 1980s mountain pine beetle outbreak aligned with a period of abundant subalpine fir regeneration (Figure 2c) and a steep decline in the fire history sample depth (Figure 2b).

FOREST HISTORY AT MINERAL PEAK

The fire-scar and age-structure samples that we collected on Mineral Peak showed no clear evidence of a disturbance-initiated cohort as the stand origin; rather, sample depth slowly increased from the beginning of the fire-history data in 1087 until the mid-1500s to mid-1600s, when the majority of whitebark pine that were sampled both for the fire history and in the age-structure plots established on the site (Figure 4). Within this general trend of increasing sample depth, potential small post-fire cohorts exist in the different areas of this site that were isolated by open talus, including a cohort of 6 trees that had similar inner dates in cluster 2 that lag behind a fire event recorded in 1497 and a small cohort of 4 trees in cluster 1 with inner rings dating to shortly after a 1591 fire. The earliest fire scars recorded by the samples collected at this site occurred in 1488 and 1497 (Figure 4a). Both fires occurred during a period of mild drought (mean PDSI from 1488 to 1500 = –1.2) (Cook *et al.*, 2004). Four fires were recorded between 1591 and 1665, but each event was recorded by only 1 tree, suggesting that these were small or low-severity fires. The next fire that was recorded in our samples scarred 4 trees in cluster 1 and occurred in 1781, which was a year of transition from relatively wet conditions to a moderate 4-y drought (mean PDSI from 1782 to 1785 = –1.8, Figure 3b). This fire closely predates the earliest inner date of subalpine fir at this site (Figure 4c). In 1834, the most widespread fire recorded at this site occurred and scarred trees in all 3 clusters of the study area. Reconstructed drought conditions were near average for this year, and above-average moisture occurred both before and after the fire event (Figure 3b). The last fire recorded in our samples from Mineral Peak burned in 1889 and scarred 3 trees in cluster 2. This was a year of extreme drought (PDSI = –4.7, Figure 3b) and was a year of widespread fire across the northwestern United States (Barrett, Arno & Menakis, 1997; Kipfmueller & Swetnam, 2000; Heyerdahl, Brubaker & Agee, 2001; Hessl, McKenzie & Schellhaas, 2004). Most subalpine fir that we were able to date established in the late 1800s and early 1900s (Figure 4c). Although a period of apparently lower subalpine fir establishment or survival occurred between 1940 and 1960, overall subalpine fir established relatively continuously up to the decade of this study.

The earliest date of mortality among whitebark pine that was likely related to mountain pine beetle activity occurred in the late 1600s. The tree that provided this evidence, along with a few others in cluster 1, had fallen onto talus and was remarkably well preserved over the centuries since its death. The outer rings of the tree had eroded away and we were therefore unable to identify beetle galleries, but the remaining sapwood clearly displayed the blue stain fungus that is suggestive of mountain pine beetle infestation (Solheim, 1995). Four beetle-killed trees provided evidence of beetle activity in this stand just before the widespread

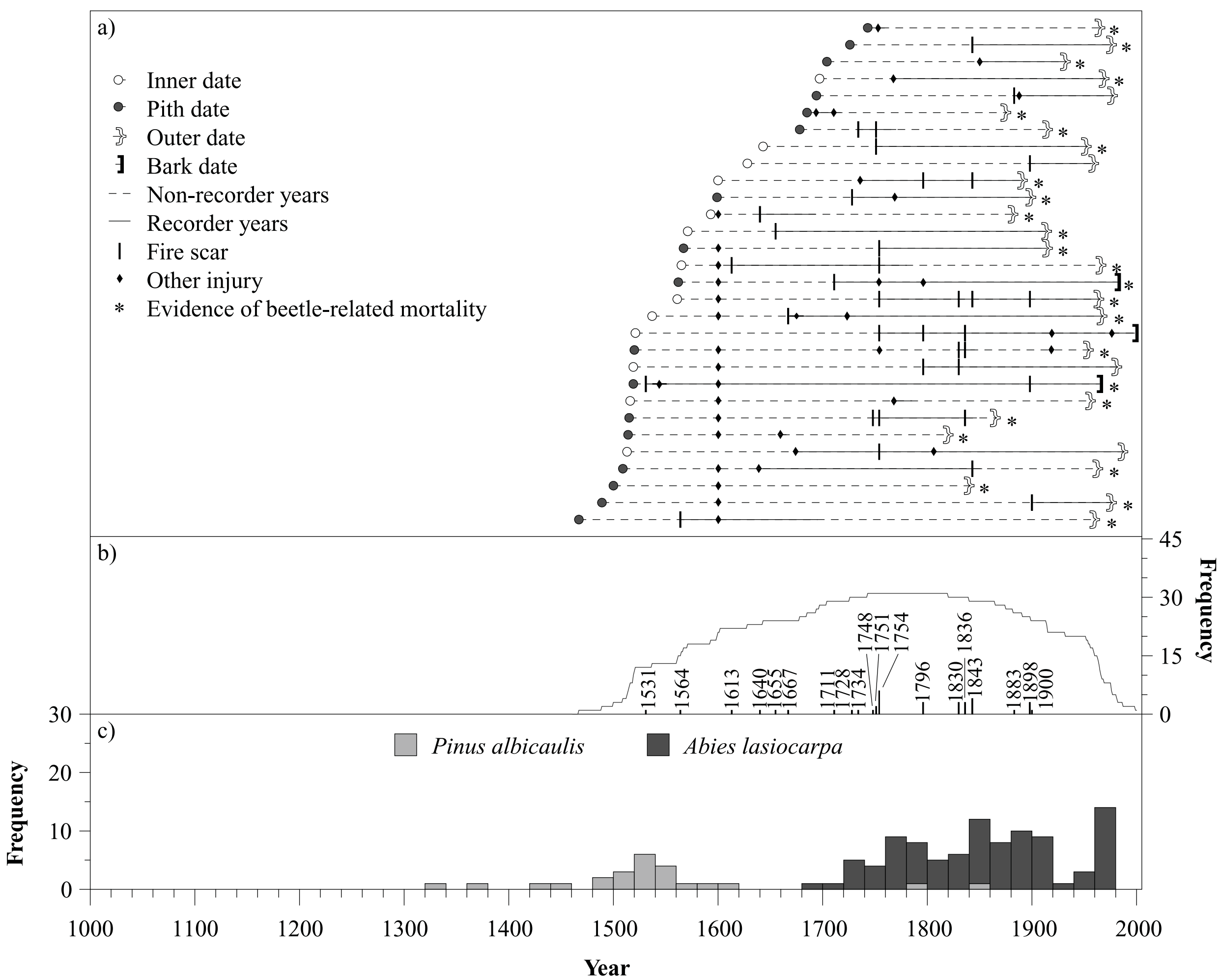

Figure 2. The a) fire history, b) fire history sample depth and master fire chronology, and c) age structure for Morrell Mountain. The synchronous "other injury" represents the number of trees that recorded the 1601 CE frost ring.

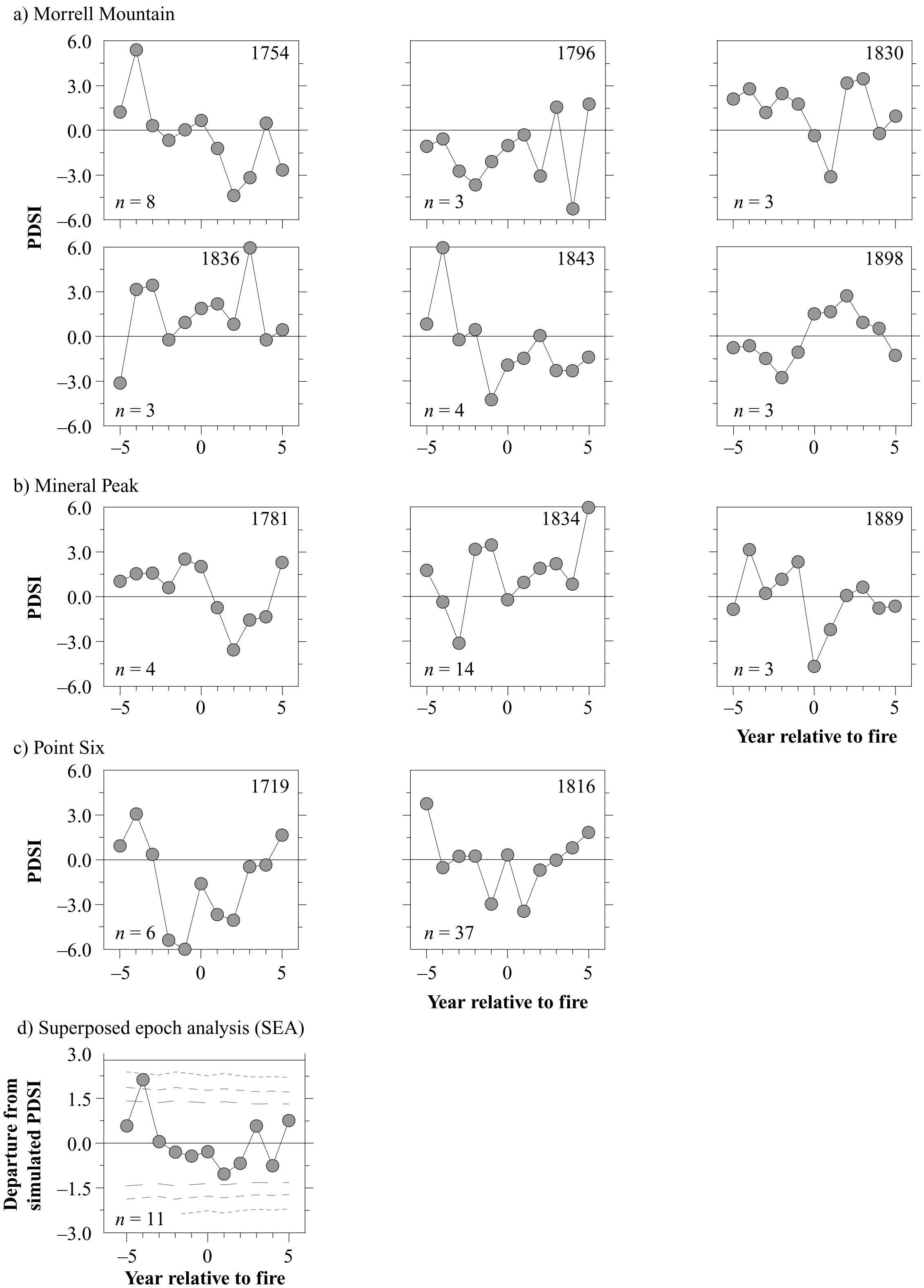

FIGURE 3. Drought conditions relative to fires that scarred at least 2 trees on a) Morrell Mountain, b) Mineral Peak, and c) Point Six and d) the results of a superposed epoch analysis (SEA) of these fires. Drought data are from grid point 83 of the Cook *et al.* (2004) Palmer Drought Severity Index (PDSI) reconstruction. The calendar year of the fire event is located in the upper-right corner of charts a)–c), while the number of trees recording that fire is located in the bottom-left corner. The x axis of each chart indicates the year of the fire event as year 0, with negative values indicating years before the fire and positive values years after the event. PDSI departures and confidence intervals in the SEA are calculated as the difference between the actual mean PDSI for each year of the window around each event and a simulated PDSI based on a Monte Carlo simulation of 1000 randomly drawn windows. The dashed lines indicate confidence intervals of 95% (long dashes), 99% (medium dashes), and 99.9% (shortest dashes).

1834 fire, and a few trees appear to have been killed by beetles in the 1930s. The majority of trees sampled at this site succumbed to relatively continuous beetle activity over the late 1900s (Figure 4b).

FOREST HISTORY AT POINT SIX

The earliest inner ring that we observed in the trees sampled for fire-history and age-structure information on Point Six dated to 1581 (Figure 5). A cohort of overstory whitebark pine established on the site a few decades later in the early 1600s (Figure 5a). The earliest fire scar was recorded by a single tree in 1661 (Figure 5a). This event was followed by a potentially widespread fire in 1719 that appears to have been of sufficient severity to initiate a second cohort of whitebark pine apparent in both the fire history sample depth (Figure 5b) and the age-structure data (Figure 5c). This fire burned in the middle of an extreme 5-y drought (mean PDSI from 1717 to 1721 = –4.2, Figure 3c) that corresponds with widespread fires throughout the Northern Rockies (Barrett, Arno & Menakis, 1997; Kipfmueller & Swetnam, 2000; Heyerdahl, Brubaker & Agee, 2001; Hessl, McKenzie & Schellhaas, 2004). A single tree recorded a fire in 1749 that coincides with the earliest inner dates of several whitebark pines sampled in the age-structure plots (Figure 5c); however, because we did not adjust the inner dates of our samples to reflect the time it took them to reach sampling height it is likely that many of these trees predated this fire and more likely established following the widespread 1719 fire. The next fire event recorded on Point Six burned in 1816 and scarred nearly every tree we sampled in the stand (Figure 5a,b). This fire burned during a year of near-normal PDSI of 0.3, but it was surrounded before and after by severe drought years (PDSI in 1815 = –3.0 and 1817 = –3.5, Figure 3c). An establishment pulse of both whitebark pine

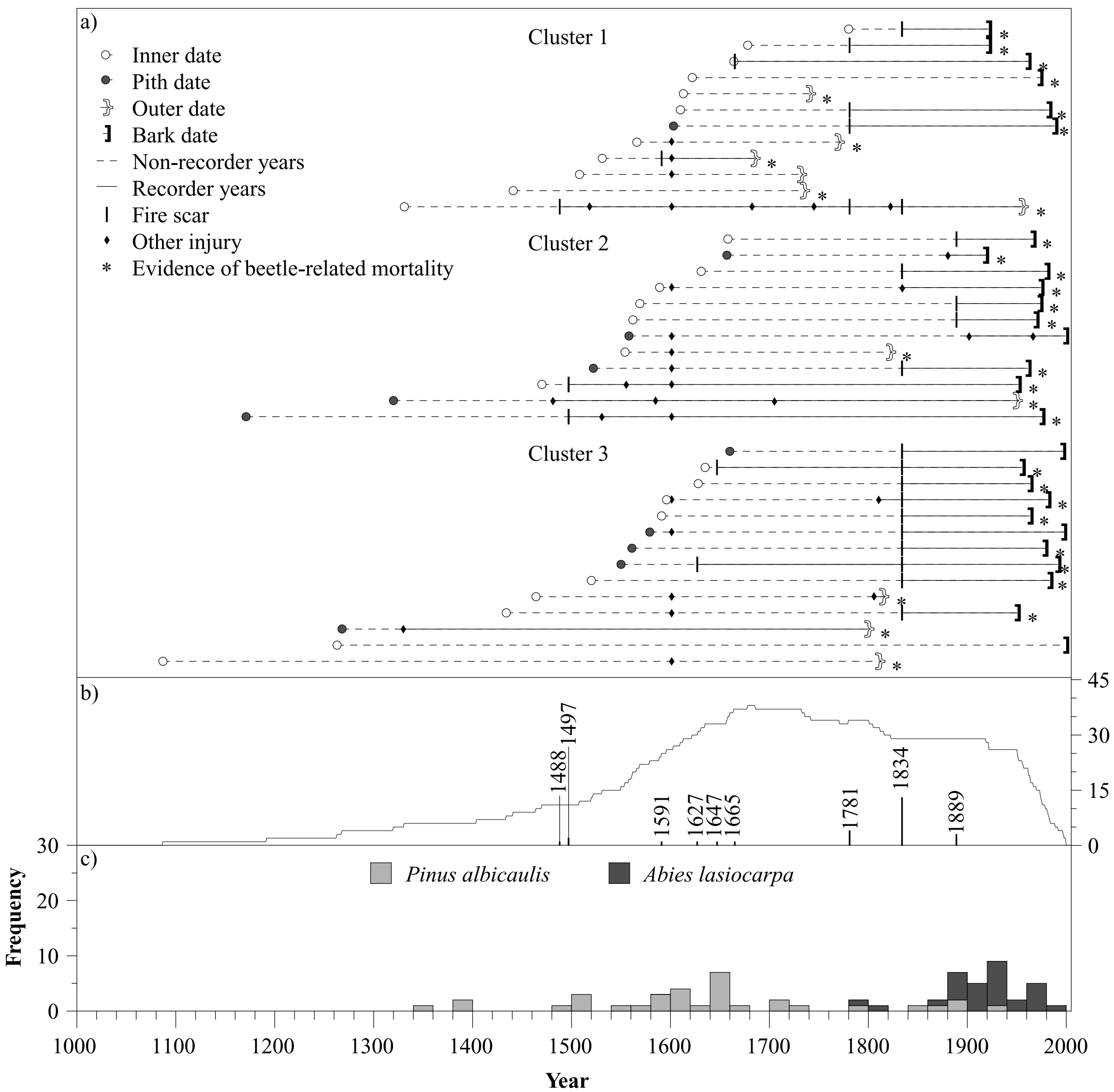

FIGURE 4. The a) fire history, b) fire history sample depth and master fire chronology, and c) age structure for Mineral Peak. The fire-scarred samples are grouped by clusters as shown in Figure 1 to emphasize the spatial variability exhibited by fires at this site.

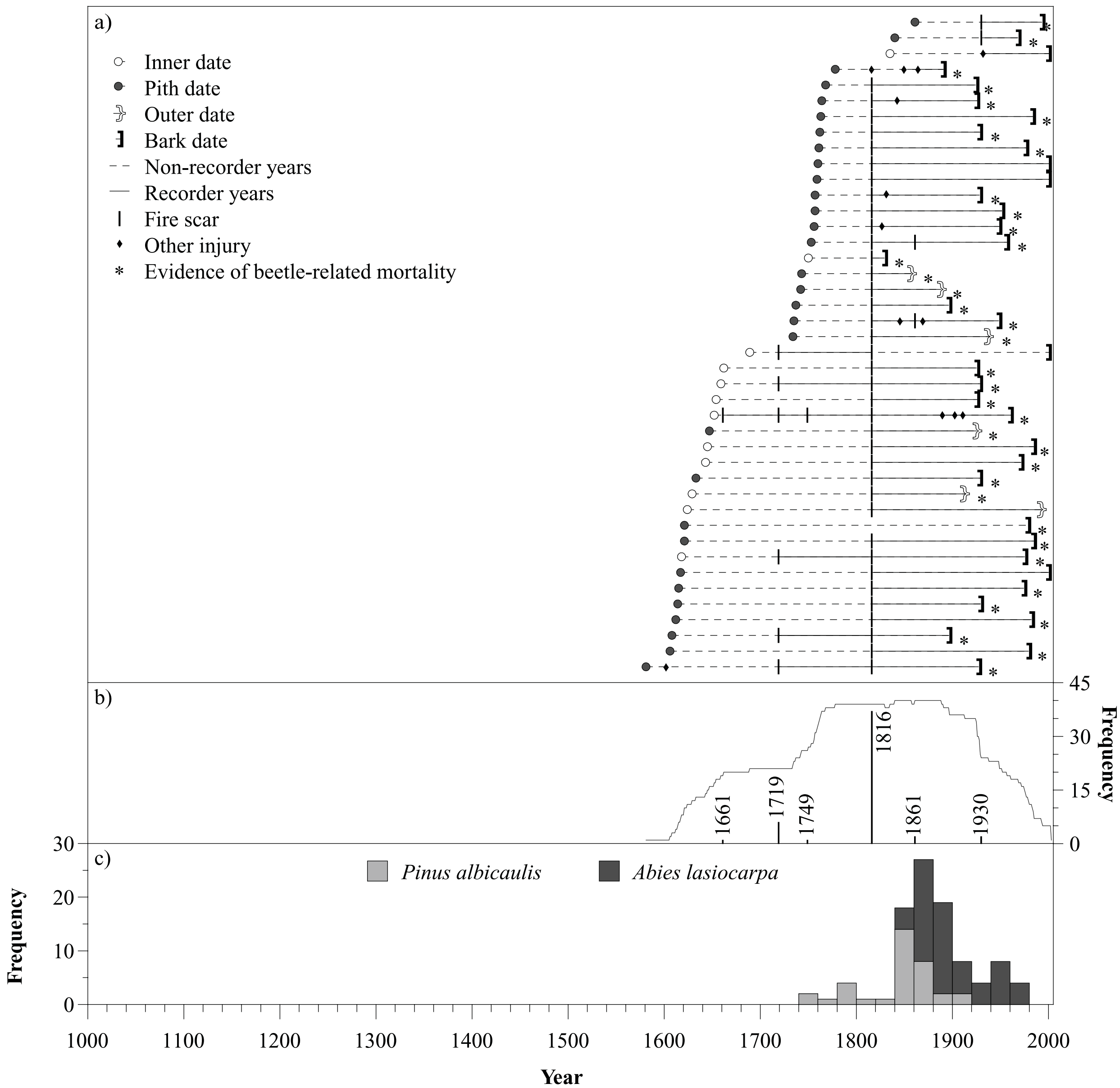

FIGURE 5. The a) fire history, b) fire history sample depth and master fire chronology, and c) age structure for Point Six.

and subalpine fir is evident in the age-structure plots following this fire, with establishment rates of both species declining in following decades. Apparently small fires scarred 2 trees each in 1861 and 1930.

The earliest evidence of mountain pine beetle activity on Point Six occurred soon after the 1816 fire, with several of the fire-scarred samples with outer rings in the mid- to late-1800s displaying blue stain fungus in their sapwood and j-shaped galleries on their outer rings. Two other periods of extensive mountain pine beetle-related mortality occurred during the 1930s and 1980s (Figure 5a). Of all of the fire-scarred samples taken from dead trees on Point Six, only 1 lacked clear evidence of beetle-related mortality.

FIRE–CLIMATE RELATIONSHIPS

The graphs of drought conditions relative to individual fire years showed no obvious or consistent relationship (Figure 3a,b,c). Some fires burned during years of severe drought (1719 on Point Six, 1889 on Mineral Peak), while the fires recorded by the largest number of trees at each site burned during nearly average moisture conditions (1754 on Morrell Mountain, 1816 on Point Six, 1834 on Mineral Peak). We therefore approached the results of the SEA cautiously. According to our SEA, significantly ($P < 0.01$) wet conditions preceded fires by 4 y (Figure 3d). No other years were significant in the remainder of the 11-y window, although the mean PDSI was generally below average for the 5 years surrounding fires.

Discussion

THE HISTORICAL ROLE OF FIRE IN WHITEBARK PINE FORESTS

Fire played an important role in the development of whitebark pine forests at all 3 sites over the past several centuries, as has consistently been observed in other whitebark pine ecosystems (Arno, 2001). The fire-history and age-structure data describe forests that developed in the context of mixed-severity fire regimes (Arno, Parsons & Keane, 2000), with fires of variable size and severity that resulted in at least 1 post-fire cohort at each site as well as periods of relatively uneven age structure. The patterns of forest development that followed these fires generally agree with previous research in whitebark pine forests (Campbell & Antos, 2003; Kipfmueller & Kupfer, 2005). The oldest trees sampled at each site were consistently whitebark pine, with additional post-disturbance cohorts on Mineral Peak and Point Six. Each site experienced at least 1 widespread fire after which subalpine fir began establishing on the site and eventually dominated the younger age classes.

We found fires to be more frequent at our sites than most other studies conducted in whitebark pine forests (Arno, 1976; Romme, 1982; Arno & Petersen, 1983; Barrett, 1994; Murray, Bunting & Morgan, 1998), including several sites within *ca* 50 km of Morrell Mountain (Keane, Morgan & Menakis, 1994). Additionally, the large number of fires that were recorded by only a single tree at our study sites suggests that it is likely that other fires may have burned at these sites that we did not observe in our fire scar record and that we may in fact be under-representing fire frequency at our sites (Baker & Ehle, 2001). Only one other study reported similar mean fire return intervals at the stand scale in whitebark pine forests (13–46 y between fires) (Morgan & Bunting, 1990). This is likely a reflection of the fine scales and higher resolution of our study and that of Morgan and Bunting (1990). This study and that of Morgan and Bunting (1990) collected numerous fire-scarred cross sections within each stand studied and used crossdating to obtain absolute calendar dates for each fire. In contrast, several of the other studies relied on temporally coarser age-structure data to identify past fires that were supplemented with relatively few fire-scarred samples that were not crossdated. Finer spatial and temporal sampling methods may be required to capture the complexity of mixed-severity fire regimes (Fulé *et al.*, 2003). However, it is important to note that the small number of fire-scarred samples used in many of these studies is due to the small number of trees that survived the severe fires that dominated the areas studied. The very presence of large numbers of fire-scarred whitebark pine in our sites highlights the variability of fire regimes in forests containing whitebark pine.

Topography also plays an important role in creating local variations in fire activity (*e.g.*, Hadley, 1994; Heyerdahl, Brubaker & Agee, 2001; Grissino-Mayer *et al.*, 2004) and may partly explain the more frequent fires that occurred at our sites. The stands we studied were located on the upper south- and western-facing slopes of the highest peaks in the immediate area. Steep, exposed aspects such as these receive more direct radiation during the warmest part of the day, which results in increased fuel dessication and probability of fire (Rollins, Morgan & Swetnam, 2002). Additionally, these "islands" of higher elevation may have acted as focal points for lightning strikes, leading to more frequent fires (Kilinc & Beringer, 2007). Such topographic influence on lightning ignitions and fire frequency has been observed in the fire regimes of the "Sky Islands" of southern Arizona (Grissino-Mayer & Fritts, 1995; Grissino-Mayer, Baisan & Swetnam, 1996), the kipuka of central Oregon (Arabas, Hadley & Larson, 2006), the lake islands of Québec (Bergeron, 1991), and convex landforms in the boreal forests of Sweden (Zackrisson, 1977), all of which experienced more frequent fire than the surrounding lower forests.

An important question to consider here, however, is what was the ecological significance of these fires? The fires responsible for the short intervals recorded at our sites left few fire scars and little to no evidence in the age structure of the stand or the timing of subalpine fir establishment at each site, suggesting that they were likely small and low severity. In fact, the site with the most frequent fires (Morrell Mountain) showed the earliest and most abundant establishment of subalpine fir. This contrasts with what has been found in some whitebark pine stands, where frequent surface fires reduced the presence of fire-intolerant tree species such as subalpine fir (*cf.*, Arno, 2001). Rather, it seems that the more widespread but less frequent fires recorded at each site may have had a greater effect on the composition and structure of each stand. At all 3 sites, subalpine fir established within 2 decades after these fires, suggesting that subalpine fir seed source was available at each site and that the environmental conditions were amenable to subalpine fir regeneration (Agee & Smith, 1984; Little, Peterson & Conquest, 1994). The establishment of shade-tolerant species such as subalpine fir and Engelmann spruce soon after fires and at the same time or soon after pioneer species such as whitebark pine has been described at several sites in the Northern Rockies (Johnson, Miyanishi & Kleb, 1994; Campbell & Antos, 2003; Kipfmueller & Kupfer, 2005). If subalpine fir had similarly established following the stand-initiating fires on Morrell Mountain and Point Six and earlier fires on Mineral Peak, then it is possible that the current abundance of subalpine fir at these sites is not unprecedented, even at these sites that experienced relatively frequent fires. Instead, the lack of evidence for subalpine fir earlier in the histories of these sites may reflect its relatively short lifespan (*ca* 200 y) (Alexander, Shearer & Shepperd, 1990) and the loss of evidence of older fir trees that died, decomposed, or burned in subsequent fires. Additional chronosequence studies similar to that employed by Campbell and Antos (2003) may help elucidate this question about whitebark pine forests in the Northern Rockies.

Variations in fire regimes of whitebark pine forests

The historical fire regimes of our study sites align well with the description of mixed-severity fire regimes (Arno, Parsons & Keane, 2000), but differences in fire frequency and fire severity at our sites highlight the diversity of disturbance regimes grouped into this broadly defined classification. The differences in fire frequency at our sites may be the product of both site characteristics and the legacy of previous fires. The vegetation at Point Six was more continuous than the vegetation at Morrell Mountain, which itself was more continuous than the highly dissected stand on Mineral Peak. Fire spread is strongly affected by fuel continuity (Miller & Urban, 2000), and the relatively continuous vegetation cover at Point Six likely allowed fires to spread throughout the stand, whereas fire spread was limited among the dissected tree clusters on Mineral Peak (*cf.*, Arabas, Hadley & Larson, 2006). The widespread fires on Point Six may have uniformly reduced fuels throughout the stand and thereby limited subsequent fire activity until a fuels complex capable of carrying a surface fire developed again. In contrast, the patchy fires on Mineral Peak and Morrell Mountain likely had little effect on the total abundance of fuels at these sites or the potential for later small fires to occur (*cf.*, Swetnam, 1993; Miller & Urban, 2000; Swetnam & Baisan, 2003). Additionally, our data support the concept that fuels accumulation may be an important factor that affects fire activity in whitebark pine forests (Morgan & Bunting, 1990; Morgan *et al.*, 1994), even though this may not be the case in other subalpine forests (Fryer & Johnson, 1988; Bessie & Johnson, 1995). Point Six received the most annual precipitation and had the most continuous forest among the 3 sites, suggesting that fuels could accumulate faster there than on the drier, more open stands on Morrell Mountain and Mineral Peak. This more rapid fuels development may be partly responsible for the more frequent widespread fires on Point Six than the other 2 sites.

The role of disturbances other than fire in whitebark pine forests

In addition to fires, blister rust infections and mountain pine beetles affected the trees at our sites. Blister rust is a non-native invasive species that infects five-needle pines and can result in the eventual death of trees of all ages (Kinloch, 2003). Since its introduction to North America in the early 1900s, blister rust has spread nearly throughout the range of whitebark pine (McDonald & Hoff, 2001), with high levels of rust-related mortality in the northern parts of the species range (Smith *et al.*, 2008). Blister rust was ubiquitous at our sites, but relatively few trees appeared to have died due to infection. Instead, the native mountain pine beetle was the dominant mortality agent for whitebark pine over the recent centuries at our sites. While most beetle-related mortality generally aligned within known beetle outbreaks in the 1930s and 1980s (Bartos & Gibson, 1990; Kipfmueller, Swetnam & Morgan, 2002), other mortality events occurred sporadically over the reconstructed history of all 3 sites. While some research has shown mountain pine beetle outbreaks to increase fuel levels and the subsequent occurrence and severity of fires in lodgepole pine forests (Geiszler *et al.*, 1980; McCullough, Werner & Neumann, 1998; Turner, Romme & Gardner, 1999), the lack of widespread fires after the early 20th century mountain pine beetle–caused mortality episodes at our sites suggest that this relationship may either not hold true in these whitebark pine stands or take longer to occur than the *ca* 70 y since these outbreaks. However, it is important to note that several trees indicated beetle-related mortality on Mineral Peak directly before the widespread 1834 fire at that site.

Interestingly, we observed blue stain fungus in the sapwood and j-shaped galleries on the boles of several whitebark pines on Morrell Mountain and Mineral Peak that died in the early 1800s. No published tree-ring–based reconstruction of mountain pine beetle activity extends this far into the past, and these observations, if replicable across other sites, indicate the potential of using remnant whitebark pines to reconstruct past episodes of mountain pine beetle activity that may have operated on landscape- to regional-scales similar to the 1930s and 1980s outbreaks. Additionally, the potential influence of beetle-driven stand dynamics on the radial growth patterns in surviving whitebark pine, if coupled with analyses of growth patterns in non-host tree species (*sensu* Swetnam & Lynch, 1989; Veblen *et al.*, 1991), may prove valuable in exploring the historical importance and ecological effects of mountain pine beetles in whitebark pine forests.

Fire–climate relationships in whitebark pine forests

The lack of a consistent pattern between drought and fire in both our analyses of individual fire years and the SEA reflects the scale-dependent relationship between fire and climate. While drought is one of the primary drivers of fire activity, individual droughts vary considerably in length, from seasonal to multi-decadal, and in severity (Karl & Koscielny, 1982; Cook *et al.*, 1999). Tree-ring width often reflects average growing conditions over the entire growing season, which limits the ability of tree-ring–based climate reconstructions to capture very short drought events or the full amplitude of extreme droughts (Fritts, 1976). In subalpine and boreal forests, extreme fire conditions can develop during long-term droughts driven by regional- and hemispheric-scale teleconnections (McCabe, Palecki & Betancourt, 2004) or short-term droughts driven by persistent high-pressure weather systems (Bessie & Johnson, 1995). The PDSI reconstruction used in our analyses was for average summer drought conditions, yet early and late-season droughts can occur even when the mean conditions for the summer are near normal (Heinselman, 1996). Additionally, the PDSI reconstruction represents a regional drought signal, yet precipitation is a patchy phenomenon across the landscape (Mock, 1996). It is therefore possible that the spatial and temporal resolution of the reconstructed PDSI were insufficient to identify the local conditions under which the fires recorded at these sites burned. Additionally, we can offer no reasonable ecological mechanism that would link significantly wet conditions 4 y prior to the fire events at our sites as indicated by our SEA. Instead, we suggest this ecologically spurious result is the product of the extremely wet conditions that occurred 4 y prior to 2 fires that burned on Morrell Mountain (1754 and 1843) and highlights the importance of using caution in the application of this method in studies based on relatively few fire events.

The lack of a single year with synchronous fires over the multi-century histories of these stands highlights the complex conditions required for the occurrence of a fire. Even when climate conditions are conducive to fire occurrence, these conditions must coincide with the right short-term weather patterns and fuels for a fire to ignite and spread. This can result in relatively weak fire–climate relationships at the stand level in subalpine settings (Gavin *et al.*, 2006), even where larger-scale analyses may find stronger relationships (*e.g.*, Kitzberger *et al.*, 2007; Heyerdahl, Morgan & Riser, 2008). This disconnect has important implications for whitebark pine management and restoration that aims to emulate natural processes, as these efforts often occur at the stand level due to economic and logistical limitations (Keane & Arno, 2001). While the recent development of fire climatology based on low-frequency variability in climate offers tremendous opportunities to better forecast fire seasons (Swetnam & Anderson, 2008), research must now focus on how to translate these findings to site-specific effects so as to inform management at the local scale.

The effects of fire suppression on whitebark pine forests

The influence of fire suppression on the forest systems of western North America is a pervasive topic in modern forest management (Arno, 1996; Zimmerman, 2003; Stephens & Ruth, 2005) and is particularly salient to the management of whitebark pine. It is commonly stated that fire suppression has exacerbated structural changes and has advanced succession in whitebark pine forests throughout its seral distribution (Keane & Arno, 1993; Keane, 2001; Tomback, Arno & Keane, 2001a). At our sites, fire suppression efforts likely limited the spread of some fires and extinguished others that may have grown from spot ignitions during the late 20th century (USDA Lolo National Forest, 2003a,b), yet subalpine fir began establishing at these sites well before fire suppression was effective in these areas (*ca* 1940, Pyne, 1982). While it is impossible to determine the potential effects of fires that were suppressed (Brown, 1994), the fires that had the greatest effects on stand structure and composition at these sites were the widespread fires that occurred relatively infrequently. Based on the frequencies of these widespread fires, only the stand on Point Six has exceeded the historical interval between events. The stand on Morrell Mountain is nearing its maximum interval between widespread fires, and Mineral Peak is well within its historical range of variability. All of these sites now contain abundant ladder fuels and coarse woody debris from the mountain pine beetle outbreaks and are potentially set to support stand-replacing fires. This suggests that despite the presence of late-successional species in these stands, the time since the last widespread fire, and hence age structure, are within the historical range of variability for Mineral Peak and Morrell Mountain. The forest on Point Six may be outside of its historical range of variability, in part due to fire suppression according to Forest Service Records.

Conclusion

Changes in fire severity and forest structure induced by fire suppression are readily apparent in many fire-dependent ecosystems, but these changes are less evident in the mixed-severity fire regimes of the Northern Rockies. Our research identified important differences between the fire regimes of 3 different whitebark pine forests that all occurred in areas assigned to the broadly defined mixed-severity fire regime type. The forest on one of the sites, Point Six, is potentially outside of its historical range of variability and provides a suitable site for restoration. The forests on Morrell Mountain and Mineral Peak remain within their historical ranges variability and do not warrant restoration at this time. These differences were likely the result of the distinct biophysical settings of each forest. Site-specific data similar to that provided in this study are necessary to help develop ecologically sound management and restoration efforts in whitebark pine forests.

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