



Climatic and structural comparison of yellow pine and mixed-conifer forests in northern Baja California (México) and the eastern Sierra Nevada (California, USA)



Mila Dunbar-Irwin^a, Hugh Safford^{b,c,*}

^a Department of Plant Sciences, University of California, Davis, CA 95616, USA

^b USDA Forest Service, Pacific Southwest Region, Vallejo, CA 94592, USA

^c Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

ARTICLE INFO

Article history:

Received 31 August 2015

Received in revised form 22 December 2015

Accepted 24 December 2015

Available online 7 January 2016

Keywords:

Jeffrey pine

Fire history

Dry conifer forest

Sierra de San Pedro Mártir

Baja California

Sierra Nevada

ABSTRACT

Effects of fire suppression policies on semi-arid yellow pine and mixed conifer (YPMC) forests in the western US have been well documented, and restoration of forest structure and natural fire regimes are high management priorities to ensure the health and resilience of such forests. However, determining reference conditions for ecological restoration is difficult due to the near absence of undegraded forests in the US. YPMC forests of the Sierra de San Pedro Mártir (SSPM) in northern Baja California, Mexico, are highly similar to forests of the Eastern Sierra Nevada, California, USA, have experienced little to no logging, and until relatively recently supported a natural fire regime. As such, these Mexican YPMC forests are thought by many to represent reference ecosystems for restoration and resource and fire management in the US. However, to this point there has been no direct climatic comparison to determine to what extent SSPM is validly compared to California YPMC sites, nor a direct statistical comparison of forest conditions to see in what ways northern California forests might differ from SSPM. We compared climatic data from SSPM with 17 meteorological stations in the range of Jeffrey pine in Alta and Baja California. Based on this comparison, we determine that SSPM clearly belongs to the general class of Jeffrey pine-dominated YPMC forests found along the eastern edge of the California Floristic Province. We used field sampling to measure forest structure, fuels, and vegetation and ground cover in SSPM and in multiple National Forests along the eastern slope of the Sierra Nevada. Live tree density was nearly twice as high in the eastern Sierra Nevada as in SSPM, and dead tree density was 2.6 times higher. Basal area was about 30% higher in the eastern Sierra Nevada, even though average tree size was larger in SSPM. Fuel loads and coarse woody debris were very similar between the two sites, and fine fuels (1-hour fuels) were actually higher in SSPM. Logging and fire suppression have resulted in denser YPMC forests dominated by smaller trees in the US, but our results suggest that fire suppression in SSPM over the last 30 years has increased fuel loads. Nonetheless, the Baja California forests still retain an overstorey structure created and maintained by centuries of frequent fire. This study provides important reference information for the management of eastern Sierra Nevada forests, and indicates that continued full fire suppression in SSPM carries significant ecological risks.

Published by Elsevier B.V.

1. Introduction

Most semi-arid forests in the western United States have been greatly affected by human management over the last 150 years, including resource extraction (timber harvest, grazing, mining,

hunting), fire exclusion, and land development (Agee, 1993; Sugihara et al., 2006; Barbour et al., 2007). Timber harvest and fire exclusion have had the most significant broad-scale impact on the forests themselves, with the former removing most large trees and the latter removing the most important ecological disturbance process. In concert, logging and fire exclusion have notably simplified forest structure and had major impacts on forest species composition and ecological function (Parsons and DeBenedetti, 1979; Skinner and Chang, 1996; Sugihara et al., 2006; Mallek et al., 2013; Dolanc et al., 2014).

* Corresponding author at: USDA Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA 94592, USA.

E-mail addresses: mdunbarirwin@gmail.com (M. Dunbar-Irwin), hughsafford@fs.fed.us (H. Safford).

In California, USA (hereafter “Alta California”), outcomes of past Euroamerican management have included forest stand densification and an increase in surface and ladder fuels (Sugihara et al., 2006). Successful fire exclusion policies implemented through most of the 20th century have resulted in the virtual absence of fire from large landscapes of yellow pine (*Pinus ponderosa*, *P. jeffreyi*) and mixed-conifer forest ecosystems (“YPMC” forests), ecosystems that experienced highly frequent, mostly low-severity fires before American settlement of Alta California began in the 1850s (Agee, 1993; Sugihara et al., 2006; Mallek et al., 2013; Safford and Stevens, in press). Many of these forests have now been subject to a 100 year fire-free period (Safford and Van de Water, 2014; Steel et al., 2015), which research suggests is unprecedented in at least the past 2000 years (Swetnam, 1993; Marlon et al., 2012). It is now well understood that the long-term lack of fire from YPMC forests is a major ecological perturbation in its own right. Recent increases in burned area, fire size, and fire severity in YPMC forests in some parts of Alta California and neighboring southwestern states appear to be the result of interactions between increasing fuels due to long-term fire suppression and the warming climate (Miller et al., 2009; Dillon et al., 2011; Miller and Safford, 2012; Mallek et al., 2013; Steel et al., 2015).

There is broad agreement that ecological restoration of western US forests should be a major focus of the federal resource agencies and other entities that manage large landscapes (Graber, 2003; USDA, 2006; SSP, 2010). At the same time, it is recognized that restoration is greatly complicated by the degraded condition of many western US forests, as well as by shifting environmental baselines caused by, among other things, global warming (Cole and Yung, 2010; Safford et al., 2012). Such issues are complications because ecological restoration traditionally relies on the identification of an undegraded reference state to guide management and to permit assessment of restoration progress (Egan and Howell, 2001). The degraded state of many modern western US forests means that contemporary reference landscapes are difficult to impossible to identify, which has resulted in a major focus on historical reference conditions (Morgan et al., 1994; Swetnam et al., 1999; Landres et al., 1999). However, the growing recognition that the changing climate, among other things, is altering the fundamental ecological conditions within which ecosystems exist is leading to fears – if sometimes exaggerated – that historical reference conditions may not provide sensible guidance if long-term sustainability is the ultimate management goal (Millar et al., 2007; Safford et al., 2012).

For researchers and managers in the southwestern US and Alta California, the less degraded condition of many nearby Mexican highland ecosystems has led to a developing recognition that the gold mine of contemporary reference landscapes may lie south of the border rather than north of it (Stephens and Fulé, 2005). Aldo Leopold may have been the first to appreciate the heuristic value of undegraded wildlands in northern Mexico to US resource management (Leopold, 1937; Leopold et al., 1947). Forest researchers in Arizona and New Mexico followed Leopold's lead and very important insights have been derived from comparative studies of southwestern US forests (mostly logged and fire-suppressed) and similar but less degraded forests in the Sierra Madre Occidental of northwestern mainland Mexico (e.g., Fulé and Covington, 1994, 1998; Meunier et al., 2014).

For Alta California, which mostly supports a different precipitation regime than the rest of the southwestern US, similarly less-degraded highland forests are found at the southern end of the California Floristic Province, in Baja California Norte. The 73,000 ha Sierra de San Pedro Mártir National Park (SSPM) is home to YPMC forests that have suffered neither long-term fire exclusion nor timber harvesting. Many researchers have recognized the

floristic and ecological similarities between the SSPM forests and semi-arid YPMC forests in Alta California, and efforts have been made to draw management and restoration lessons from the conditions that exist in the SSPM. Scientific study in the SSPM has described, among other things, forest phytosociology (Peinado et al., 1997), phytogeography (Peinado et al., 1994a, 1994b), floristics (Passini et al., 1989; Thorne et al., 2010), forest structure and mortality (Stephens and Gill, 2005), fuel loads and snags (Stephens, 2004), post-fire regeneration (Stephens and Fry, 2005), spatial patterns of wildfire (Stephens et al., 2008), fire history (Minnich et al., 2000; Stephens et al., 2003; Evett et al., 2007a; Skinner et al., 2008), and forest disease (Maloney and Rizzo, 2002).

For US managers interested in YPMC forest and fire restoration in Alta California, these studies might potentially provide valuable reference information, however there are a few important limitations in this body of work. First of all, very few of the studies have carried out direct statistical comparisons between SSPM and Alta California forests. Exceptions include Savage (1997), who compared forest mortality after drought between SSPM and the San Bernardino Mountains in southern Alta California; and Fry et al. (2014), who compared spatial patterns in forest structure between two 4-ha stem-mapped plots in SSPM and two similar Jeffrey pine-mixed conifer plots in the southern Sierra Nevada, Alta California. Second, almost all of the detailed forest structural data we have from SSPM come from an array of permanent plots found in a small area of relatively homogenous terrain and forest; forest characteristics in different landscape positions and in other parts of SSPM have yet to be quantified through on-the-ground measurement. Third, to this point no one has carried out a rigorous comparative analysis of the climate of SSPM and the climates of YPMC sites in Alta California where SSPM-derived reference information might be applied. Without such an analysis, managers and restoration practitioners run the risk of employing SSPM reference conditions in locations where their use is not well justified.

The eastern slopes of the Sierra Nevada in Alta California support YPMC forests and landscapes that are remarkably similar to the SSPM (Fig. 1). Dominant tree species are mostly shared, the most common shrubs and herbs are congeners or conspecifics, geologic substrates are mostly granitic or metamorphic in both areas, and both are found on the continental margins of the North American Mediterranean climate zone, also known as the California Floristic Province. On the surface, the major differences appear to be the geographic location (SSPM is 500–1100 km to the south), and legacies of past and current human management, where most of the Sierra Nevada forests have experienced some level of timber harvest and a century or more of fire exclusion, and SSPM has not been logged and lacked effective fire suppression until the last three decades. However some authors have questioned whether climates are sufficiently similar between SSPM and Alta California sites to permit SSPM's use as a reference ecosystem (Keeley, 2006).

Because researchers have advocated use of SSPM reference information in YPMC forests in Alta California (e.g., Minnich et al., 1995, 2000; Stephens and Fulé, 2005), and because managers and restorationists in the eastern Sierra Nevada have already begun to use reference information from SSPM in resource management planning and project development (e.g., USDA, 2015), we resolved to carry out a study that directly compared forest structure and climate in the two areas. Our principal purposes were (1) to explore how, in the context of differing management histories, modern eastern Sierra Nevada YPMC forests compare structurally to similar forests in SSPM; and (2) to determine whether climates in the two areas (and other YPMC areas in Alta California with Jeffrey pine) are sufficiently similar to justify the application of SSPM reference information to restoration projects in the eastern Sierra Nevada.



Fig. 1. General aspect, Jeffrey pine forest in three locations in the eastern Sierra Nevada, Alta California, and the Sierra de San Pedro Mártir, Mexico.

2. Study areas

2.1. Sierra de San Pedro Mártir National Park, Baja California, Mexico

The Sierra de San Pedro Mártir (SSPM) National Park (31°37'N, 115°59'W) is located approximately 250 km south southeast of San Diego in northern Baja California, Mexico (Fig. 2). The SSPM forms part of the Peninsular Mountain Range that begins in southern Alta California. Like most of Alta California, the northern Baja California forests are within the North American Mediterranean climate zone (a.k.a California Floristic Province), but at its southern end (Fig. 2). Winters are cool and moist, and summers are warm and dry. January mean minimum temperatures at 2080 m (near the lowest elevation at which continuous conifer forest grows) are about -1.0° , and July mean maximum temperatures are about 24.9°C ; mean annual precipitation is about 570 mm (Table 1; Minnich et al., 2000), most of which falls as snow in the winter months (SSPM receives 10–20% of its precipitation in the summer from monsoonal influences).

The highlands of the SSPM support conifer and oak forests whose dominant species are all shared with drier yellow pine and mixed conifer forests in Alta California (Passini et al., 1989; Delgadillo, 2004): Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), lodgepole pine (*Pinus contorta*), single-leaf pinyon pine (*Pinus monophylla*), quaking aspen (*Populus tremuloides*), and canyon live oak (*Quercus chrysolepis*); incense cedar (*Calocedrus decurrens*) is also present in SSPM but it is relatively rare. There is also a minor component of other oak (*Quercus* spp.) and conifer species (*Cupressus montana*, *Pinus quadrifolia*) that are either Baja endemics or shared with lower

forest types in southern Alta California and Arizona (Delgadillo, 2004). Above 1800 m, most forests fall within the general definition of YPMC forest, with many sites dominated completely by Jeffrey pine, others showing a mixture of species, and moister north slopes supporting stands dominated by white fir and sugar pine (Passini et al., 1989; Minnich and Vizcaino, 1998). The dominant genera of shrubs (e.g., *Ceanothus*, *Arctostaphylos*, *Artemisia*, *Ericameria*, *Salvia*) and herbs are also shared with YPMC forests in Alta California, and many individual species are shared as well (Delgadillo, 2004; Thorne et al., 2010). Soils have only been broadly classified in the SSPM, but the most common parent materials are Late Mesozoic granitic rocks with some areas of high-grade metamorphics (Stephens and Gill, 2005).

Limited fire suppression began in the SSPM in the 1970s. In the last two to three decades fire suppression has become steadily more effective and today almost all fire starts within the YPMC area are extinguished within one day of ignition (G. de León Giron, pers. comm.); in a typical year 7–15 fire ignitions are extinguished (H. Rivera, pers. comm.). Timber harvest has been essentially absent in SSPM, although a few localities at the parks boundaries have experienced incursions of illegal logging over the last century. As in much of Alta California, livestock grazing began centuries ago, and it continues today, with effects ranging from light to heavy, depending on the location and time of year (Minnich and Vizcaino, 1998).

2.2. Eastern Sierra Nevada, Alta California, USA

The Alta California sites chosen for this study fall within the drier eastern portion of the range of Jeffrey pine, which is distributed primarily along the continental margins of the North

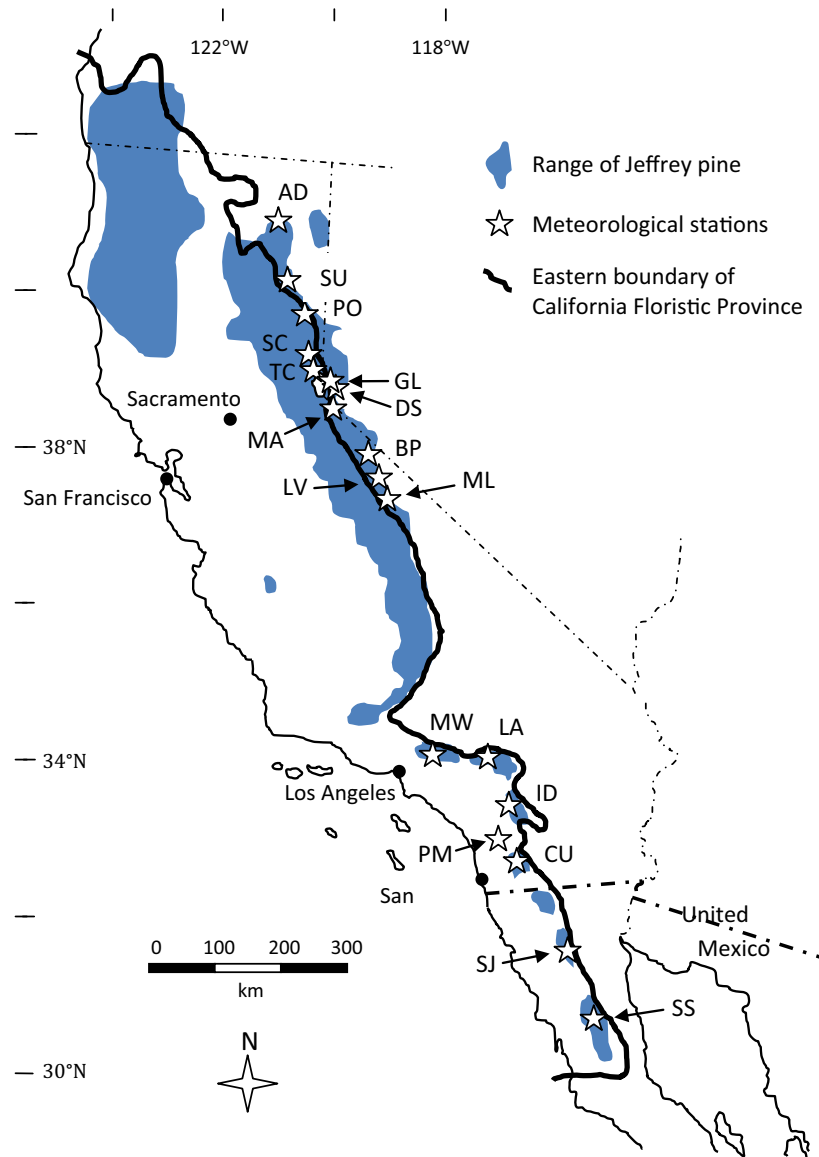


Fig. 2. Map of California Floristic Province (coincident with North American Mediterranean climate zone), the range of Jeffrey pine, and locations of meteorological stations used in the climate analysis.

American Mediterranean climate zone (Fig. 2). Except for a few plots near Antelope Lake on the Plumas National Forest, all of the Alta California sites are found east of the Sierra Nevada crest, from near Janesville, CA (40°17'N, 120°31'W) to Bishop, CA (37°21'N, 118°23'W); we refer to this area as the eastern Sierra Nevada (hereafter “ESN”). In Fig. 2, ESN plot locations stretch from between meteorological stations PO and SU in the north to ML in the south. The ESN sites support broadly similar climates to the Baja California sites, although all of them are cooler than the BC sites in winter, and most have less summertime rainfall (see climate analysis below). Substrates in the Alta California sites were all granitic in derivation (or, rarely, metamorphic), similar to the SSPM. ESN plots were mostly of lower elevation than the SSPM sites in order to compensate for the lower latitude position of the latter. Plots were located on the Plumas, Tahoe, Humboldt-Toiyabe, and Inyo National Forests, and the Lake Tahoe Basin Management Unit of the US Forest Service.

Like the SSPM, dominant tree species in the Alta California sites are Jeffrey pine, white fir, sugar pine, lodgepole pine, and quaking aspen; incense cedar is found in moister areas and single-leaf

pinyon in drier areas. In our ESN plots we also found western juniper (*Juniperus occidentalis*), and whitebark pine (*Pinus albicaulis*) on the Inyo National Forest.

All of our ESN plots fall in areas that were logged at some time in the past. Most sites were selectively cut in the late 1800s and/or early 1900s, but the Lake Tahoe Basin and most of the Plumas and Tahoe National Forest plots were clear cut in the late 1800s. Livestock grazing has been present in our ESN study area since the mid to late 1800s, and all of our plots except those on the Lake Tahoe Basin and the Inyo National Forest are found in active grazing allotments.

For the purposes of comparison between the US and Mexican sites, we report here only data from forests initially classified as yellow pine and mixed conifer (see below). The areas sampled on the Plumas and Tahoe National Forests include a YPMC forest type called “eastside pine” where Jeffrey and ponderosa pine can be co-dominant depending on the elevation. Though these two species are closely related and occasionally hybridize, Jeffrey pine is considered more tolerant of environmental stresses and replaces ponderosa pine between 1800 m and 2100 m elevation on the west

Table 1
Meteorological stations and data used in the climate analysis.

| Site | Code | Elevation (m) | Mean annual temp (°C) | January mean min temp (°C) | July mean max temp (°C) | Mean annual precip. (mm) | % precip. falling JJA | Inter-annual CV precip. | Years |
|-----------------------|------|---------------|-----------------------|----------------------------|-------------------------|--------------------------|-----------------------|-------------------------|--|
| Adin | AD | 1277 | 12.3 | −6.7 | 29.0 | 305 | 0.13 | 0.345 | 1977–1994 |
| Susanville (Airport) | SU | 1301 | 9.6 | −7.1 | 31.7 | 305 | 0.09 | 0.419 | 1975–1994 |
| Portola | PO | 1472 | 8.2 | −7.3 | 29.5 | 557 | 0.06 | 0.355 | 1977–1994 |
| Sagehen Creek | SC | 1935 | 5.0 | −10.7 | 25.7 | 854 | 0.05 | 0.390 | 1977–1994 |
| Tahoe City | TC | 1899 | 6.7 | −7.2 | 25.4 | 793 | 0.05 | 0.371 | 1977–1994 |
| Glenbrook | GL | 1951 | 8.1 | −4.6 | 25.5 | 415 | 0.08 | 0.455 | 1977–1994 |
| Daggett Summit | DS | 2234 | 5.9 | −6.3 | 23.8 | 609 | 0.09 | 0.369 | 1989–1998 |
| Markleeville | MA | 1689 | 8.0 | −7.3 | 29.0 | 575 | 0.08 | 0.339 | 1991–2000 |
| Bridgeport | BR | 1941 | 6.4 | −13.3 | 29.0 | 230 | 0.18 | 0.514 | 1977–1994 |
| Lee Vining | LV | 2073 | 9.0 | −7.0 | 28.5 | 366 | 0.10 | 0.482 | 1989–1998 |
| Mammoth Lakes | ML | 2400 | 5.8 | −8.1 | 25.4 | 582 | 0.07 | 0.351 | 1994–2003 |
| Mt Wilson | MW | 1740 | 13.9 | 3.2 | 27.9 | 1114 | 0.02 | 0.498 | 1977–1994 |
| Lake Arrowhead | LA | 1594 | 11.0 | −1.8 | 27.3 | 1113 | 0.02 | 0.529 | 1977–1994 |
| Idyllwild | ID | 1646 | 11.5 | −2.2 | 28.0 | 753 | 0.07 | 0.454 | 1977–1994 |
| Palomar Mtn | PM | 1707 | 13.1 | 1.6 | 28.8 | 766 | 0.06 | 0.548 | 1977–1994 |
| Cuyamaca | CU | 1423 | 11.5 | −1.8 | 28.4 | 836 | 0.05 | 0.501 | 1977–1994 |
| Sierra Juarez | SJ | 1580 | 11.7 | −1.1 | 28.9 | 566 | 0.21 | 0.389 | 1976–1986 |
| SSPM | SS | 2080 | 10.9 | −1.0 | 24.9 | 569 | 0.14 | 0.520 | 1977–1979, 1984, 1989–1992, 1993–1994 ^a |
| Overall averages | | 1775 | 9.4 | −4.9 | 27.6 | 628 | 0.09 | 0.435 | |
| Overall std deviation | | | 2.7 | 4.3 | 2.0 | 257 | 0.05 | 0.073 | |

^a 1989–1992 data from Minnich et al. (2000).

slope of the Sierra Nevada (Haller, 1959; Barbour and Minnich, 2000; Safford and Stevens, in press), and essentially entirely replaces ponderosa pine on the east slope. Sierra Nevada plots in this study ranged from 1513 m to 2626 m and were almost entirely on the east slope (some plots on the Plumas National Forest were just west of the crest, near Antelope Lake), hence nearly all of the yellow pines we sampled were Jeffrey pine. Ponderosa pine does not occur in Baja California.

3. Methods

3.1. Climate data

Temperature and precipitation data were analyzed from 16 meteorological (“met”) stations in Alta California, and 2 met stations in Baja California, including SSPM and a site in the Sierra Juarez. We did not include met stations from northwest California as Jeffrey pine in this part of California is almost entirely found on azonal sites with soils derived from ultramafic rocks. Site characteristics are provided in Table 1, and locations are shown in Fig. 2. All met stations were found within or at the edge of Jeffrey pine-dominated forest types. Alta California data came from the COOP meteorological station data made available by the Western Regional Climate Center, at <http://www.wrcc.dri.edu/summary/Climsmnca.html>, <http://www.wrcc.dri.edu/summary/Climsmcca.html>, and <http://www.wrcc.dri.edu/summary/Climsmsca.html>. We focused on data from 1977 to 1994, as this period included the relatively sparse records we have from the Baja California sites, but a few stations include data from years outside this period due to periods of met station inoperability.

Temperature data for SSPM came from Meteorological Station #2105 of the Comisión Nacional del Agua (CONAGUA; data from the Base de Datos Climáticos del Noroeste de México at: <http://peac-bc.cicese.mx/datosclim/dcbc.php#>) at 2080 m elevation (Lat: 30°58′00″; Long: 115°34′54″). This station was located at the CONAFOR (Comisión Nacional Forestal) fire brigade barracks, which is near the lower edge of Jeffrey pine distribution in SSPM. January mean minima were calculated from the years

1977–1980, and 1984–1985 (all other years were missing all or almost all daily data); July mean maxima were calculated from the years 1977–1985 and 1991–1997. Precipitation data came from Met Station 2105 for the years 1977–1979, 1984, and 1993–1994. Station 2105 was often out of service and these were the years with one month or less of missing data. For October 1977 we replaced the missing data with the long-term mean for October from 1978 to 1997. For December 1984 we replaced the missing data using the regression between Met Station 2105 and the station at Santa Cruz (CONAGUA #2060), which is 11 km SSE of #2105 (regression $R^2 = 0.75$). Precipitation data for 1989–1992 were obtained from Minnich et al. (2000; Minnich’s station was close to station 2105). The mean precipitation value in Table 1 is the average of station 2105 and Minnich’s data. We did not directly use data from the Mexican National Astronomical Observatory met station (“MNAO”, 2800 m elevation; data online at <http://www.astrossp.unam.mx/weather15/>) in our analysis because the station is at a higher elevation than our plots, it came on line only relatively recently, and until 2014 did not measure snowfall, which comprises most of the precipitation in SSPM.

The second Baja California site was CONAGUA’s Met Station #2066, in the Sierra Juarez (Lat: 32°00′13″, Long: 115°56′54″); we accessed data from 1977 to 1986 (the station went out of service in 1986), also from <http://peac-bc.cicese.mx/datosclim/dcbc.php#>. This station was located at the ejido at the Arroyo del Sauzal, also at the lower edge of Jeffrey pine distribution in the Sierra Juarez. For all met stations we also calculated the proportion of annual precipitation that falls during the summer months of June–August, to gauge the importance of monsoonal precipitation at each site. Finally, we calculated the interannual coefficient of variation (CV; the standard deviation divided by the mean) for precipitation for each met station for the period of record.

Statistical ordination of climate variables (mean annual temperature, January mean minimum temperature, July mean maximum temperature, annual precipitation, interannual CV for precipitation, and proportion of annual precipitation falling June through August) was carried out using nonmetric multidimensional scaling (NMS) in PC-ORD 6, run on autopilot using Relative Euclidean dis-

tance (since there were negative numbers in the dataset). Based on measures of ordination stress (McCune and Grace, 2002), we ran the NMS for two dimensions. We also carried out correlations between the meteorological variables and the ordination axes. PC-ORD 6 was also used to carry out a cluster analysis of the 18 sites based on the same climate variables, also using Relative Euclidean distance, with the group average linkage method.

3.2. Fire data

We assembled data on time since last fire (TSLF) for each sampled site to permit assessment of whether differences between our study areas might be driven partly by fire history. For ESN, we overlaid our plot locations with the US Forest Service Fire Return Interval Departure (FRID) geodatabase (<http://www.fs.usda.gov/main/r5/landmanagement/gis>; Safford and Van de Water, 2014), version 2013, which provides annually updated TSLF data for all Forest Service lands in California.

For SSPM, we used two sources. First, we obtained fire perimeters from a LANDSAT-based study of fire severity in SSPM since 1984 (Rivera et al., in press) and overlaid those fires with our plot locations (there were only four intersections, as very few fires occur on the SSPM plateau anymore due to fire exclusion policies of the Mexican Park Service). Second, we digitized the dated fire perimeters from 1925 to 1991 found in Minnich et al. (2000; we were not able to obtain the original GIS data) and overlaid the resulting map with the SSPM plot locations. Note that the Minnich et al. (2000) data were organized in classes of five to six years, so we were only rarely able to assign exact fire years.

3.3. Field data collection

For both study areas, plots were selected using a stratified random sampling method on vegetation maps produced by the US Forest Service Remote Sensing Laboratory in Sacramento, CA. There were 14 vegetation classes for SSPM and 8 classes for ESN. Vegetation classes were delineated first by dominant canopy species and then further divided by average diameter of the canopy trees in the stand. Potential sampling points were randomly located using Arc-GIS in polygons identified as either Jeffrey pine, “eastside pine” (mix of Jeffrey and ponderosa pine), or mixed conifer. Plots to be sampled were selected based on access, geographic location (to ensure adequate dispersion of plots across the sampled landscapes), and site characteristics such as slope and aspect (to ensure environmental comparability between the SSPM and ESN datasets). We used the US Forest Service FACTS (Forest Activity Tracking System) database to determine if any of the potential ESN sites had experienced management disturbance in the last two decades and we avoided such sites. We did not purposefully avoid locating sites in areas that experienced management more than 20 years ago, and we also did not try to avoid recent fires (but none happened to fall in such places). In a few cases we found evidence of recent cutting when we visited plots in the field; we did not sample such sites. In total, we sampled 86 plots in SSPM in the field seasons of 2012 and 2013, and 64 plots in ESN in the summer of 2013. Mean elevation of plots in SSPM was about 2450 m (range 2100–2750 m), in ESN it was about 2100 m (range 1513–2630 m).

3.3.1. Common stand exams

Forest structure, understory composition, and ground surface cover data were collected in accordance with the protocols of the USDA Forest Service’s Pacific Southwest Region 5 Common Stand Exam Field Guide (http://www.fs.fed.us/nrm/documents/fsveg/cse_user_guides/R5FG.pdf).

Field plots were 11.3 m radius, 405 m² in area (1/10 acre). Plots were located using a GPS and general plot information for each plot

was taken including characteristics such as slope, aspect, and visual estimates of ground surface cover. For each woody individual in the plot with a diameter at breast height (dbh; measured at 1.37 m) greater than 7.6 cm, we tagged, recorded species, and measured dbh, height, canopy width, height to live crown, and crown class. Snags were tagged, dbh measured, and a decay class (from the Common Stand Exam Field Guide) assigned if they had a height of more than 1.37 m and dbh greater than 7.6 cm. Finally, seedlings (trees <1.37 m tall) and saplings (≥ 1.37 m tall but with dbh <7.6 cm) were identified to species (whenever possible) and aged by counting terminal bud scars in a circular subplot of 4.37 m radius (60 m²) centered on plot center.

Ocular cover estimates were made for every species within the plot. Species identifications were made according to Wiggins (1980), Delgado (2004), Thorne et al. (2010), and Baldwin et al. (2012). J. Delgado (Universidad Autónoma de Baja California) and E. Kentner (consulting botanist, San Diego) also aided in plant identification.

3.3.2. Fuels data

Data on woody fuels were collected in accordance with the Brown’s Fuels protocol (Brown, 1974). Four transects, one in each of the four cardinal directions, were surveyed in each plot and values were averaged. Slope for each transect was recorded only if it was greater than 20% to allow for area correction necessary in steeper terrain (Brown, 1974). Woody debris (fuels) intersecting the transect tape in 0.0–0.64 cm diameter (1-hour fuels) and 0.64–2.5 cm diameter (10-hour fuels) classes were counted along the first 2 m of the transect starting at the outermost point. Fuels in the 2.5–7.6 cm diameter class (100-hour fuels) were counted along the first 4 m of the transect from the outermost point, and 1000-hour fuels (a.k.a coarse woody debris [“cwd”], >7.6 cm diameter) were counted along the entire 11.3 m. The length, and diameters at both ends and the transect intersection of each individual piece of cwd were also recorded. Litter, duff, and fuel depths were measured at the transect initiation point and at 4 m.

3.4. Statistical analysis of field data

Field data were entered into an Access database, extracted as .csv and analyzed using R. Hierarchical agglomerative cluster analysis was performed on all plots using Ward’s minimum variance criterion (Ward, 1963) and `hclust()` function in R. We tested both Euclidean and Jaccard’s distance matrices calculated from percent cover of dominant tree and shrub species separately on plots at each site. For Jaccard’s distance matrix, conversion to presence/absence data was performed first, and for Euclidean distance, a regular standardization was applied. Each distance method produced one large group of plots and a few smaller groups that contained unique species. Further dividing the clusters produced the same large group but the other groups were divided into sub-groups, which we interpreted as lending credibility to the large group as the main body of similar plots. Plots belonging to these clustering outliers tended to be strongly dominated by species like quaking aspen, white fir, lodgepole pine, or pinyon pine and they did not floristically fit within either Jeffrey pine or mixed conifer forest; these plots were dropped from the analysis. Plots at each site in which the majority of species were not shared by the other site were also dropped from analysis. Final sample numbers were 70 plots for SSPM and 58 for ESN.

Descriptive statistics for fuels were calculated using appropriate equations developed for California forests (Brown, 1974, van Wagtendonk et al., 1996). Descriptive statistics for everything else including live and dead trees per hectare, and distributions of tree diameter size classes were calculated in R. For each field variable, we also calculated the coefficient of variation (CV) among all plots

sampled in ESN, as well as among all plots sampled in SSPM, so as to get a rough relative idea of the spatial variability in these variables in each study region.

Site comparisons were carried out using generalized linear models with location as a predictor and the variable of interest as the outcome. Data distributions dictated distribution choice for the models – often negative binomial or poisson, with zero-inflation specified where appropriate. Generalized linear mixed effects models were used for negative binomial distributions with location as a predictor and PlotID as a random effect. AIC scores were used to choose the best model. Statistical models for fuels were run using the `glmmadmb()` function in the “glmmADMB” package for R. Coarse woody debris was compared with linear models. All others were run using the `glmer()` and `zeroinfl()` function in the R packages “lme4” and “pscl.” Confidence intervals were calculated using function `precis()` in the package “rethinking.”

4. Results

4.1. Climate

January mean minima for the Alta California met stations ranged from -13.3°C to 3.2°C (mean = -5.0°C). The January mean minimum at the SSPM station was -1.0°C (Table 1). July mean maxima ranged from 23.8°C to 31.7°C in Alta California (mean = 27.7°C), and was 24.8°C for the SSPM. In the Alta California sites, total average annual precipitation ranged from 230 mm (Bridgeport, CA, which 6 km east of the edge of Jeffrey pine distribution) to 1114 mm (mean = 619 mm), and was 569 mm in SSPM. The proportion of annual precipitation that fell between June and August was between 2% and 18% at the US stations, and 14% in the SSPM. The interannual CV for precipitation averaged 0.431 in the Alta California sites, compared to 0.520 in SSPM (Table 1). Climatic variables for SSPM fall within (mostly much less than) a standard deviation of the overall averages in Table 1, except for the interannual CV for precipitation. ESN met stations within the geographic area sampled in our field study averaged -8.0°C January mean minimum temperature, 26.9°C July mean maximum, 554 mm precipitation, and 8.4% of precipitation falling between June and August, and had a mean interannual CV for precipitation of 0.404. The ESN sites are thus very similar to SSPM in growing season temperatures and annual precipitation, but they are colder in winter than the SSPM station (the main area of forest in SSPM is 300–500 m higher than the met station, so probably roughly 1.5–2.5° colder using lapse rates), they tend to receive somewhat less summer precipitation than SSPM (although one site, BR [Bridgeport], has higher summer precipitation – proportionally speaking – than SSPM), and interannual variability in precipitation in ESN is generally less than in SSPM (although again, BR is similar to SSPM).

The NMS ordination and cluster analysis (not shown) of climate variables delineated four major groups of our meteorological stations (Fig. 3): (1) A set of very dry, continental sites from the western Great Basin with appreciable monsoonal influence, situated near the eastern edge of the distribution of Jeffrey pine forest (lower right group in Fig. 3); (2) A group of Sierra Nevada sites found within Jeffrey pine-dominated forest, with mostly average climatic values (central group in blue circle in Fig. 3); (3) A group comprising the southern California and Baja California sites (upper group in red circle in Fig. 3), trending from relatively wet sites (MW, LA) to the relatively dry Baja California sites (SS, SJ); (4) The cluster analysis also identified a group comprised of the Baja California sites plus PO, GL, and MA from ESN (group within dashed black circle in Fig. 3). Site locations within the NMS ordination were best explained by annual precipitation, the proportion of

precipitation falling between June and August, and the January mean minimum temperature (Fig. 3). The interannual CV for precipitation was not a useful predictor of site differences, and mean annual temperature and July mean maximum temperature were relatively weakly correlated with one axis.

4.2. Recent fire history

The median time since fire was 62 years in SSPM and 100 years in ESN (with 100 being our default maximum). Using the same default maximum, mean time since last fire was lower in SSPM (56 vs 67 years). Fig. 4 compares the number of fires that have occurred in plots in our two study areas since our records began. 37 ESN plots (63.8% of the ESN total) had not burned since at least 1908 (the earliest fire mapping for which we have reasonably accurate data; Miller et al., 2009), while 13 plots in SSPM (18.6% of the SSPM total) had not burned since at least 1925 (our earliest fire mapping date). The median number of fires over the period of record was two in SSPM and zero in ESN. No plots in ESN burned more than once, while 36 (51%) burned more than once in SSPM (28 twice, 5 three times, 2 four times, and 1 plot burned five times; Fig. 4). At the time of the imposition of effective fire suppression in SSPM (early-1980s), the median time since last fire was 32 years, and the mean was 37 years. The last plots burned in SSPM were in 2003, the last plots burned in ESN were in 2006. Adding years since last fire as a random effect did not show significance in any of our statistical tests.

4.3. Trees: density, basal area, and diameter

The mean density of live trees per hectare was 352.1 (range 25–1175) in ESN and 187.9 (0–600) in SSPM (Table 2). This difference was strongly statistically significant. The coefficient of variation for live tree density (SD/mean) among plots was similar in both areas (0.67 in SSPM, 0.75 in ESN). Dead tree (snag) densities in ESN were also much higher (by 2.6 times) than in SSPM (Table 2). Mean snag density was 31.2 (range 0–400) in ESN, and 12.1/ha (range 0–150) in SSPM. The coefficient of variation for snag density was slightly lower in SSPM (1.91) than in ESN (2.19). Mean seedling density in SSPM was 420/ha (range 0–6474) and in ESN it was 1052/ha (range 166–6806). Mean sapling density in SSPM was 131/ha (range 0–3154) and in ESN it was 231/ha (range 0–996). Coefficient of variation for seedlings and saplings was much higher in SSPM than in ESN (seedlings: 2.76 SSPM, 1.14 ESN; saplings: 3.07 SSPM, 0.76 ESN). Differences between means were highly significant for both seedlings and saplings ($P < 0.0001$).

Live basal area was highly significantly different between the two study areas (Table 2). SSPM forests supported 30% less live basal area on average (mean $22.5\text{ m}^2/\text{ha}$, range 0–46) than ESN (mean $31.8\text{ m}^2/\text{ha}$, range 1–114). Coefficients of variation for live basal area were slightly lower in SSPM (0.55) than in ESN (0.66). Dead basal area differences were also significant between the two sites, with the SSPM plots supporting a mean of $2.6\text{ m}^2/\text{ha}$, range 0–14) and the ESN plots supporting a mean of $4.6\text{ m}^2/\text{ha}$ (range 0–171); in both cases the median values were zero (Table 2). The coefficient of variation for dead basal area was 4.97 in ESN and only 1.57 in SSPM. As noted above, time since last fire was not a significant factor for either basal area or trees per hectare between the two regions.

When comparing reproductive trees ($\geq 7.6\text{ cm dbh}$), the differences in average dbh between SSPM and ESN were found to be highly significant. ESN trees were on average 19% smaller than SSPM trees. The mean dbh in SSPM was 39.1 cm (range 7.5–146.7) and the mean dbh in ESN was 31.9 cm (range 7.5–147.8) (Table 2). The CV for live dbh was nearly identical in the two study areas (0.67 SSPM, 0.66 ESN). The mean dbh of dead trees ($>7.6\text{ cm}$

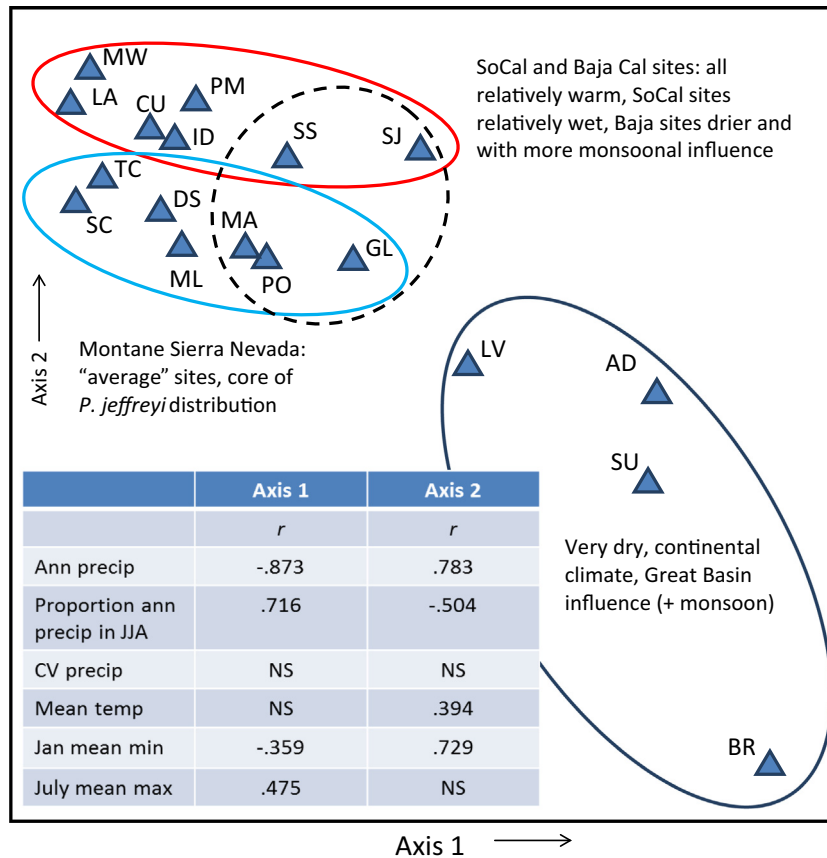


Fig. 3. Non-metric Multidimensional Scaling (NMS) ordination results, and correlations between meteorological data and Axes 1 and 2. Similar met station groups circled. The group bordered by the dashed black line was identified in cluster analysis.

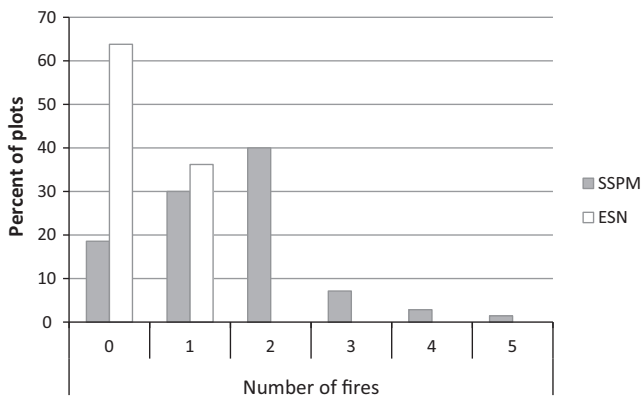


Fig. 4. Distribution of number of fires occurring at the plot locations we sampled in the Sierra de San Pedro Mártir (SSPM) and the eastern Sierra Nevada (ESN) since the beginning of spatial fire records (SSPM – 1925; ESN – 1908).

dbh) in the SSPM was 50.5 cm, versus 28.8 cm in ESN. As in all of the other comparison, time since last fire was not a significant factor in explaining the differences in dbh between the two areas.

Fig. 5 portrays the average distribution of trees by size class in terms of tree density (stems/ha), excluding seedlings and saplings. The stands sampled in ESN generally follow an inverse-J distribution, whereas the SSPM stands support a flatter distribution where more of the biomass is proportionally in larger trees. The ESN stands support two to three times as many trees as SSPM in every size class below 60–70 cm dbh (Fig. 5).

4.4. Fuels, litter and duff

Fuels loads were similar between the SSPM and ESN plots, with the exception that 1-hour fuels (0.0–0.64 cm diameter) were higher on average in SSPM than in ESN. CVs for 1-hour fuels were about 1.0 in both study areas. 10-hour fuels were marginally higher in ESN, and CVs were very similar again (0.7 SSPM vs.

Table 2

Summary statistics for comparisons of tree density, basal area, and diameter between the Sierra de San Pedro Mártir (SSPM) and the eastern Sierra Nevada (ESN). Only trees ≥ 7.6 cm dbh are included.

| | SSPM | | | ESN | | | <i>P</i> |
|--------------------------------------|------|--------|------|------|--------|------|----------|
| | Mean | Median | s.e. | Mean | Median | s.e. | |
| Live trees/ha | 188 | 162 | 15.1 | 352 | 250 | 34.1 | <0.0001 |
| Dead trees/ha | 12 | 0 | 2.8 | 31 | 0 | 8.7 | <0.0001 |
| Seedlings/ha | 420 | 0 | 142 | 1052 | 913 | 195 | <0.0001 |
| Saplings/ha | 131 | 0 | 49.2 | 231 | 166 | 28.3 | <0.0001 |
| Live basal area (m ² /ha) | 22.5 | 23 | 1.5 | 31.8 | 28 | 2.8 | <0.0001 |
| Dead basal area (m ² /ha) | 2.6 | 0 | 0.5 | 4.6 | 0 | 3.1 | 0.0034 |
| Dbh (cm) | 34.1 | 26 | 0.72 | 24.8 | 20.3 | 0.87 | <0.001 |

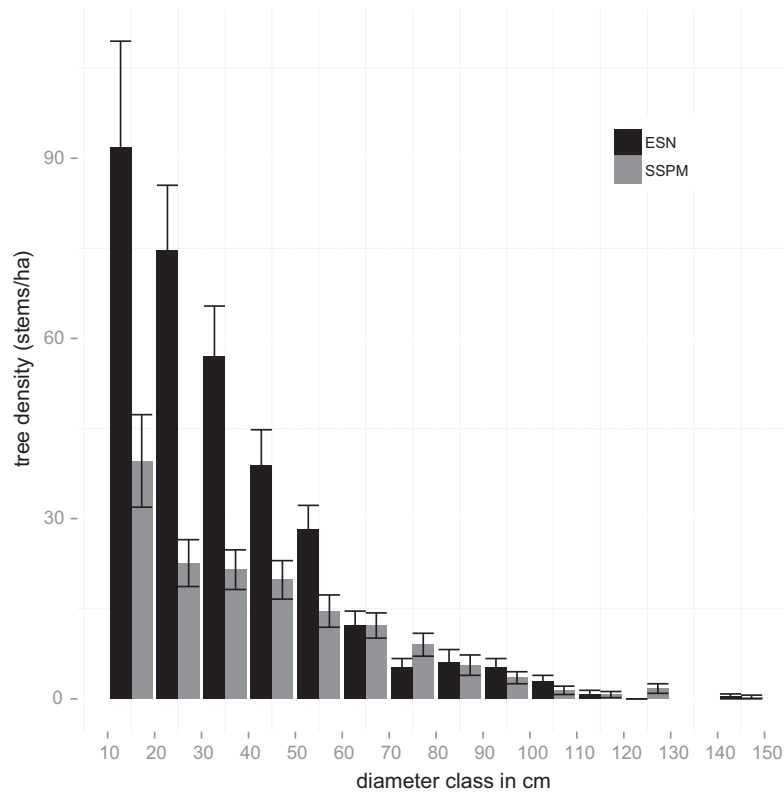


Fig. 5. Average distribution of tree size classes, in stems per hectare, in the Sierra de San Pedro Mártir (SSPM) and the eastern Sierra Nevada (ESN). Error bars represent standard error.

0.67 ESN). 100-hour and 1000-hour fuels (coarse woody debris) did not differ between the two study areas (Table 3). CVs for 100HR fuels were 0.95 in SSPM and 1.11 in ESN, CVs for 1000-hour fuels (cwd) were higher in SSPM than in ESN (2.1 vs 1.7), and the range of cwd loads was also higher in SSPM (0–300 t/ha vs. 0–198 t/ha in ESN). Total fuels loads were very similar between the two areas (Table 3).

Litter depth was significantly higher in ESN than in SSPM (Table 3), but the variability among sites was higher in SSPM (CV = 0.8 vs 0.5 in ESN). Duff depths were low and did not differ significantly between the two areas (Table 3).

4.5. Vegetation cover

Tree cover was higher in the ESN sites than in SSPM (Fig. 6), but the difference was only marginally significant (mean = 24.9% SSPM and 32.5% ESN; $P = 0.07$). The highest tree covers we sampled were 65% in SSPM and 75% in ESN, and the median tree cover in SSPM was 17%, vs 30% in ESN. The CV for tree cover was higher in the SSPM (0.78 vs 0.49 ESN). Mean shrub and forb cover were not significantly different between SSPM and ESN (Fig. 6), but the median shrub cover was much higher in ESN (5%) than in SSPM (1%), and the CV for shrub cover was higher in SSPM (1.4 vs 0.9 ESN). Forb cover was very variable, with CVs at 2.3 for SSPM and 2.9 for ESN. Graminoid cover was higher in ESN (means = 5.5% vs. 1% SSPM; $P = 0.012$), and variability between plots was exceptionally high. The CV for graminoid cover in SSPM was 4.6, and in ESN, 2.8.

5. Discussion

The strong floristic, geologic, and – as documented here – climatic similarities between YPMC forest sites in the northern Baja California mountains and Alta California suggest to us broad ecological comparability and support the validity of using relatively

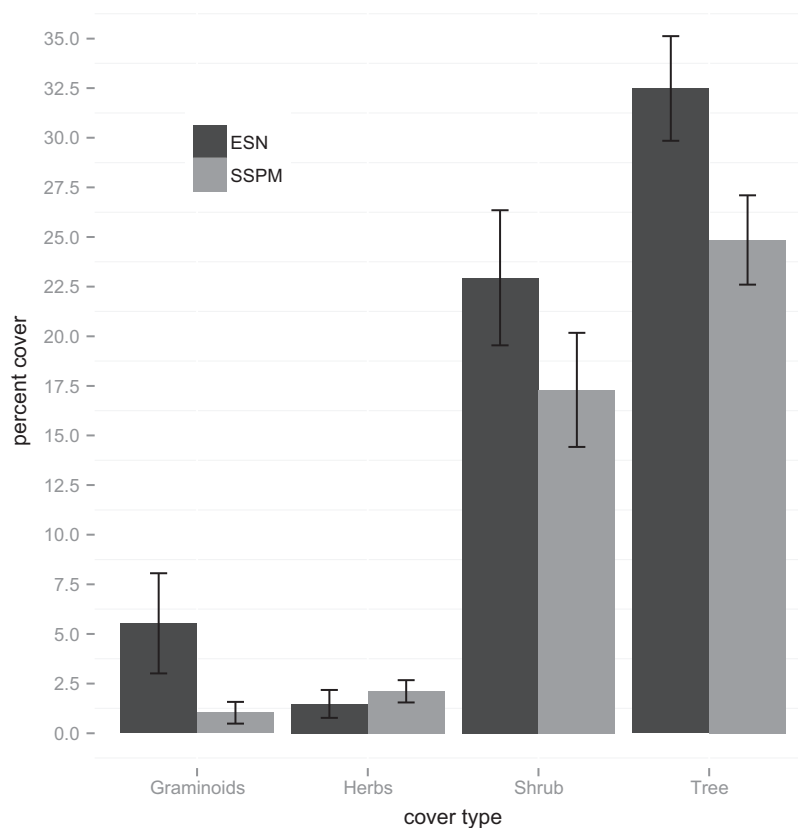
undegraded Mexican YPMC forests as reference systems for restoration and fire and resource management in Jeffrey pine-dominated forests (as well as mixed ponderosa-Jeffrey pine forests) in Alta California. It is true that the Sierra de San Pedro Mártir (SSPM) is found at the very southern end of the North American Mediterranean climate zone, but in almost all of the climatic variables we assessed, it is well within the range of variation expected for Jeffrey pine forest sites in western North America. For SSPM, our cluster analysis demonstrated especially strong climatic similarities with the Portola (PO), Glenbrook (GL), and Markleeville (MA) stations in the eastern Sierra Nevada (ESN), which are located close to a large number of our ESN plots. Ongoing fire suppression in SSPM threatens its value as a restoration reference however; we elaborate on this issue below.

It has been claimed that the monsoonal influence in Baja California may invalidate the use of SSPM reference information in Alta California YPMC forests (Keeley, 2006). However, some stations in Alta California receive similar or even higher proportions of their annual precipitation in the summer months (e.g., Table 1). In addition, the particular time period for which we have complete meteorological data for SSPM (see Table 1) turns out to be a period in southern California in which the proportion of annual precipitation falling between June and August was about 45% higher than the long-term mean (average of COOP met station data for southern California sites CU, ID, MW, and PM); we infer that the values in Table 1 for SSPM and the Sierra Juarez are probably somewhat inflated when compared to the Alta California sites. As Keeley (2006) notes, it is important that better and more consistent meteorological data be collected in the Baja California mountains, but contrary to Keeley (2006), we believe the available data show quite clearly that the climates of SSPM and most of the Alta California sites are similar enough to warrant ecological comparisons. In this, we agree with many other authors, including Delgadillo (1994), Minnich et al. (1995, 2000), Peinado et al. (1997; who

Table 3

Summary statistics for comparisons of woody fuels, litter, and duff between the Sierra de San Pedro Mártir (SSPM) and the eastern Sierra Nevada (ESN).

| | SSPM | | | ESN | | | P |
|--|------|--------|------|------|--------|------|--------|
| | Mean | Median | s.e. | Mean | Median | s.e. | |
| 1-hour fuels (t/ha) | 0.56 | 0.28 | 0.07 | 0.26 | 0.15 | 0.04 | <0.001 |
| 10-hour fuels (t/ha) | 1.24 | 0.96 | 0.11 | 1.54 | 1.31 | 0.14 | 0.098 |
| 100-hour fuels (t/ha) | 2.9 | 2.31 | 0.33 | 3.03 | 2.31 | 0.43 | 0.63 |
| ≥1000-hour fuels (t/ha) (=cwd ^a) | 28.9 | 4.8 | 6.8 | 25.1 | 5.9 | 5.9 | 0.57 |
| Total fuels (t/ha) | 33.6 | 10.4 | 6.9 | 29.7 | 11 | 6 | 0.56 |
| Litter depth (cm) | 2.96 | 2.62 | 0.27 | 3.63 | 3.33 | 0.25 | 0.008 |
| Duff depth (cm) | 1.18 | 0.81 | 0.16 | 1.21 | 0.71 | 0.17 | 0.9 |

^a cwd = coarse woody debris.**Fig. 6.** Comparisons of vegetation cover between the Sierra de San Pedro Mártir (SSPM) and the eastern Sierra Nevada (ESN). Error bars represent standard error.

floristically and climatically recognize a class of Jeffrey pine-dominated forests common to the east side of the Sierra Nevada, drier mountain sites in southern California, and the mountains of northern Baja California), and Stephens and colleagues (many papers, cited elsewhere).

With respect to our comparisons of forest structure, four general results stand out. First, as we expected, the ESN forests we sampled were much denser than forest in SSPM, trees were smaller on average, and stand basal area was higher as well. Second, although tree cover was higher in ESN, grass cover was lower in SSPM. Third, structures important to wildlife, like coarse woody debris and standing dead trees, were as abundant (cwd) or more abundant (snags) in ESN than in SSPM. Finally, fuels were surprisingly similar in the two study areas. We discuss each of these salient results below.

We expected to find that the YPMC forests sampled in our ESN sites were denser and more dominated by smaller trees than our SSPM plots, as numerous previous studies have made the same

finding (although generally without actually carrying out statistical comparisons) (Minnich et al., 1995, 2000; Delgadillo, 2004; Stephens and Gill, 2005). Indeed, densities of trees ≥ 7.6 cm dbh were nearly twice as high in ESN as in SSPM, with 80% of the difference found in trees <40 cm dbh, and 60% in trees <30 cm dbh. Assuming moderate and low site indices (measures of site productivity), trees <40 cm dbh are <110 years old on average in ESN and <145 years on average in SSPM (tree growth rates range from 19% to 28% faster in our ESN sites than in SSPM; Minnich et al., 2000, Safford, unpublished data; Stephens and Fry, unpublished data). This strong pulse of smaller trees in ESN that is absent in SSPM recruited primarily after the cessation of heavy logging in most of our ESN sites (mostly ending by the 1910s or 1920s) and was not subsequently culled by fire, which was for the most part excluded in ESN after the beginning of the 20th century (Safford and Stevens, in press). The surprisingly high density of seedlings and saplings in our SSPM plots (more than $3\times$ higher than the densities sampled by Stephens and Gill in 1998 [Stephens and Gill,

2005]) seems likely to be the result of the three decades of fire suppression in the National Park, a management decision that is changing SSPM forests in other ways as well (see below).

Large tree (>70 cm dbh) densities are higher in SSPM than ESN, thus higher basal areas in our ESN plots come about entirely through the very high abundance of small trees in the Alta California forests. The lower-than-expected densities of large trees in ESN must be due either to the effects of earlier logging, or some other mortality factor, or both. Multiple studies have found increases in overall YPMC density in the Sierra Nevada, but losses in large trees (Lutz et al., 2009; Van Mantgem et al., 2009; Safford and Stevens, in press). Basal areas in our SSPM plots (22.5 m²/ha, range 0–46) were very similar to those measured by other studies of YPMC forests in the National Park. Passini et al. (1989) reported a mean of 22 m²/ha for their Jeffrey pine forest plots (but 51 m²/ha for their [very few] Jeffrey pine-white fir-sugar pine plots), Minnich et al. (2000) reported a range from 21 to 34 m²/ha, depending on species composition, and Stephens and Gill (2005) reported 19.9 m²/ha for their Jeffrey pine-mixed conifer plots.

Although overstory cover was lower in SSPM than ESN, we found that grass cover was lower in the former. This was somewhat surprising, for two reasons. First, SSPM receives somewhat more monsoonal precipitation on average than most of our ESN sites, and summertime rain is a major driver of understory vegetation growth (Safford and Stevens, in press). Second, lower tree cover means more incident light at the ground surface, which benefits understory species. Evett et al. (2007) carried out a study of soil grass phytoliths in SSPM and determined that phytolith densities were too low to indicate extensive cover of grass over the previous centuries, as far back as before the original introduction of livestock in the mountain range by Spanish missionaries. Evett et al. (2007) postulated that, in the excessively drained upland soils that support YPMC forest in SSPM, even more summertime precipitation than SSPM normally receives might be necessary to generate a strong response in the graminoid members of the understory. In years of high monsoonal precipitation in SSPM we have personally seen relatively strong responses of understory grasses in forest soils adjoining meadow complexes, where ground water may be close to the surface and where soil water holding capacity is enhanced by the presence of clay minerals, but little change in the understory of upland soils, which is where most of our plots were; we have also seen most of this extra grass biomass consumed quickly by cattle. Minnich et al. (2000) also noted that livestock presence was much lower in upland forests than in riparian and meadow areas. Although grazing is not officially permitted in Mexican National Parks, livestock owners from the SSPM highlands use the Park's forests as a source of dry-season forage and attempts to remove the cattle have met with strong political resistance. Grazing is currently completely unmanaged in SSPM, aside from a few local exclosures. We saw cattle sign in many of our plots in SSPM, but less sign of livestock in our ESN plots. Both study areas supported substantial numbers of cattle and sheep for more than a century (and more than two centuries in SSPM). Less intensive grazing continues in both areas today, but only in SSPM is grazing currently carried out without regard to ecological impacts.

It has been suggested that woody structures important to wildlife are relatively lacking in modern Alta California YPMC forests (e.g., Franklin and Fites-Kaufmann, 1996; Zack et al., 2002). However our data for snags and coarse woody debris within the ESN study area suggest that these important wildlife elements are at least as common as in reference forests in SSPM (Tables 2 and 3). We found mean densities of 31 snags/ha in ESN, which falls at the higher end of the range of 4–36 snags/ha suggested by Safford and Stevens (in press) to broadly represent the natural range of variation (NRV) for dead tree densities in undegraded YPMC forests in the Sierra Nevada. Our measures of coarse woody

debris similarly suggest that current ESN YPMC forests support cwd values that are at the higher end of NRV. According to Safford and Stevens (in press), cwd in undegraded YPMC forests would be expected to range from 0 to 34 tons/ha (mean = 15.5 tons/ha \pm 2 sd); our ESN sites averaged 25.1 tons/ha. Assuming that SSPM forest structure can be treated as a less degraded reference for Alta California Jeffrey pine sites (and we believe we and others have made a strong case for this), our data support Safford and Stevens' (in press) conclusions that changes in YPMC forest structure in the Sierra Nevada from the pre-Euroamerican settlement era include increases in both average snag density and coarse woody debris, not decreases as surmised by earlier accounts which focused on wildlife benefits and considered only the cwd and snag creating function of fire rather than the complete cycle of fuel creation and consumption (see Agee (2002), and Skinner (2002) for more holistic considerations of this issue).

A further surprising result of our study was our finding that fuel loads in ESN and SSPM were very similar. After all, our ESN plots contained many more trees than our SSPM plots, the Sierra Nevada has been managed under strict fire suppression for much longer (\pm 100 years vs. \pm 30 years), and an earlier study reported very low fuel loads in SSPM forests (Stephens, 2004). Fine fuel loads in our SSPM plots were almost double those in Stephens (2004), who conducted field work in 1998. We believe our results suggest two things: First, the limited geographic area (1.44 km²) sampled in Stephens (2004) is not necessarily representative of the broader landscape in SSPM. Second, fuels have been increasing in SSPM forests in the three or four decades since fire suppression policies began. We believe that both are probably true. Stephens (2004) purposefully sampled from a small area of relatively homogenous forest (same substrate and forest type, flat ground, same fire history) to minimize the effects of other factors. However, we also sampled many plots in similar forest, and even in those plots our means and ranges were different from the Stephens et al. data. We don't question the value of the Stephens (2004) data, but the differences between our results and his point to the need for both locally intensive and spatially extensive data when comparing landscape-level patterns. More importantly, our results compared to those of Stephens (2004) suggest that the institution of organized fire suppression in SSPM in the 1980s is a major driver of the surprisingly high fine fuels we found in our SSPM plots, i.e. that the nearly two fire-free decades between Stephen's original field campaign and ours have led to the fuel accumulations we measured. We attempted to directly test the effect of time since last fire in our fuels comparisons, but the temporal resolution of our SSPM fire data was poor, and most of our plots in both study areas were not coincident with fires that occurred within the last three to four decades.

Based on Jeffrey pine fuel deposition rates measured by van Wagtenonk and Moore (2010), fuels in the 1-, 10-, 100-, and even 1000-hour size classes could have accumulated in SSPM in the three decades since fire suppression began. Van Wagtenonk and Moore (2010) also showed that the rate of 1-hour fuel deposition (mass per unit area) is more than five times higher for large diameter trees than for smaller trees (using Jeffrey pine as an example). Given that ESN densities were about twice those in SSPM, and the density contrast is driven entirely by smaller trees, the differential in fine fuel deposition between large and small trees could account for the disparity in fuel loads of 1- and 10-hour size classes between the two sites. It has been shown that decomposition rates in yellow pine-dominated forests are very slow, falling to almost zero during the dry season (Murphy et al., 1998). Hart et al. (1992) showed that litter decomposition rates in ponderosa pine forest in the Sierra Nevada were about 7% per year in old growth and 15% per year in young growth: in other words, it takes twice as long for old growth litter to decompose completely than the

litter of young forest stands (c. 12–15 years vs. c. 6–7 years). Combining the larger mean dbh in SSPM with the faster growth rates in ESN, the average age of trees in our ESN plots was certainly much younger than the average age in our SSPM plots. In summary, compared to current ESN forests, current SSPM forests may combine higher fuel deposition with slower decomposition (due not to intrinsically higher deposition or decomposition rates, but to the older and larger canopy trees), which may lead to higher susceptibility of fuel loads to the exclusion of fire.

In contrast to 1-hour fuels, litter depth was higher in our ESN plots than in SSPM. In our study areas, litter is primarily composed of needles fallen from trees. Surface litter is consumed by fire, and 60% of plots in the ESN did not have fires on record, whereas only 19% of plots in the SSPM had no fires on record. However, using the decomposition rates above, litter cycles about every 7–15 years in these forests, so since very few plots in either study area had fires within the last 15 years, the explanation must lie elsewhere. Denser stands of trees in the ESN sites probably result in greater competition for resources and greater stress, which can lead to early leaf drop and higher rates of mortality (Allen et al., 2010). Certainly the higher densities of standing dead trees (and higher median loading for CWD) in the ESN sites suggest that mortality rates are higher there than in SSPM. A number of studies have shown that mortality in the Baja conifer forests during recent droughts was much lower than in Alta California (Savage, 1997; Stephens, 2004), and enhanced surface litter in ESN may or may not be related to this pattern. Murphy et al. (1998) found that ponderosa pine litter decomposition is faster at higher elevations where moisture is higher, and additionally that extended periods of low precipitation decrease decomposition rates. Overall, SSPM receives somewhat more summertime precipitation than our ESN sites, so perhaps litter decomposition rates are higher in SSPM? This seems unlikely however, given that most decomposition in our dry study areas occurs under snow (Stark, 1973). In addition, unpublished direct measurements of decomposition rates in SSPM suggest that litter remains on the ground for many years (D. Fry, UC-Berkeley, pers. comm.).

Although surface fuels were broadly similar in the two study areas, live fuels were much higher in ESN, driven by higher densities of small trees, which act as ladder fuels to carry surface fires into the forest canopy, and the tree canopy was denser as well, which is more likely to permit crown fires to propagate (Agee and Skinner, 2005). Overall, the risk of severe fires in ESN continues to be much higher than in SSPM, even though fire suppression policies in the latter are increasing both dead and live fuels. Differences in forest fire severity between our two study areas are extreme. Miller et al. (2009) and Miller and Safford (2008, 2012) showed that fires since 1984 in Sierra Nevada YPMC forests have burned an average of over 30% of their area at high severity (>90% canopy tree mortality), whereas recent work in SSPM shows an average of <5% high severity fire during the same period (Rivera et al., in press). Rivera et al. also note, however, that high severity patch size within fires is rising in SSPM, which is a worrisome trend probably linked to the increases in surface fuel and small trees we saw on the ground.

On the surface, the similar coefficients of variation and medians in most of our structural and fuels data suggest a similar level of spatial heterogeneity in our ESN and SSPM study areas. This is not something we expected, based on past research (Stephens, 2004; Stephens et al., 2008). Of course, the spatial scales of our two study areas were quite different, so it may be that the heterogeneity we are comparing is statistically incompatible, and CVs calculated among plots are hardly the most robust way of assessing spatial variation. It might have been better to compare CVs within our geographic plot groups in ESN (rather than the overall mean from all plots) to the SSPM data, since the spatial scale would have

been more comparable, but these groups included only 4–7 plots each (see Fig. 2), vs. the 70 we sampled and used statistically in SSPM. Note that for forest types like YPMC, which are generally characterized by fine-scale spatial variability (Safford and Stevens, in press), scattered plots across the landscape might not capture heterogeneity as effectively as plots on a small grid (Fry and Stephens, 2010).

5.1. Management implications

In SSPM, our results suggest strongly that fire suppression actions are increasing fuels and forest density. In places in SSPM (although they are admittedly still rare) we have personally seen fuel accumulations that rival some of the heavier accumulations regularly encountered in YPMC forests in Alta California. It seems impossible that continuation of these policies will not result ultimately in an increase in forest fire severity and forest mortality, such as has been seen in Alta California. The high severity patch size trends reported in Rivera et al. (in press) are a clear warning sign. The Mediterranean zone of northwestern Mexico is recognized as its own biogeographic province, and a hotspot of plant and animal species found nowhere else in the nation (Peinado et al., 1994; Delgadillo, 2004). Recent wildfires in the Sierra Nevada have burned areas as large as the forested plateau of SSPM in one or two days. It would be a tragedy to lose such a biologically important ecosystem to short-sighted fire management policies, but this is the path that SSPM currently finds itself on.

Current Mexican National Park policies do not permit the harvest of living trees, and even the cutting of dead trees is difficult. Mexican national fire management policy was recently changed from fire suppression under all conditions to fire management (mirroring US changes in the 1970s), but the regulations and executive actions necessary to actually implement these changes have yet to happen. At this point prescribed fire and wildland fire use (managed natural ignitions) in most National Park units are possible in theory but not in practice. This means that the dozen or so natural ignitions that occur in YPMC forest in SSPM every summer will continue to be put out and fuels will continue to accumulate. A complicating factor in SSPM is the presence of the Mexican National Astronomical Observatory (MNAO). SSPM is famous for its clear, dry skies – hence the presence of MNAO – and prescribed fire and wildland fire use clearly threaten the clarity of the summer sky. As a result, MNAO, which is run by the National Autonomous University of Mexico (UNAM), is supportive of minimizing fire occurrence, but recent directors of the installation have expressed willingness to talk about ecological needs of the park and potential compromises. Major observatories in the southwestern US (e.g., Mt. Graham, Mt. Wilson, Mt. Palomar, Mt. Lemmon) have had to deal with fire and fuels management in their immediate surroundings for decades, and their experiences may help chart a way forward. Certainly there is a general desire to avoid the fate of the important Mt. Stromlo Observatory in Australia, which was destroyed by a forest fire in 2003. The observatory was surrounded by dense vegetation, and no fuel reduction by prescribed fire or other means had been carried out around the site.

Clearly, SSPM is not a perfect restoration reference site for Jeffrey pine-dominated forests in the US, as Mexican fire managers have successfully excluded fire from SSPM conifer forests for the last three decades. Our data show that this has led to predictable changes in forest fuels and seedling densities, and probably in forest stand structure as well. However, tree growth rates in SSPM are slower on average than in ESN, and since logging has not occurred in SSPM and tree mortality rates are low (e.g., Stephens and Gill, 2005), general stand structure has not yet changed enough to obscure broad patterns created by centuries of frequent fire. As such, it seems perfectly reasonable to use contemporary

Table 4
Maximum elevations at which management reference information from the Sierra de San Pedro Mártir is climatically appropriate.^a

| Distance to the north of SSPM (km) | Maximum elevation (m) | | | Examples of appropriate US management landscapes |
|------------------------------------|-------------------------|--------------------------|-------------------------|---|
| | Lapse rate = 0.4°/100 m | Lapse rate = 0.45°/100 m | Lapse rate = 0.5°/100 m | |
| 300 | 2687 | 2660 | 2633 | San Jacinto Mountains |
| 400 | 2616 | 2580 | 2544 | Eastern San Bernardino Mountains |
| 500 | 2545 | 2500 | 2455 | Southern Sequoia National Forest |
| 600 | 2474 | 2420 | 2366 | Southern Inyo National Forest |
| 700 | 2403 | 2340 | 2277 | Northern Inyo National Forest |
| 800 | 2332 | 2260 | 2188 | Bridgeport District, Humboldt-Toiyabe National Forest |
| 900 | 2261 | 2180 | 2099 | Lake Tahoe Basin; Carson District, Humboldt-Toiyabe National Forest |
| 1000 | 2190 | 2100 | 2010 | Eastern Tahoe and Plumas National Forests |
| 1100 | 2119 | 2020 | 1921 | Eastern Lassen NF |

^a Assuming preponderance of Jeffrey pine (current or historical), and mean annual precipitation <800 mm.

inventories of mature-tree stand structure from SSPM to help guide restoration efforts in more degraded Jeffrey pine-dominated forests in Alta California. On the other hand, contemporary measures in SSPM of more rapidly mutable forest attributes like fine fuels, seedlings, and saplings may not be as representative of historic reference conditions in Alta California. In these cases, earlier inventories than ours, for example the Stephens and colleagues papers based on data collected in 1998 (e.g., Stephens, 2004; Stephens and Gill, 2005), may provide more accurate reference information for forest restoration purposes in Alta California.

Our climatic comparison suffers from a relative lack of data from the Baja California sites. We were able to collect only 10 years of data from the Sierra Juarez, and 6–15 years (depending on data type) from SSPM, and these were from decades ago. The MNAO began to collect some meteorological data soon after its construction in 1967, but the protocol for data collection depended on the availability of personnel, which resulted in <70% of days receiving measurements, and an even lower percentage (c. 50% of days) in December and January, when most staff would be on holidays (Tapia, 1992); precipitation was not measured. Automated data collection, including precipitation, began in 2006, but MNAO lacked snow measurement capability until last year (H. Rivera, UABC, pers. comm.), so the data record to this point either completely lacks precipitation (until 2006), or lacks most of the precipitation (until 2014). There is a clear need to develop a data record of temperature and precipitation for SSPM, as there is in the Parque Nacional Constitución de 1857, which is found in Jeffrey pine forest in the Sierra Juarez. Such a record would help in work such as ours here, but also in better understanding the relationships between vegetation and climate and climate and disturbance, it would permit more robust modeling of likely climate change impacts to SSPM and other Baja California mountain landscapes, and it would allow for modern fire and fuel modeling, which will be necessary if the National Park begins to use fire as a management tool. Another related issue is the location of the Baja California met stations. The CONAGUA stations in SSPM and the Sierra Juarez were both at the lower edge of the distribution of Jeffrey pine, and outside the main area of forest. We would recommend that newer stations should be installed within the main areas of forest in both locations.

In Alta California, the places for which data from SSPM can be reasonably used as management references are mostly at lower elevations. This is because of the relationship between the latitudinal temperature gradient (about 5.6°/1000 km along the west coast of California; Safford and Van de Water, 2014) and the adiabatic lapse rate (c 0.3–0.65° per 100 m elevation depending on the location and the season). Assuming an average western US lapse rate somewhere between 0.4° and 0.5°/100 m (Major, 1995; Harlow et al., 2004; Blandford et al., 2008; Minder et al., 2010), it can be

calculated that the latitude-to-elevation relationship through northern Baja California and Alta California is such that moving one km of horizontal distance along a line of longitude is equivalent to 0.7–0.9 m in elevation change. The highest elevation YPMC forests in SSPM grow at about 2900 m. Thus, at a radius of 300 km north of SSPM (e.g., San Jacinto Mountains) it would be climatically most reasonable to apply management activities based on SSPM reference information in Jeffrey pine and mixed conifer forests below elevations of about 2690 m (2900 – [0.7 * 300]). Table 4 calculates approximate compensating elevations for distances up to 1100 km north of SSPM, and lists those major federal management units affected. Three lapse rates are compared in Table 4: we recommend using the more liberal value of 0.4°/100 m, since climate warming is causing upward migration of biota throughout Alta California (Kelly and Goulden, 2008; Moritz et al., 2008; Tingley et al., 2009; Forister et al., 2010).

The continuance of current fire and fuel management policies in SSPM seriously threatens both the sustainability of forested ecosystems in the park, and the ability of US managers to use contemporary and future information gathered from SSPM to inform management in Alta California. The warming climate is a further serious complication, as is the increasing number of human ignitions in the chaparral belt below the park. However, we believe that there is still time to make a course-correction in SSPM. 30+ years of fire suppression have been enough to increase surface fuels and seedling and sapling densities and to promote the development of some heavy fuel jackpots, but overall the forest in SSPM is still much less dense than in most climatically and floristically comparable sites in Alta California. Rivera et al.'s (in press) study of fire severity patterns shows that fires in SSPM are still burning at much lower severity than similar forests in Alta California, and most lightning ignitions on the SSPM plateau are still extinguished with little effort. Yosemite and Sequoia-Kings Canyon National Parks in Alta California transitioned from full fire suppression to progressive wildland fire use (WFU) policies after as much as a century of fire exclusion, and both WFU programs are hailed as great successes today (Collins and Stephens, 2007; Miller et al., 2012). Nearby National Forests have also made important strides in wildland fire use (Meyer, 2015). With some forethought and fortitude, similar steps in the Sierra de San Pedro Mártir can help to guarantee the long-term persistence of these unique conifer forests.

Acknowledgements

Funding was provided by US Forest Service International Programs, the US Forest Service Pacific Southwest Region Ecology Program, the UC-Davis Ecology Graduate Group, the UC-Davis Plant

Sciences Department, and the Comisión Nacional de Áreas Naturales Protegidas (CONANP). Field crews in the SSPM included Zayra Pena, Jessica Trujillo, Ibes Davila, and Hiram Rivera from Mexico; and John Williams, Kevin Hickenbottom, Haley Wiggins, and Ed Kentner from the US. In the ESN, Clark Richter, Amy Jirka, Amy Sturgill, Maggie Mansfield, Haley Wiggins, and Deb Scolnick carried out most of the field work. Botany help was provided by Onkar Singh and Ed Kentner. At UC-Davis, members of the Young Lab provided theoretical and analytical ideas and editing, with particular support from Gabrielle Bohlman. Brendan Barrett provided extensive statistical help. Truman Young edited many drafts of the manuscript.

References

- Agee, J.K., 1993. *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, DC.
- Agee, J.K., 2002. Fire as a coarse filter for snags and logs. In: General Technical Report PSW-GTR-181. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 359–368.
- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. *For. Ecol. Manage.* 211, 83–96.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684.
- Baldwin, B.G., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T.J., 2012. In: *The Digital Jepson Manual: Vascular Plants of California*, second ed. University of California Press, <<http://ucjeps.berkeley.edu/IJM.html>>.
- Barbour, M.G., Minnich, R.A., 2000. Californian upland forests and woodlands. In: Barbour, M.G., Billings, W.D. (Eds.), *North American terrestrial vegetation*. Cambridge University Press, Cambridge, UK, pp. 162–202.
- Barbour, M.G., Keeler-Wolf, T., Schoenherr, A.A. (Eds.), 2007. *Terrestrial Vegetation of California*, third ed. Univ California Press, Berkeley, CA, USA.
- Blandford, T.R., Humes, K.S., Harshburger, B.J., Moore, B.C., Walden, V.P., Ye, H., 2008. Seasonal and synoptic variations in near-surface air temperature lapse rates in a mountainous basin. *J. Appl. Meteorol. Climatol.* 47, 249–261.
- Brown, J.K., 1974. *Handbook for Inventorying Downed Woody Material*. Gen. Tech. Report INT-16. U.S. Department of Agriculture Forest Service, Intermountain Forest and Range Experiment Station.
- Cole, D.N., Yung, L., 2010. *Beyond Naturalness: Rethinking Park and Wilderness Stewardship in an Era of Rapid Change*. Island Press, Washington, DC, USA.
- Collins, B.M., Stephens, S.L., 2007. Managing natural wildfires in Sierra Nevada wilderness areas. *Front. Ecol. Environ.* 5, 523–527.
- Delgadillo, J., 2004. *El bosque de coníferas de la Sierra de San Pedro Mártir*. Instituto Nacional de Ecología, Baja California.
- Dillon, G.K., Holden, Z.A., Morgan, P., Crimmins, M.A., Heyerdahl, E.K., Luce, C.H., 2011. Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. *Ecosphere* 2, art130.
- Dolanc, C.R., Safford, H.D., Dobrowski, S.Z., Thorne, J.H., 2014. Twentieth century shifts in abundance and composition of vegetation types of the Sierra Nevada, CA, US. *Appl. Veg. Sci.* 17, 442–455.
- Egan, D., Howell, E. (Eds.), 2001. *The Historical Ecology Handbook: A Restorationist's Guide to Reference Ecosystems*. Island Press, Washington, DC.
- Evvett, R.R., Franco-Vizcaino, E., Stephens, S.L., 2007a. Comparing modern and past fire regimes to assess changes in prehistoric lightning and anthropogenic ignitions in a Jeffrey pine – mixed conifer forest in the Sierra San Pedro Mártir, Mexico. *Can. J. For. Res.* 37, 318–330.
- Evvett, R.R., Franco-Vizcaino, E., Stephens, S.L., 2007b. Phytolith evidence for the absence of a prehistoric grass understory in a Jeffrey pine – mixed conifer forest in the Sierra San Pedro Mártir, Mexico. *Can. J. For. Res.* 37, 306–317.
- Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J., Waejen, D.P., Shapiro, A.M., 2010. Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proc. Natl. Acad. Sci.* 107, 2088–2092.
- Franklin, J.F., Fites-Kaufmann, J.A., 1996. Assessment of late-successional forests of the Sierra Nevada. In: *Sierra Nevada Ecosystem Project: Final Report to Congress. Volume II: Assessments and Scientific Basis for Management Options*. University of California, Centers for Water and Wildland Resources, Davis, CA, pp. 627–635.
- Fry, D.L., Stephens, S.L., 2010. Stand-level spatial dependence in an old-growth Jeffrey pine – mixed conifer forest, Sierra San Pedro Mártir, Mexico. *Can. J. For. Res.* 40, 1803–1814.
- Fry, D.L., Stephens, S.L., Collins, B.M., North, M.P., Franco-Vizcaino, E., Gill, S.J., 2014. Contrasting spatial patterns in active-fire and fire-suppressed mediterranean climate old-growth mixed conifer forests. *PLoS ONE* 9, e88985.
- Fule, P.Z., Covington, W.W., 1994. Fire-regime disruption and pine-oak forest structure in the Sierra Madre Occidental, Durango, Mexico. *Restor. Ecol.* 2, 261–272.
- Fulé, P.Z., Covington, W.W., 1998. Spatial patterns of Mexican pine-oak forests under different recent fire regimes. *Plant Ecol.* 134, 197–209.
- Graber, D., 2003. Ecological restoration in wilderness: natural versus wild in National Park Service wilderness. *George Wright Forum* 20 (3), 34–41.
- Haller, J.R., 1959. Factors affecting the distribution of ponderosa and Jeffrey pines in California. *Madroño* 15, 65–71.
- Harlow, R.C., Burke, E.J., Scott, R.L., Shuttleworth, W.J., Brown, C.M., Petti, J.R., 2004. Research note: derivation of temperature lapse rates in semi-arid south-eastern Arizona. *Hydrol. Earth Syst. Sci. Discuss.* 8 (6), 1179–1185.
- Hart, S.C., Firestone, M.K., Paul, E.A., 1992. Decomposition and nutrient dynamics of ponderosa pine needles in a Mediterranean-type climate. *Can. J. For. Res.* 22, 306–314.
- Keeley, J.E., 2006. South coast bioregion. In: Sugihara, N.G., van Wagtenonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), *Fire in California's Ecosystems*. University of California Press, Berkeley, CA, pp. 350–390.
- Kelly, A.E., Goulden, M.L., 2008. Rapid shifts in plant distribution with recent climate change. *Proc. Natl. Acad. Sci.* 105 (33), 11823–11826.
- Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* 9, 1179–1188.
- Leopold, A., 1937. *Conservationist in Mexico*. *Am. For.* 43, 118–119.
- Leopold, A., Sows, L.K., Spencer, D.L., 1947. A survey of over-populated deer ranges in the United States. *J. Wildl. Manage.* 11, 162–183.
- Lutz, J.A., van Wagtenonk, J.W., Franklin, J.F., 2009. Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA. *For. Ecol. Manage.* 257, 2296–2307.
- Major, J., 1995. California climate in relation to vegetation. In: Barbour, M.G., Major, J. (Eds.), *Terrestrial Vegetation of California*, second ed. California Native Plant Society, Sacramento, CA, pp. 11–78.
- Mallek, C., Safford, H., Viers, J., Miller, J., 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere* 4, art153.
- Maloney, P.E., Rizzo, D.M., 2002. Pathogens and insects in a pristine forest ecosystem: the Sierra San Pedro Mártir, Baja, Mexico. *Can. J. For. Res.* 32, 448–457.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323, 521–524.
- Marlon, J.R., Bartlein, P.J., Gavin, D.G., Long, C.J., Anderson, R.S., Briles, C.E., Brown, K. J., Colombaroli, D., Hallett, D.J., Power, M.J., Scharf, E.A., Walsh, M.K., 2012. Long-term perspective on wildfires in the western USA. *Proc. Natl. Acad. Sci.* 109, E535–E543.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Designs, Gleneden Beach, OR, USA.
- Meunier, J., Romme, W.H., Brown, P.M., 2014. Climate and land-use effects on wildfire in northern Mexico, 1650–2010. *For. Ecol. Manage.* 325, 49–59.
- Meyer, M.D., 2015. Forest fire severity patterns of resource objective wildfires in the southern Sierra Nevada. *J. Forest.* 113, 49–56.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151.
- Miller, J.D., Collins, B.M., Lutz, J.A., Stephens, S.L., van Wagtenonk, J.W., Yasuda, D. A., 2012. Differences in wildfires among ecoregions and land management agencies in the Sierra Nevada region, California, USA. *Ecosphere* 3 (9), art80.
- Miller, J.D., Safford, H.D., 2008. *Sierra Nevada fire severity monitoring: 1984–2004*. Technical Report R5-TP-027. USDA Forest Service, Pacific Southwest Region, Vallejo, CA.
- Miller, J.D., Safford, H.D., 2012. Trends in wildfire severity 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, USA. *Fire Ecol.* 8, 41–57.
- Miller, J.D., Safford, H.D., Crimmins, M., Thode, A.E., 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12, 16–32.
- Minder, J.R., Mote, P.W., Lundquist, J.D., 2010. Surface temperature lapse rates over complex terrain: lessons from the Cascade Mountains. *J. Geophys. Res.: Atmos.* 115 (D14).
- Minnich, R.A., Barbour, M.G., Burk, J.H., Fernau, R.F., 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. *Conserv. Biol.* 9, 902–914.
- Minnich, R.A., Barbour, M.G., Burk, J.H., Sosa-Ramirez, J., 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Mártir, Baja California, Mexico. *J. Biogeogr.* 27, 105–129.
- Minnich, R.A., Vizcaino, E.F., 1998. *Land of Chamise and Pines: Historical Accounts and Current Status of Northern Baja California's Vegetation*. University of California Press.
- Morgan, P., Aplet, G.H., Haufler, J.B., Humphries, H.C., Moore, M.M., Wilson, W.D., 1994. Historical range of variability: a useful tool for evaluating ecosystem change. *J. Sustain. For.* 2, 87–111.
- Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C., Beissinger, S.R., 2008. Impact of a century of climate change of small-mammal communities in Yosemite National Park, USA. *Science* 322, 261–266.
- Murphy, K.L., Klopatek, J.M., Klopatek, C.C., 1998. The effects of litter quality and climate on decomposition along an elevational gradient. *Ecol. Appl.* 8, 1061–1071.
- Parsons, D.J., DeBenedetti, S.H., 1979. Impact of fire suppression on a mixed-conifer forest. *For. Ecol. Manage.* 2, 21–33.
- Passini, F.M., Delgadillo, J., Salazar, M., 1989. L'écosystème forestier de Basse Californie: composition floristique, variables écologiques principales, dynamique. *Acta Oecologica Plantarum* 10 (3), 275–293.

- Peinado, M., Aguirre, J.L., Delgadillo, J., 1997. Phytosociological, bioclimatic and biogeographical classification of woody climax communities of western North America. *J. Veg. Sci.* 8, 505–528.
- Peinado, M., Alcaraz, F., Delgadillo, J., Aguado, I., 1994a. Fitogeografía de la península de Baja California, México. *Anales del Jardín Botánico de Madrid* 51 (2), 255–277.
- Peinado, M., Batrolomé, C., Delgadillo, J., Aguado, I., 1994b. Pisos de vegetación de la Sierra de San Pedro Mártir, Baja California, México. *Acta Botánica Mexicana* 29, 1–20.
- Rivera Huerta, H., Safford, H.D., Miller, J.D., Patterns and trends in burned area and fire severity 1984–2010 in the Sierra de San Pedro Mártir, Baja California, México, *Fire Ecology*, in press.
- Safford H.D., Stevens J.T., Natural Range of Variation (NRV) for yellow pine and mixed conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. General Technical Report PSW-GTR-___, USDA Forest Service, Pacific Southwest Research Station, Albany, CA, in press.
- Safford, H.D., Hayward, G.D., Heller, N.E., Wiens, J.A., 2012. Historical ecology, climate change, and resource management: can the past still inform the future? In: Wiens, J.A., Hayward, G.D., Safford, H.D., Giffen, C.M. (Eds.), *Historical Environmental Variation in Conservation and Natural Resource Management*. John Wiley & Sons Ltd., pp. 46–62.
- Safford, H.D., Van de Water, K.M., 2014. Using Fire Return Interval Departure (FRID) analysis to map spatial and temporal changes in fire frequency on National Forest lands in California. USDA For. Serv. Res. Pap. PSW-RP-166, 1–59.
- Savage, M., 1997. The role of anthropogenic influences in a mixed-conifer forest mortality episode. *J. Veg. Sci.* 8, 95–104.
- Skinner, C.N., 2002. Influence of fire on the dynamics of dead woody material in forests of California and southwestern Oregon. USDA For. Serv. General Tech. Rep. PSW-GTR 181, 445–454.
- Skinner, C.N., Burk, J.H., Franco-Vizcaino, E., Stephens, S.L., 2008. Long-term influences of climate on fire regimes in montane forests of northwestern Mexico. *J. Biogeogr.* 35, 1436–1451.
- Skinner C.N., Chang C., 1996. Fire regimes, past and present. Sierra Nevada Ecosystem Project: Final Report to Congress. Volume II: Assessments and scientific basis for management options, Centers for Water and Wildland Resources, University of California–Davis, 1042–1069.
- SSP, 2010. Framework for cooperative conservation and climate adaptation for the southern Sierra Nevada and Tehachapi Mountains. Southern Sierra Partnership, California, USA. Online at: <http://www.southernsierrapartnership.org/uploads/2/3/7/6/23766303/ssp_framework_-_volume_1.pdf>.
- Stark, N.M., 1973. Nutrient Cycling in a Jeffrey Pine Ecosystem. Institute for Microbiology, University of Montana, Missoula, MT.
- Steel, Z.L., Safford, H.D., Viers, J.H., 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere* 6, Art 8.
- Stephens, S.L., Fulé, P.Z., 2005. Western pine forests with continuing frequent fire regimes: possible reference sites for management. *J. Forest.* 103, 357–362.
- Stephens, S.L., 2004. Fuel loads, snag abundance, and snag recruitment in an unmanaged Jeffrey pine-mixed conifer forest in Northwestern Mexico. *For. Ecol. Manage.* 199, 103–113.
- Stephens, S.L., Fry, D.L., 2005. Spatial distribution of regeneration patches in an old-growth *Pinus Jeffrey-mixed* conifer forest in northwestern Mexico. *J. Veg. Sci.* 16, 693–702.
- Stephens, S.L., Fry, D.L., Franco-Vizcaino, E., 2008. Wildfire and spatial patterns in forests in Northwestern Mexico: the United States wishes it had similar fire problems. *Ecol. Soc.* 13.
- Stephens, S.L., Gill, S.J., 2005. Forest structure and mortality in an old-growth Jeffrey pine-mixed conifer forest in north-western Mexico. *For. Ecol. Manage.* 205, 15–28.
- Stephens, S.L., Skinner, C.N., Gill, S.J., 2003. Dendrochronology-based fire history of Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir, Mexico. *Can. J. For. Res.* 33, 1090–1101.
- Sugihara, N.G., van Wagtenonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), 2006. *Fire in California's Ecosystems*. University of California Press, Berkeley, CA.
- Swetnam, T.W., 1993. Fire history and climate change in giant sequoia groves. *Science* 262, 885–885.
- Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied historical ecology: using the past to manage for the future. *Ecol. Appl.* 9, 1189–1206.
- Tapia, M., 1992. Twenty years of weather and observing statistics in San Pedro Mártir, Baja California, Mexico. *Revista Mexicana de Astronomía y Astrofísica* 24, 179–186.
- Thorne, R.F., Moran, R.V., Minnich, R.A., 2010. Vascular plants of the high Sierra San Pedro Mártir, Baja California, Mexico: an annotated checklist. *Aliso* 28, 1–57.
- Tingley, M.W., Monahan, W.B., Beissinger, S.R., Moritz, C., 2009. Birds track their Grinnellian niche through a century of climate change. *Proc. Natl. Acad. Sci.* 106, 19367–19643.
- USDA, 2006. *Ecosystem Restoration: A Framework for Restoring and Maintaining the National Forests and Grasslands*. US Department of Agriculture, Forest Service, Washington, DC. Online at: <http://www.fs.fed.us/restoration/documents/RestFramework_final_010606.pdf>.
- USDA, 2015. Lake Tahoe Basin Management Unit Draft Forest Plan. USDA Forest Service, South Lake Tahoe, CA.
- Wagtenonk, J.W., Benedict, J.M., Sydorik, W.M., 1996. Physical properties of woody fuel particles of Sierra Nevada conifers. *Int. J. Wildland Fire* 6, 117–123.
- Van Wagtenonk, J.W., Moore, P.E., 2010. Fuel deposition rates of montane and subalpine conifers in the central Sierra Nevada, California, USA. *For. Ecol. Manage.* 259, 2122–2132.
- Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. *J. Am. Stat. Assoc.* 58, 236–244.
- Wiggins, I.L., 1980. *Flora of Baja California*. Stanford University Press, Stanford, Calif.
- Zack, S., George, T.L., Laudenslayer Jr., W.F., 2002. Are there snags in the system? Comparing cavity use among nesting birds in “snag-rich” and “snag-poor” eastside pine forests. In: General Technical Report PSW-GTR-181. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.