

RESEARCH ARTICLE

CORROBORATING EVIDENCE OF A PRE-EURO-AMERICAN LOW- TO MODERATE-SEVERITY FIRE REGIME IN YELLOW PINE–MIXED CONIFER FORESTS OF THE SIERRA NEVADA, CALIFORNIA, USA

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ABSTRACT

Fire was the dominant ecological process controlling forest structure and succession in western North American conifer forests for thousands of years. Because fires are now suppressed, and because widespread logging has greatly altered vegetation structure, land managers often use estimates of pre-Euro-American settlement forest conditions to help guide restoration actions. It follows that it is important to fully understand the characteristics of pre-Euro-American settlement fire regimes. Percentages of high-severity fire, fire rotation period, and proportions of early, mid, and late developmental forests are intricately and inextricably linked. Early twentieth century vegetation maps that appear to reflect aspects of pre-settlement forest conditions demonstrate that large patches of montane chaparral, which is often an early seral community in yellow pine-mixed conifer forests, were mostly restricted to steep south-facing canyon slopes at higher

RESUMEN

El fuego fue el proceso ecológico dominante, que controló la estructura y sucesión en los bosques de coníferas del oeste de Norte América por miles de años. Dado que los fuegos son ahora extinguidos rápidamente y que la tala extensiva ha alterado la estructura original de la vegetación, los gestores de tierras se remiten frecuentemente a las condiciones de los bosques previas a la colonización europea para ayudar a guiar acciones de restauración. De esto se deduce la importancia de entender completamente las características de los regímenes de fuegos previos a la llegada de la colonización europea. Los porcentajes de fuegos de alta severidad, el período de rotación de los fuegos, y las proporciones de bosques en estados serales de desarrollo inicial, medio, y maduro son intrincados e inexorablemente ligados entre sí. Los mapas de vegetación de principios del siglo XX, que parecieran reflejar aspectos de las condiciones de los bosques previos a la colonización, demuestran que grandes parches de chaparral montano, que es frecuentemente una comunidad seral inicial en bosques mixtos de pino amarillo, estaban mayormente restringidos a laderas escarpadas con orientación sur y en ele-

elevations associated with fir or subalpine forests. When resampled to a 16 ha minimum mapping unit, we found that an early twentieth century vegetation map shows montane chaparral occupied only about five percent of the landscape outside of areas that were highly impacted by gold rush era mining. We found that successional modeling suggests that similar levels (7%) of high severity per fire in pre-settlement yellow pine-mixed conifer forests in the Sierra Nevada would permit about half of the forested area to reach late development state, consistent with other estimated amounts of pre-settlement old-growth forests. In contrast, we found that high levels (30%) of high severity per fire—the current average—would result in only about 13% of forests in a late development state. We do not see evidence that large proportions of high-severity fire were typical during pre-settlement fires in yellow pine-mixed conifer forests in our study area.

vaciones altas, asociadas a abetos o bosques subalpinos. Cuando re-muestreamos una unidad mínima de mapeo equivalente a 16 ha, encontramos que un mapa de vegetación de principios del siglo XX muestra que el chaparral montano ocupaba solo el 5% del paisaje por fuera de las áreas que habían sido altamente impactadas por la minería desarrollada durante la era correspondiente a la fiebre del oro. Encontramos que el modelado sucesional sugiere que previo a la colonización europea, similares niveles (7%) de alta severidad de cada fuego en bosques mixtos de pino amarillo, permitiría que casi la mitad del área boscosa llegara al último estadio de desarrollo seral, lo que es consistente con otras estimaciones de abundancia de bosques maduros en el período previo a la colonización. En contraste con esto, encontramos que altos niveles de severidad (30%) de cada fuego (el promedio actual) resultaría en que solo el 13% de los bosques lleguen al estado de desarrollo seral maduro. No encontramos evidencia de que grandes proporciones de incendios altamente severos fuesen típicos durante el período previo a la colonización en bosques de pino amarillo in nuestra área de estudio.

Keywords: California, fire severity, mixed conifer, pre-settlement, Sierra Nevada, southern Cascades, succession, yellow pine

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INTRODUCTION

In many ecosystems throughout the western USA, fire is the key ecological process influencing, among other things, forest structure, wildlife and plant habitat, and subsequent fire behavior (Pyne 1982, Sugihara *et al.* 2006a). Because fire has been excluded from most of these ecosystems for the last century, land managers often use estimates of pre-Euro-American settlement fire regimes and forest conditions to help develop forest restoration

goals (Landres *et al.* 1999, North *et al.* 2009, Long *et al.* 2014). Since little is known about how a changing climate and projected increases in fire activity will affect future species distributions and forest structures, specific restoration targets based solely upon restoring and maintaining historical conditions may be inappropriate (Millar *et al.* 2007, Halofsky *et al.* 2014). Nonetheless, historical reference information is valuable for understanding how current conditions arose, as well as for developing a mechanistic understanding of ecosystem dy-

namics that may permit predictions of future conditions (Swetnam *et al.* 1999; Fulé 2008; Safford *et al.* 2012a, b).

Sugihara *et al.* (2006a) described seven fundamental attributes of a fire regime: seasonality, fire frequency (or its inverse, fire return interval [FRI]), fire size, spatial complexity (e.g., high-severity patch size and distribution), intensity, severity, and fire type (i.e., surface, passive crown, active crown, or independent crown). Fire frequency (fire rotation, defined as the time needed for an area the size of the study area to burn, is the areal equivalent) and either fire type or severity (as a surrogate for intensity) are often used by ecologists to characterize different fire regimes (e.g., frequent, low severity; infrequent, high severity; etc.) as they are relatively easily measured, and their relationship is broadly inverse and fairly well understood (Heinselman 1978, Hardy *et al.* 2001, Steel *et al.* 2015).

One of the most profound effects of Euro-American settlement in California was the near extinction of fire as an ecological process, beginning with the decimation of the Native American population in the nineteenth century, and followed by a policy of fire exclusion in the early twentieth century (Cook 1978, Kilgore and Taylor 1979, Anderson 2005, Stephens *et al.* 2007, Mallek *et al.* 2013). In the last few decades, there has been an increase in the amount of high-severity fire observed in some of these California forests (Miller *et al.* 2009, Miller and Safford 2012, Mallek *et al.* 2013, Stephens *et al.* 2016), and the evidence is strong that this trend is driven by an interaction between the warming climate and forest fuel accumulations resulting from the long-term absence of fire (Safford and Van de Water 2014, Steel *et al.* 2015, Safford and Stevens 2017). In California, the trend of increasing fire severity is most strongly seen in yellow pine and mixed conifer forest types in the Sierra Nevada, which historically supported fire regimes of very frequent, mostly lower-severity fire (van Wagtendonk *et al.* 2017, Fites-

Kaufman *et al.* 2007, Van de Water and Safford 2011).

Yellow pine forests in California are characterized by the occurrence of one or both of the yellow pine species: ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Jeffrey pine (*P. jeffreyi* Balf.). Many other tree species overlap the geographic distribution of yellow pine in California, including sugar pine (*P. lambertiana* Douglas), white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), incense-cedar (*Calocedrus decurrens* [Torr.] Florin), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and black oak (*Quercus kelloggii* Newberry) (Sawyer *et al.* 2008). Difficulties in differentiating obvious forest types have led to the general recognition of a mixed conifer type (e.g., Fites-Kaufman *et al.* 2007). Yellow pine-mixed conifer (YPMC) forests are the focus of much attention in California because: (1) they are the most widespread forest type on land managed by the federal resource agencies; (2) they support most of the habitat for several old-forest obligate carnivores and raptors, whose declining populations are of conservation concern; and (3) they include a majority of the wildland urban interface (USDA 2004, Zielinski *et al.* 2013, Tempel *et al.* 2014). The preponderance of existing literature describes YPMC forests in California to have historically supported fire regimes characterized by frequent low- to moderate-severity fires that maintained a heterogeneous uneven-aged forest structure with large fire-resistant trees by opening small canopy gaps and thinning out most regenerating trees (see Safford and Stevens 2017 for a summary). However, fire frequency and patterns of severity varied due to factors such as topographic position and complexity, and site water balance (Beaty and Taylor 2001, Long *et al.* 2014, Kane *et al.* 2015).

Recently, a few authors (e.g., Baker 2014, 2015; Odion *et al.* 2014) have challenged the low- to moderate-severity paradigm for YPMC forests, and assert that fires in these forests

previously resulted in extensive amounts of high-severity fire and high-severity patch sizes similar to modern fires. These authors reached their conclusions by comparing estimates of modern high-severity fire rotations to pre-settlement fire rotations calculated from fires that occurred during the California Gold Rush era (e.g., Leiberger 1902) or through the use of methods that are based upon an assumption that tree establishment is primarily linked to high-severity fire. These methods are problematic for several reasons. First, effects of fires caused by California Gold Rush era activities did not necessarily represent the pre-settlement fire regime (Safford and Stevens 2017). Second, tree establishment in dry forests is more closely linked to periodic wet episodes or longer fire-free periods (Fulé *et al.* 2014). Finally, comparing high-severity rotations does not answer the question of how fire behavior differs in individual modern fires, on average, compared with pre-settlement fires. The difference between the two questions is important. The average proportion of high severity per fire is typically used as a description of the fire regime (Sugihara *et al.* 2006a). Proportion of high severity per fire is important because it is related to high-severity patch size (van Wagtenonk and Lutz 2007). In Sierra Nevada YPMC forests, high-severity patches often result in early seral shrub patches, which subsequently nearly always burn at high severity (van Wagtenonk 2012, van Wagtenonk *et al.* 2012). It is the average proportion of high severity, therefore, that, when coupled with fire rotation, describes how fire would have driven high-severity patch size, subsequent successional patterns, and the amount of young and old forests that could exist on a landscape (Sugihara *et al.* 2006a).

In this manuscript, we investigate underexploited data sources to provide insight into the amount of high-severity burning that characterized the average pre-settlement fire. These include late nineteenth and early twentieth century accounts and datasets, as well as con-

temporary forest dynamics modeling. Accounts and data from near the turn of the twentieth century are valuable because (1) at that time, FRIs were likely still within or near their long-term range of variability (Van de Water and Safford 2011); and (2) because it can take many decades for forests to reestablish in severely burned areas, these early sources from areas relatively less impacted by Euro-American settlement activities may also contain useful insights about pre-settlement rates of high-severity fire (Wilken 1967, Russell *et al.* 1998, Nagel and Taylor 2005, Knapp *et al.* 2013). Based on these and other data sources, modeling efforts can be used to develop mechanistic models of forest and fire dynamics that can provide insight into the amount of young versus old forest conditions that would likely result from different scenarios of fire frequency and severity (Swetnam and Brown 2010).

We use these early accounts and datasets to ask the following questions. First, how does the amount of early seral vegetation in early twentieth century vegetation maps in areas highly impacted by California Gold Rush activities compare with areas that were less impacted? And how do the early twentieth century vegetation maps compare with late twentieth century maps? Second, using state-and-transition simulations, we compare proportions of early, mid, and late development mixed conifer forests that would result from two different proportions of fire severities representing the best estimates for the pre-settlement regime and the modern regime, retaining well-established pre-settlement FRIs in both cases.

METHODS

Study Area

This study primarily focused on areas managed under the Sierra Nevada Forest Plan Amendment (SNFPA) by the USDA Forest Service (USDA 2004), and National Park Ser-

vice managed lands within the SNFPA boundary. This region is approximately the area assessed by the Sierra Nevada Ecosystem Project (SNEP) and is often called the SNEP area (Figure 1). The SNEP study area consists primarily of the Sierra Nevada, but also includes the Modoc Plateau and Warner Mountains, the White-Inyo Mountains, and portions of the southern Cascades. Because the original Wieslander vegetation-type maps (VTM, described below) that we used were created by drawing polygons directly on United States Geological Survey (USGS) quadrangle map sheets (Kelly and Allen-Diaz 2005) that do not conform to the SNEP boundary, we restricted most of our analyses to the least common denominator boundary defined by the VTM, national parks, and national forests (NF) in the Forest Service's Pacific Southwest Region that intersect the SNEP area (Figure 2).

Our study focused primarily on two conifer-dominated forest types in the study region: yellow pine forests and woodlands dominated by ponderosa pine or Jeffrey pine, and mixed conifer forests with three or more co-dominant conifer species, including various mixtures of ponderosa pine, Jeffrey pine, sugar pine, white fir, incense-cedar, Douglas-fir, and giant sequoia (*Sequoiadendron giganteum* [Lindl.] J. Buchholz), plus hardwoods such as black oak, canyon live oak (*Quercus chrysolepis* Liebm.), interior live oak (*Q. wislizenii* A. DC.), and tanoak (*Notholithocarpus densiflorus* [Hook. & Arn.]). Sawyer *et al.* (2008) describe almost 20 forest alliances that make up the montane mixed conifer forest, but, for this study, we follow common practice (e.g., Barbour *et al.* 2007, Steel *et al.* 2015, Safford and Stevens 2017) and treat mixed conifer forests as a single type. The lower elevation of ponderosa pine dominated forests is 300 m to 400 m in the northern portion of the study area and increases to over 1000 m in the southern Sierra Nevada, but also depends upon aspect, soil depth, etc. (Storer and Utsinger 1963, Fites-Kaufman *et al.* 2007). Jeffrey pine dominated

forests occur mostly between 1500 m and 2400 m in the northern subregion, and from 1700 m to 2800 m in the southern Sierra Nevada (Barbour and Minnich 2000, Fites-Kaufman *et al.* 2007). A large area east of the Sierra Nevada crest supports a mixed yellow pine forest co-dominated by ponderosa and Jeffrey pine, commonly referred to as eastside pine. The upper elevation of yellow pine and lower elevation of mixed conifer overlap. At the upper elevational limit of mixed conifer (1700 m to 2200 m in elevation, depending on latitude), red fir (*A. magnifica* A. Murray bis), western white pine (*Pinus monticola* Douglas ex D. Don), and lodgepole pine (*Pinus contorta* Douglas ex Loudon) can be found (Safford and Stevens 2017).

We combine yellow pine and mixed conifer forests in this study for two reasons. First, under most ecological circumstances, they are successional related (Safford and Stevens 2017). Historically, frequent fire that usually burned at low to moderate severity led to the maintenance of yellow pine dominated stands, primarily found in relatively more xeric topographic settings, by removing more fire sensitive shade tolerant fir and cedar species. Mixed conifer forests would have had slightly longer fire return intervals and would have occurred in more mesic settings. Over the last century, yellow pine forests have become rare on the west side of the Sierra Nevada due to logging and fire suppression-driven succession to mixed conifer stands dominated by more shade tolerant and fire intolerant species like white fir and incense-cedar (Parsons and DeBenedetti 1979, North *et al.* 2007, Thorne *et al.* 2008, Scholl and Taylor 2010). Second, other than the slightly different fire return intervals, yellow pine and mixed conifer forests in California have very similar fire regime characteristics (Weaver 1974, Sugihara *et al.* 2006b, Van de Water and Safford 2011, Safford and Stevens 2017).

In this study, we also focus on montane chaparral, which is often the early seral result

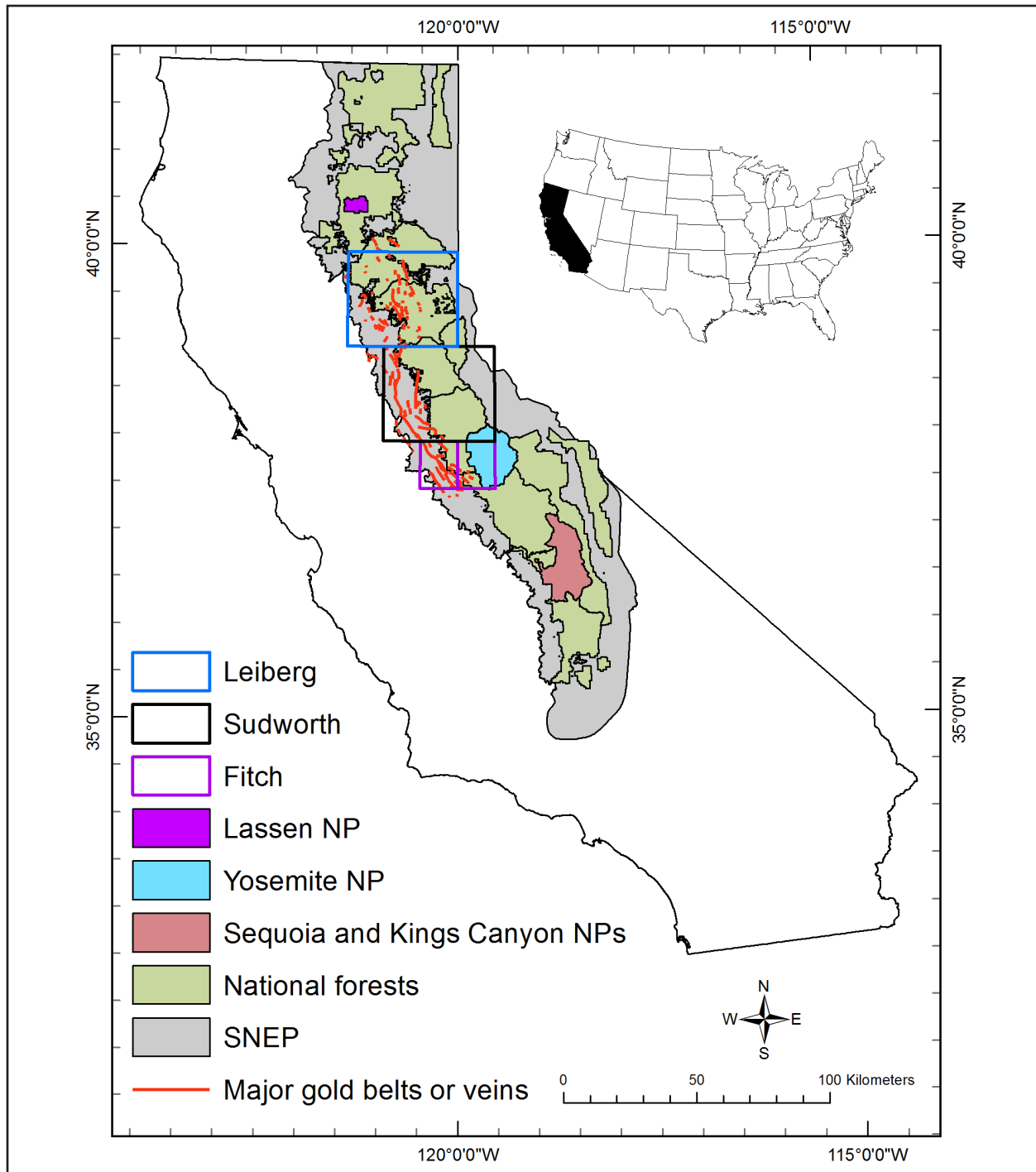


Figure 1. Sierra Nevada Ecosystem Project (SNEP) study area showing the areas surveyed by Leiberg (1902), Sudworth (1900), and Fitch (1900a, b; Sonora and Yosemite quadrangles, left to right, respectively) in the late nineteenth century. National Forests (NF) and National Parks (NP) north to south include Modoc NF, Lassen NF, Lassen NP, Plumas NF, Tahoe NF, Lake Tahoe Basin Management Unit, Eldorado NF, Stanislaus NF, Yosemite NP, Inyo NF, Sierra NF, Sequoia and Kings Canyon NPs, and Sequoia NF. Within Leiberg's study area, major gold belts or veins occur within national forest boundaries (Plumas and Tahoe NFs), but they primarily occur below the elevation of the national forests south of Leiberg's study area (gold belts or veins adapted from Clark 1970).

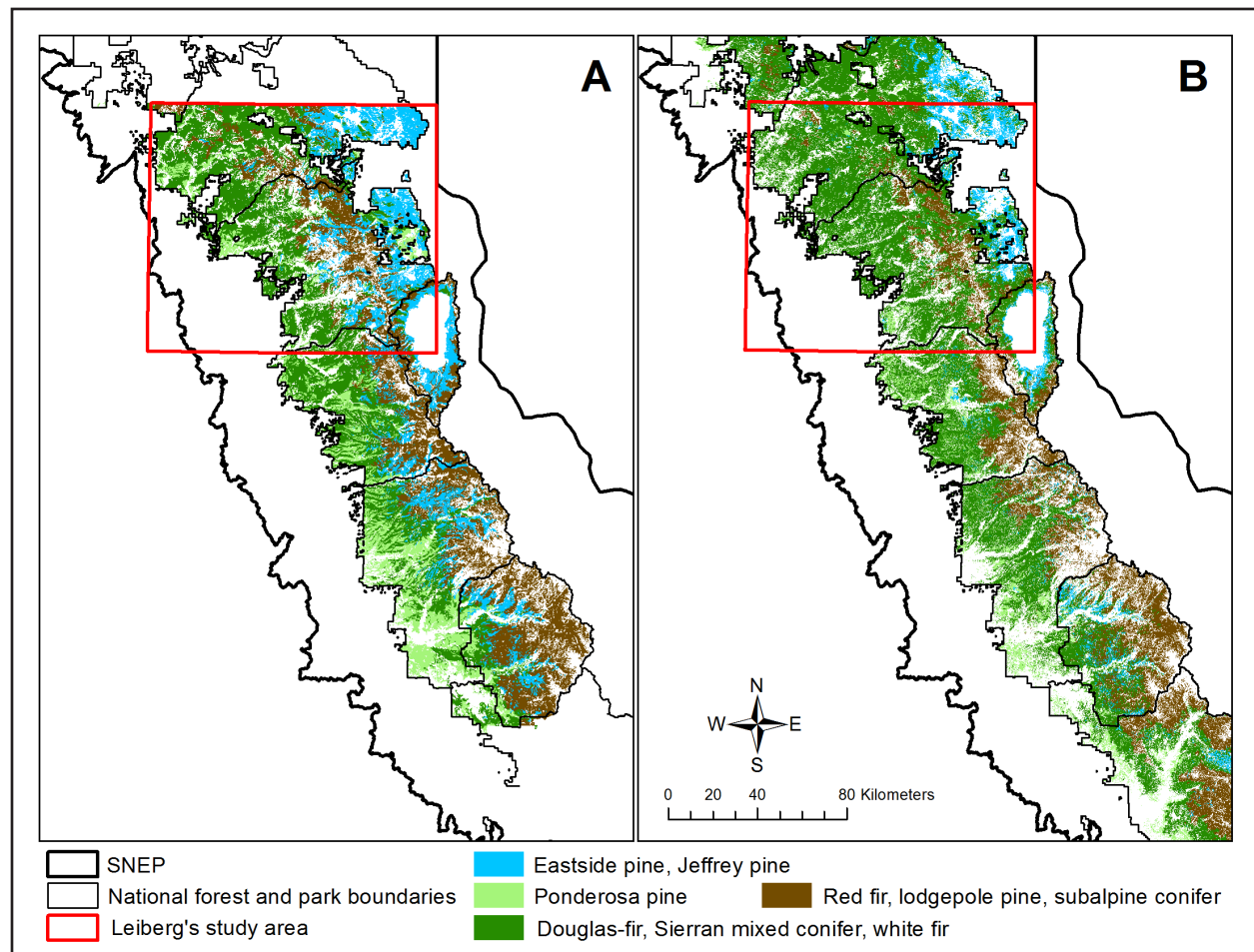


Figure 2. Major conifer vegetation types in the early and late twentieth century A) Wieslander vegetation type map (VTM) (Thorne *et al.* 2006, Thorne *et al.* 2008), and B) existing vegetation (CALVEG) (Keller-Wolf 2007) circa 2000 to 2009 (online at <http://www.fs.usda.gov/detail/r5/landmanagement/resource-management/?cid=stelprdb5347192>). Data are restricted to National Forests (NF) and National Parks (NP) boundaries, listed north to south: Lassen NF, Plumas NF, Tahoe NF, Lake Tahoe Basin Management Unit, Eldorado NF, Stanislaus NF, Yosemite NP, and Sierra NF.

of severe disturbance in YPMC forests (e.g., logging, fire, or erosion; Risser and Fry 1988, Kaufmann and Martin 1991). Montane chaparral is composed of one or more shrub species such as deerbrush (*Ceanothus integerrimus* Hook. & Arn.), mountain whitethorn (*Ceanothus cordulatus* Kellogg), snowbrush ceanothus (*C. velutinus* Douglas ex Hook.), or greenleaf manzanita (*Arctostaphylos patula* Greene). After severe fire, montane chaparral may delay conifer establishment for many decades, and it may persist for centuries in the event of recurrent fires (Wilken 1967, Pinder

et al. 1997, Taylor and Skinner 2003, Nagel and Taylor 2005, Lauvaux *et al.* 2016). In some cases, montane chaparral can also form an edaphic quasi-climax community on shallow, low productivity soils (Risser and Fry 1988), but these sites can also succeed to conifer over a longer time frame. Montane chaparral occurs throughout the range of YPMC forests and should not be confused with other, lower elevation chaparral types dominated by shrub species that are not typically seral to conifer forest (e.g., chamise [*Adenostoma fasciculatum* Hook. & Arn.], buckbrush [*Ceanothus*

cuneatus {Hook.} Nutt.], toyon [*Heteromeles arbutifolia*], silk tassel bush [*Garrya* spp.], chaparral pea [*Pickeringia montana* Nutt.], or shrub oaks like *Q. berberidifolia* Liebm.). These lower elevation chaparral types are probably best viewed as climax vegetation types, and tend to occur on drier sites with thin soils; at higher elevations, they are often restricted to steep south and west facing canyon slopes (England 1988*a, b*; Risser and Fry 1988).

Background on Late Nineteenth and Early Twentieth Century Accounts and Datasets

After the establishment of the federal Forest Reserves, beginning in 1891, the USGS and Forest Service produced a series of reports that inventoried and described merchantable timber. Most of the surveys conducted in California provide at least qualitative information on fire effects that can be used to infer severity (Fitch 1900*a, b*; Sudworth 1900; Cooper 1906; Larson and Woodbury 1916; Figure 1). Leiberg (1902) includes several maps detailing areas burned for a portion of the northern Sierra Nevada that have been used by some researchers as evidence of extensive pre-settlement high-severity fire (e.g., Baker 2014, 2015; Odion *et al.* 2014). Leiberg's study area encompassed not only YPMC forests but also upper montane forests dominated by red fir. The elevational boundary between mixed conifer and red fir forests in the Sierra Nevada coincides with a major ecological transition zone that corresponds to the approximate elevation of freezing in mid-winter storms, and the transition from rain-dominated to snow-dominated climate regimes (Safford and Van de Water 2014). Like yellow pine, pre-settlement mixed conifer forests in California were largely "fuel-limited" and characterized by frequent, lower-severity wildfires, whereas red fir forests were more "climate-limited" and thus characterized by less frequent, more severe wildfires (Barbour *et al.*

2002, Sugihara and Barbour 2006, Barbour *et al.* 2007, Safford and Van de Water 2014, Steel *et al.* 2015). Leiberg's study area had also been highly impacted by California Gold Rush era logging, mining, and grazing activities. Indeed, nearly all the major gold veins that occur on Forest Service lands in the Sierra Nevada are in Leiberg's study area (Figure 1). Forty-six out of 49 of the largest-scale hydraulic mining operations in the Sierra Nevada were found in Butte, Plumas, Yuba, Sierra, Nevada, and Placer counties, which comprise the majority of Leiberg's study area (Clark 1970). Logging activities prior to 1900 were not all well documented; however, existing records indicate that they were mostly associated with mining activities or supported development of local settlements (McKelvey and Johnston 1992, Beesley 1996). Leiberg (1902) reported that 44% of forests in his study area had been affected by some degree of logging, compared with 21% of Sudworth's study area (Sudworth 1900). Fitch (1900*a, b*) reported that there was not any logging activity in his study areas at the time of his surveys; however, at least some logging had occurred earlier (Hurt 1941). In summary, impacts from mining and logging at the time of the surveys had been far greater in northern Sierra Nevada compared with the central and southern Sierra Nevada (Clark 1970, Beesley 1996, Gruell 2001).

In the early twentieth century, the USDA Forest Service published a series of reports that supported the imposition of a full fire exclusion policy. The reports provide the most detailed broad scale summary information on vegetation and fire effects in pine dominated forests produced up until that time for California, including information on number of ignitions, ignition sources, and fire sizes (Show and Kotok 1923); fire statistics stratified by vegetation type (Show and Kotok 1929); and tree mortality due to fire (Show and Kotok 1924, 1925).

The Vegetation Type Map (VTM) project funded by the Forest Service and headed by

Albert Wieslander developed the first comprehensive vegetation map for portions of California (Wieslander 1935*a, b*). Beginning in 1928 and continuing up until World War II, the project surveyed over 17000 vegetation plots and mapped the vegetation for approximately 35 % of the state and about 60 % of Forest Service lands, including the areas surveyed by Leiberg, Sudworth, and Fitch (online at <http://vtm.berkeley.edu>). The vegetation maps provide the extent (polygons) and the plots provide composition and structure. The maps were created by surveyors by drawing polygons directly onto USGS topographic maps. Plots were then established within the polygons to measure representative conditions (Wieslander 1935*a*). The plot data have most often been used to contrast early and late twentieth century forest conditions (e.g., Dolanc *et al.* 2013, 2014). The map data have only been infrequently used to this point, but the map sheets were recently digitized and georeferenced, and vegetation types crosswalked to equivalent types in late twentieth century maps (Thorne *et al.* 2006, 2008). As a result, the map data are now usable for spatial analysis and can be used to provide broad-scale spatial estimates of vegetation-type cover.

Limitations of Early Accounts and Datasets

When extrapolating information presented in late nineteenth and early twentieth century reports and datasets to pre-settlement forests, it is important to understand that changes in ignition patterns, and extensive mining, logging, and grazing had already begun to transform the conifer forests of California when these data were collected and reports written. Lightning ignition patterns likely did not substantially change between pre-settlement times and the early twentieth century, but human ignition patterns undoubtedly did. The occurrence of lightning strikes decreases from east to west, and is low in the western foothills and lower slopes of the Sierra Nevada where Na-

tive American populations were densest (Cook 1978, van Wagtendonk and Cayan 2008). There is disagreement among researchers as to the extent of the impact of Native American ignitions on the Sierra Nevada landscape (Parker 2003), but the high pre-Euro-American settlement fire frequencies seen in oak woodlands and lower elevation conifer forests in the Sierra Nevada were likely due in part to Native American practice. In at least some locations, there is evidence that ignitions by Native Americans associated with foraging practices played a role in reducing surface fuels and thinning lower to middle elevation mixed conifer and pine forests (Reynolds 1959, Anderson 2005, Morgan 2008). Historical accounts indicate that many fires ignited by Native Americans were ignited in the fall when negative impacts to food resources would be minimized (Anderson 2005, Morgan 2008). In contrast, most human ignited fires during the early part of the twentieth century occurred in July and August when there is a higher risk of escaping control and extreme fire behavior (Show and Kotok 1923). Ignitions by Native Americans had largely been eliminated by the mid 1800s as the Native American population had been reduced by >80 % by 1855, and most of the remaining population removed to reservations (Cook 1978, Kilgore and Taylor 1979, Dutschke 1988).

Logging practices contributed greatly to the spread and severity of early settlement forest fires. Logging practices in those days left all slash (tree limbs, tops, and discarded parts) on site, which greatly increased surface fuels. As a result, settler-ignited fires were much more likely to result in severe effects to the forest than fires before settlement commenced (Sudworth 1900, Leiberg 1902). Organized, active suppression of fires in California began after the establishment of Yosemite, Sequoia, and General Grant national parks in 1890, the first Forest Reserves in 1892, and the Forest Service in 1905 (Cermak 2005, van Wagtendonk 2007). As a result, most fire history stud-

ies show a dramatic decrease in fires after about 1900 throughout the Sierra Nevada (Kilgore and Taylor 1979, Caprio and Swetnam 1995, Taylor 2000, Collins and Stephens 2007, Scholl and Taylor 2010).

Vegetation Data

We used two spatial vegetation datasets in this study: 1) Wieslander VTM, and 2) the most recent version of the Forest Service CALVEG (Classification and Assessment with Landsat of Visible Ecological Groupings) existing vegetation maps.

The VTM from the 1930s is the earliest comprehensive vegetation map for California (Barbour and Major 1988). Recently, the VTM map sheets covering a contiguous 30236 km² area of the Sierra Nevada, stretching from the southern half of the Plumas NF south through Yosemite National Park (NP), were digitized and the VTM vegetation types were crosswalked to the California Wildlife Habitat Relationship (CWHR) types (Mayer and Laudenslayer 1988; Thorne *et al.* 2006, 2008; Figure 2). Although there are map polygons smaller than 1 ha, the minimum mapping unit (MMU) was typically around 16 ha (Wieslander *et al.* 1933, Thorne *et al.* 2006).

Technically, CALVEG is a vegetation classification scheme used by the Forest Service in California to map existing vegetation (Matyas and Parker 1980, Keeler-Wolf 2007, USDA 2014). However, we follow standard practice and also refer to the vegetation map data as CALVEG. The CALVEG MMU is considered to be approximately 1 hectare. We used the most recent CALVEG vegetation data with mapping dates 2000 to 2009 (USDA 2014). In addition to being labeled by CALVEG vegetation type, map polygons are also labeled with CWHR type (Mayer and Laudenslayer 1988), which we used for our analyses to facilitate comparison with the VTM. We modified the CALVEG data where some forested areas on the Plumas NF that had been severely burned just prior to being mapped in 2000 were

mapped as barren. For this study, we counted those areas as early seral montane chaparral.

Analyses

Vegetation data. Montane chaparral is often an early seral condition for YPMC forests in the Sierra Nevada (Risser and Fry 1988, Kaufmann and Martin 1991). Montane chaparral can persist for more than a century, and will only transition back to conifer forest if not reburned in a subsequent fire (Wilken 1967, Russell *et al.* 1998, Nagel and Taylor 2005). The occurrence of montane chaparral in the VTM is therefore a possible source of remnant evidence for the amount of high-severity fire that may have occurred since the California Gold Rush period and possibly before. It could thus be expected that there would be a larger amount of montane chaparral in the VTM map in areas that had experienced larger amounts of high-severity fire (e.g., during the California Gold Rush period) compared to those areas that had not. We therefore compared the VTM inside and outside Leiberg's (1902) study area to determine whether the documented differences in California Gold Rush era impacts between Leiberg's study area and further south were reflected in the amounts of montane chaparral (Figures 2 and 3). We also compared the VTM to CALVEG, both within and outside Leiberg's study area, to assess the impacts that the fire suppression era has had on the distribution of vegetation types.

Because the VTM and CALVEG datasets have different MMUs, and MMU can influence the proportion of map categories, we resampled both maps to 400 m × 400 m pixels (16 ha) before making any comparisons (Saura 2002). When resampling, we assigned pixels the value of the vegetation type with the maximum area within each 16 ha pixel. Comparisons were restricted to NF and Yosemite NP boundaries. Both Forest Service and privately managed lands within NF boundaries were included.

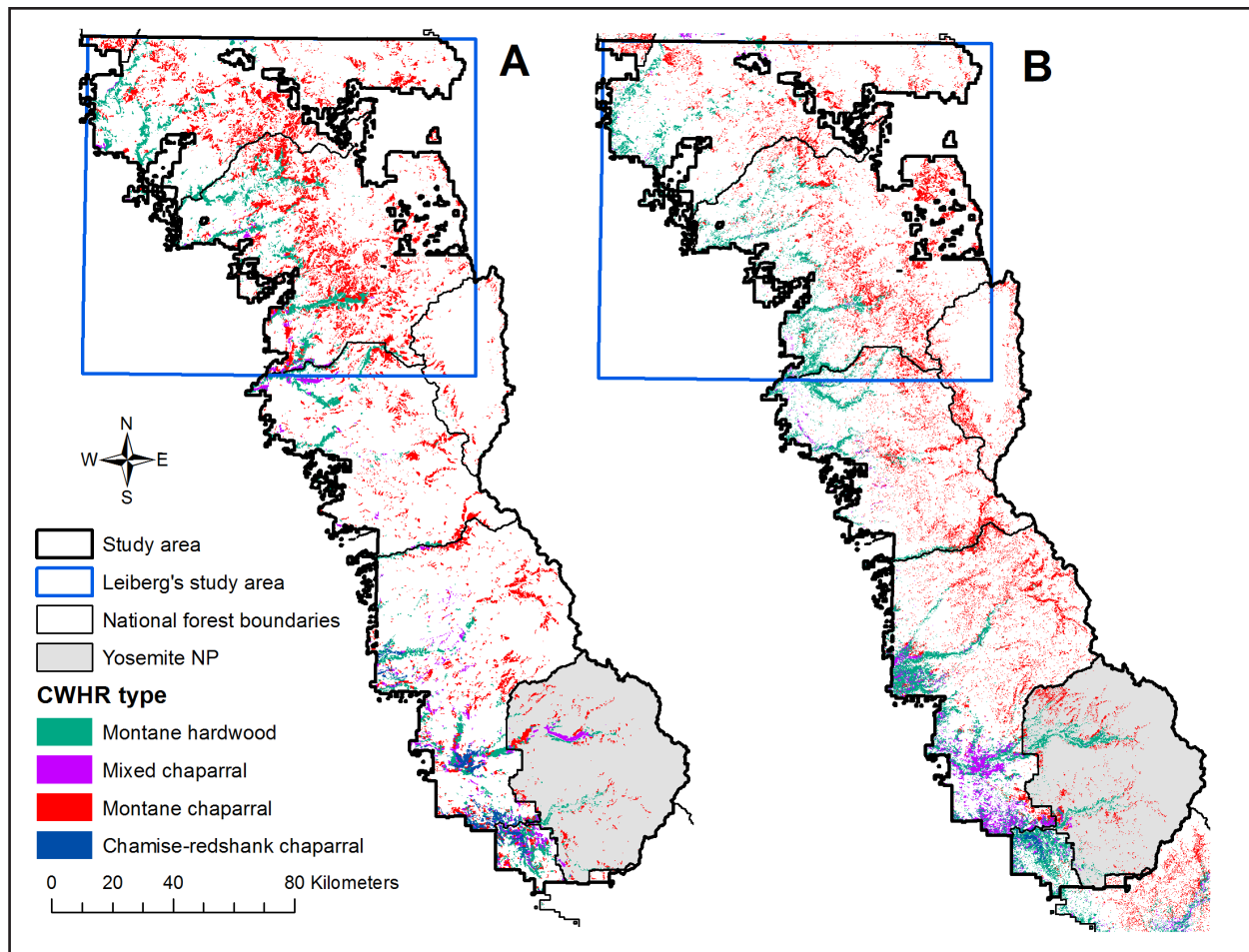


Figure 3. Comparison of areas mapped as chaparral and hardwood California wildlife habitat relationship (CWHR) types mapped in A) the Wieslander VTM and B) CALVEG. National Forests (NF) north to south include Plumas NF, Lake Tahoe Basin Management Unit, Tahoe NF, Eldorado NF, Stanislaus NF, and Sierra NF. Areas of extensive chaparral in the VTM that do not appear in CALVEG are primarily restricted to Leiberg's (1902) study area. Displayed data are in the original minimum mapping units (MMUs; i.e., not resampled).

Succession modeling. To estimate the proportion of young and old pre-settlement YPMC forests, we used the Vegetation Dynamics Development Tool (VDDT; ESSA 2007). The VDDT is an aspatial, nonequilibrium state-and-transition model (Stringham *et al.* 2003) that incorporates multiple ecosystem states linked by pathways representing deterministic and probabilistic transitions. The VDDT is a Monte Carlo simulator that uses random draws to determine the order and occurrence of disturbances, which may then drive probabilistic transitions (ESSA 2007).

We used the default LANDFIRE VDDT model for Mediterranean California Dry-Mesic mixed conifer forest and woodland (model 0610270; model and metadata available at http://www.landfire.gov/national_veg_models_op2.php) to represent pre-settlement YPMC forests. LANDFIRE VDDT models use the terminology of early, mid, and late development to designate growth stages (i.e., early = young forests, and late = old forests), and surface, mixed, and replacement for fire behavior and effects. We used the same growth stage terminology of early, mid, and

late in our manuscript to remain consistent. The VDDT state-and-transition models do not associate specific tree mortality thresholds with their fire effects terms. Surface fire usually results in the mortality of few overstory trees, whereas replacement fire usually means sufficient tree mortality to convert forest to non-forest (i.e., tree canopy cover of <10% [Brohman and Bryant 2005]). We therefore assumed, for the purpose of this manuscript, that the model's fire effects terms equate to low, moderate, and high severity (surface, mixed, and replacement, respectively). Fire frequency and severity vary substantially among the five states (development stage-structure combination; Table 1), in the model, but the overall mean FRI is approximately 11 years and the overall mean distribution of high-, moderate-, and low-severity fire is 7:30:63. These FRI and fire severity values are very close to pre-settlement reference values (e.g., Leiberg 1902, Van de Water and Safford 2011, Rivera-Huerta *et al.* 2016, Safford and Stevens 2017). To contrast forest conditions resulting from a hypothetical situation that reflects the proportions of severity in modern fires but retains all other aspects of the pre-settlement fire regime, we retained the structure of the 0610270 model, but proportionally and iteratively changed the fire transition probabilities among states until the distribution of fire severities approximated 30:22:48 (high:moderate:low), the mean severity distribution of Sierra Nevada fires between 1984 and 2010 (Mallek *et al.* 2013). Hereafter, we refer to these two models as the pre-settlement and hypothetical models. We began each simulation with 100% of the landscape in a late development closed state (late seral, closed forest, with canopy cover >50%). Both models were run for 10 simulations of 1000 years each, using the pre-settlement FRI of 11 years. We plotted the average percentage of the modeled landscape in each of three development states: early, mid, and late over time.

RESULTS

Vegetation Data

The percentage of montane chaparral within Leiberg's study area compared with outside was 2.4 times greater in the 1930s VTM map (12.0% versus 5.0%), but was only 1.2 times greater in modern CALVEG map (7.2% versus 5.8%; Table 2). Overall, the percentage of montane chaparral was 1.3 times greater in the VTM map than in CALVEG (8.2% versus 6.5%, respectively). However, the difference between VTM and CALVEG was largely restricted to Leiberg's study area. The VTM chaparral cover was 1.7 times greater than CALVEG inside Leiberg's study area (12.0% versus 7.2%, respectively) compared with 1.2 times less outside (5.0% versus 5.8%, respectively).

Most areas of montane chaparral in the VTM south of Leiberg's study area correspond to steep south-facing canyon slopes at upper elevations associated with red fir and subalpine conifer forests that match similar patches and locations in CALVEG (Figures 2 through 4; before resampling to 16 ha MMU, VTM mean, standard deviation, and maximum montane chaparral patch size = 33.2 ha, 82.3 ha, and 1640.2 ha, respectively). Areas of montane chaparral that appear in CALVEG but not the VTM are primarily due to recent fires or the smaller CALVEG minimum mapping unit of 1 ha versus 16 ha for the VTM (Figure 3). There are also minor differences due to discrepancies in areas mapped as hardwood versus chaparral vegetation types.

Comparing YPMC in the VTM to CALVEG, the percentage of yellow pine (CWHR types ponderosa pine, Jeffrey pine, and eastside pine) decreased by a factor of 2.6 times (28.2% versus 10.7%, respectively), and mixed conifer forests (CWHR types Douglas-fir, Sierran mixed conifer, and white fir) increased by a factor of 1.7 times (29.3% versus 48.8%, respectively), but combined,

Table 1. Vegetation states for the LANDFIRE biophysical setting Mediterranean California dry-mesic mixed conifer forest and woodland (LANDFIRE zone 6 model number 0610270, online at http://www.landfire.gov/national_veg_models_op2.php).

Class	Development state	Structure	Cover (%)	Height (m)	Tree diameter (cm)	Transition description
A	Early	All	0 to 100	0 to 10	<12.7	Either tree seedlings develop a nearly continuous canopy and class moves to Class B or C, or chaparral conditions may dominate. Replacement fire mean return interval (MFRI) = 50 yr, mixed fire MFRI = 200 yr. Annually, there is 0.01 probability of succeeding to Class B, and 0.005 probability of succeeding to Class C. After 50 yr, succeeds to Class B.
B	Mid	Closed	51 to 100	10.1 to 25	12.7 to 63.5	Replacement fire MFRI = 75 yr, 80 % of mixed fire (MFRI = 20 yr) moves area to Class C, 20 % of mixed fire stays in Class B. Surface fire MFRI = 36 yr. Insect or disease occurs ~200 yr, usually with little effect, but 20 % of occurrences move the area to Class C. After 50 yr, succeeds to Class E.
C	Mid	Open	0 to 50	10.1 to 25	12.7 to 63.5	Replacement fire MFRI = 315 yr, 83 % of mixed fire (MFRI = 30 yr) keeps area in Class C, 17 % of mixed fire resets area to Class A. Surface fire MFRI = 15 yr. Insect or disease occurs ~500 yr, usually with little effect. After ~35 yr without fire, these stands move to Class B. Patches stay in Class C >100 yr.
D	Late	Open	0 to 50	≥25.1	>63.5	Replacement fire MFRI >1000 yr. Mixed fire (MFRI = 30 yr) usually leaves patch in Class D, but rarely it can move to Class A. Surface fire MFRI = 11 yr maintains Class D. Insect or disease is rather rare (annual probability = 0.001). After 35 yr without fire, this class will transition to Class E.
E	Late	Closed	51 to 100	≥25.1	>63.5	Replacement fire MFRI = 160 yr, 50 % of mixed fires (MFRI = 60 yr) cause no transition, but mixed fire can move area to Class A (MFRI = 70 yr), or Class D (MFRI = 330 yr). Surface fires MFRI = 50 yr. Insect or disease mean return = 250 yr, and usually has little effect on stand structure, but 25 % of the time can move area to Class D.

the percentage of yellow pine and mixed conifer only slightly increased (57.5% versus 59.5%, respectively) (Table 2). The trends of decreasing yellow pine and increasing mixed conifer was consistent both inside and outside of Leiberg's study area.

Succession Modeling

State-and-transition simulations, using the original LANDFIRE 0610270 VDDT model representing 7% high severity (pre-settlement model), stabilized at around 700 years with

Table 2. Comparison of the Wieslander VTM and CALVEG for Forest Service and National Park Service lands within the VTM study area delineated in Figures 2A and 3A.

California wildlife habitat relationship (CWHR) type	Wieslander vegetation type map (VTM) ^a		VTM for Leiberg's study area ^a		VTM outside Leiberg's study area ^a		CALVEG ^a		CALVEG for Leiberg's study area ^a		CALVEG outside Leiberg's study area ^a	
	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%
Annual grassland	11 888	0.6	5 808	0.7	6 080	0.6	20 976	1.1	8 464	1.0	12 512	1.2
Aspen	2 352	0.1	320	0.0	2 032	0.2	640	0.0	0	0.0	640	0.1
Bitterbrush	2 176	0.1	1 040	0.1	1 136	0.1	864	0.0	864	0.1	0	0.0
Blue oak- foothill pine	8 992	0.5	1 296	0.1	7 696	0.7	1 984	0.1	448	0.1	1 536	0.2
Blue oak woodland	640	0.0	96	0.0	544	0.1	576	0.0	0	0.0	576	0.1
Chamise-redshank chaparral	12 608	0.6	0	0.0	12 608	1.2	1 488	0.1	0	0.0	1 488	0.1
Closed-cone pine-cypress	1 088	0.1	144	0.0	944	0.1	2 272	0.1	576	0.1	1 696	0.2
Douglas-fir	35 264	1.8	28 224	3.2	7 040	0.7	74 720	4.0	74 112	8.6	608	0.1
Eastside pine	33 664	1.7	16 464	1.8	17 200	1.6	70 688	3.8	70 096	8.1	592	0.1
Jeffrey pine	268 928	13.8	153 392	17.2	115 536	11.0	48 160	2.6	5 376	0.6	42 784	4.2
Juniper	6 720	0.3	464	0.1	6 256	0.6	10 960	0.6	128	0.0	10 832	1.1
Lodgepole pine	123 120	6.3	10 720	1.2	112 400	10.7	38 288	2.0	5 264	0.6	33 024	3.3
Low sage	3 184	0.2	2 416	0.3	768	0.1	160	0.0	112	0.0	48	0.0
Mixed chaparral	25 040	1.3	4 944	0.6	20 096	1.9	27 328	1.5	1 808	0.2	25 520	2.5
Montane chaparral	159 456	8.2	106 688	12.0	52 768	5.0	121 504 ^b	6.5	62 800 ^b	7.2	58 704	5.8
Montane hardwood-conifer	736	0.0	144	0.0	592	0.1	47 392	2.5	28 368	3.3	19 024	1.9
Montane hardwood	86 192	4.4	48 304	5.4	37 888	3.6	126 416	6.7	41 488	4.8	84 928	8.4
Montane riparian	1 376	0.1	352	0.0	1 024	0.1	3 888	0.2	1 312	0.2	2 576	0.3
Perennial grassland	0	0.0	0	0.0	0	0.0	19 888	1.1	1 264	0.1	18 624	0.0
Ponderosa pine	245 088	12.6	58 752	6.6	186 336	17.7	81 568	4.3	15 872	1.8	65 696	6.5
Red fir	218 352	11.2	114 480	12.8	103 872	9.9	223 712	11.9	76 032	8.8	147 680	14.6
Sagebrush	27 456	1.4	18 896	2.1	8 560	0.8	25 328	1.3	24 544	2.8	784	0.1
Sierran mixed conifer	412 336	21.2	235 552	26.4	176 784	16.8	736 832	39.2	355 264	41.0	381 568	37.7
Subalpine conifer	111 696	5.7	18 784	2.1	92 912	8.8	80 048	4.3	1 680	0.2	78 368	7.7
Wet meadow	23 520	1.2	6 240	0.7	17 280	1.6	6 432	0.3	1 200	0.1	5 232	0.5
White fir	122 016	6.3	57 744	6.5	64 272	6.1	105 808	5.6	89 328	10.3	16 480	1.6

^a Although there are polygons <1 ha, the minimum mapping unit was typically about 16 ha (Wieslander *et al.* 1933, Thorne *et al.* 2006). Polygons were resampled to 400 m × 400 m pixels for comparing CALVEG to the VTM.

^b Includes areas on the Plumas NF that burned at high severity but mapped in 2000 as barren in the 1999 Bean Creek, 1999 Bucks, 1999 Devils Gap, 1999 Horton2, 1999 Pidgen, 1999 Stag, and 2000 Storrie fires.

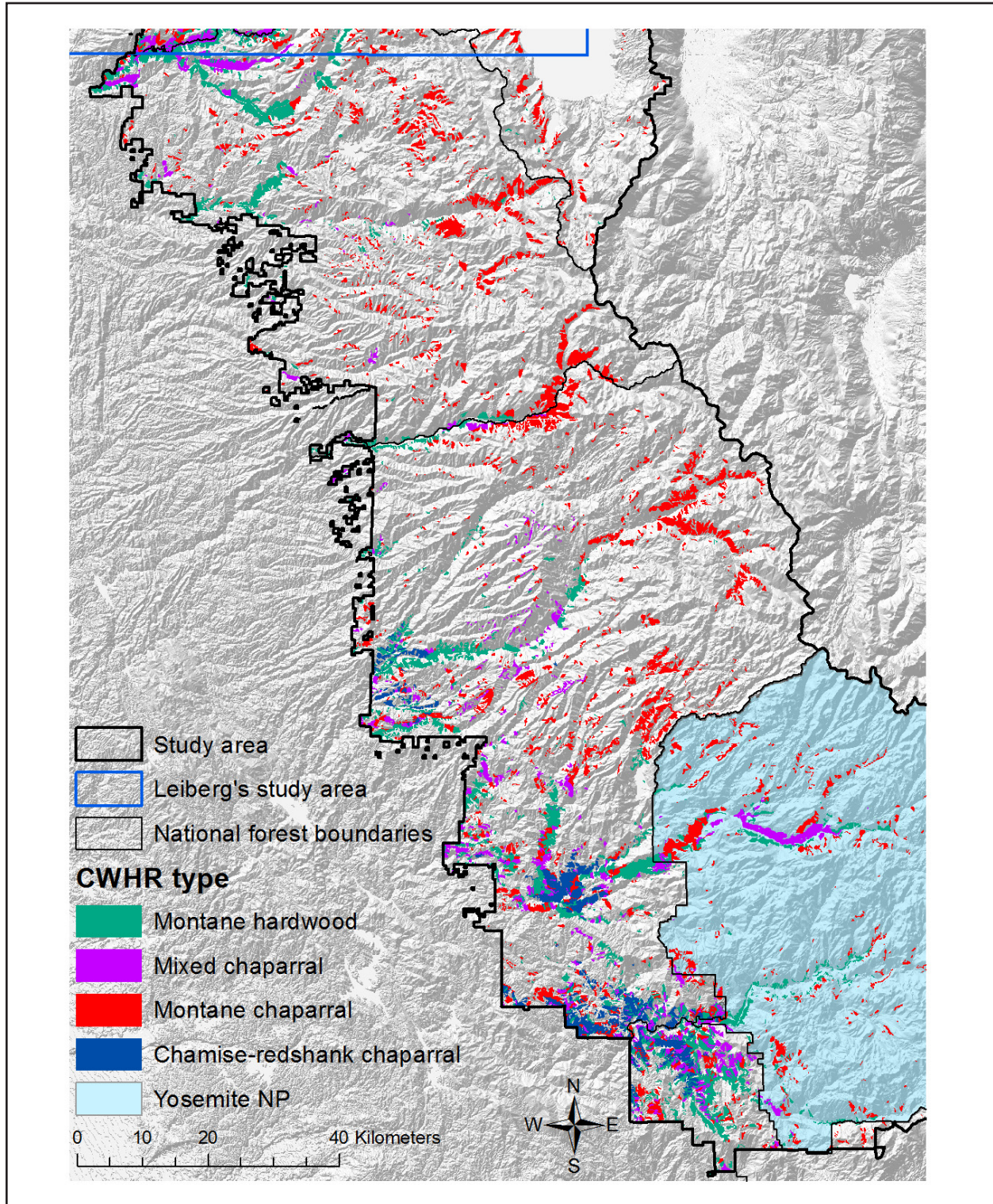


Figure 4. Areas mapped as chaparral and hardwood California wildlife habitat relationship (CWHR) types mapped in the Wieslander VTM. National Forests (NF) north to south include Lake Tahoe Basin Management Unit, Eldorado NF, and Stanislaus NF. Areas of extensive chaparral in the VTM mostly correspond to steep southerly facing canyon slopes. Displayed data are in the original minimum mapping units (i.e., not resampled).

mean proportions across the 10 model runs of YPMC forests in early, mid, and late development state of about 20%, 35%, and 45%, re-

spectively (Figure 5A). The hypothetical model (30% high severity) stabilized much earlier in the simulation at around 400 years,

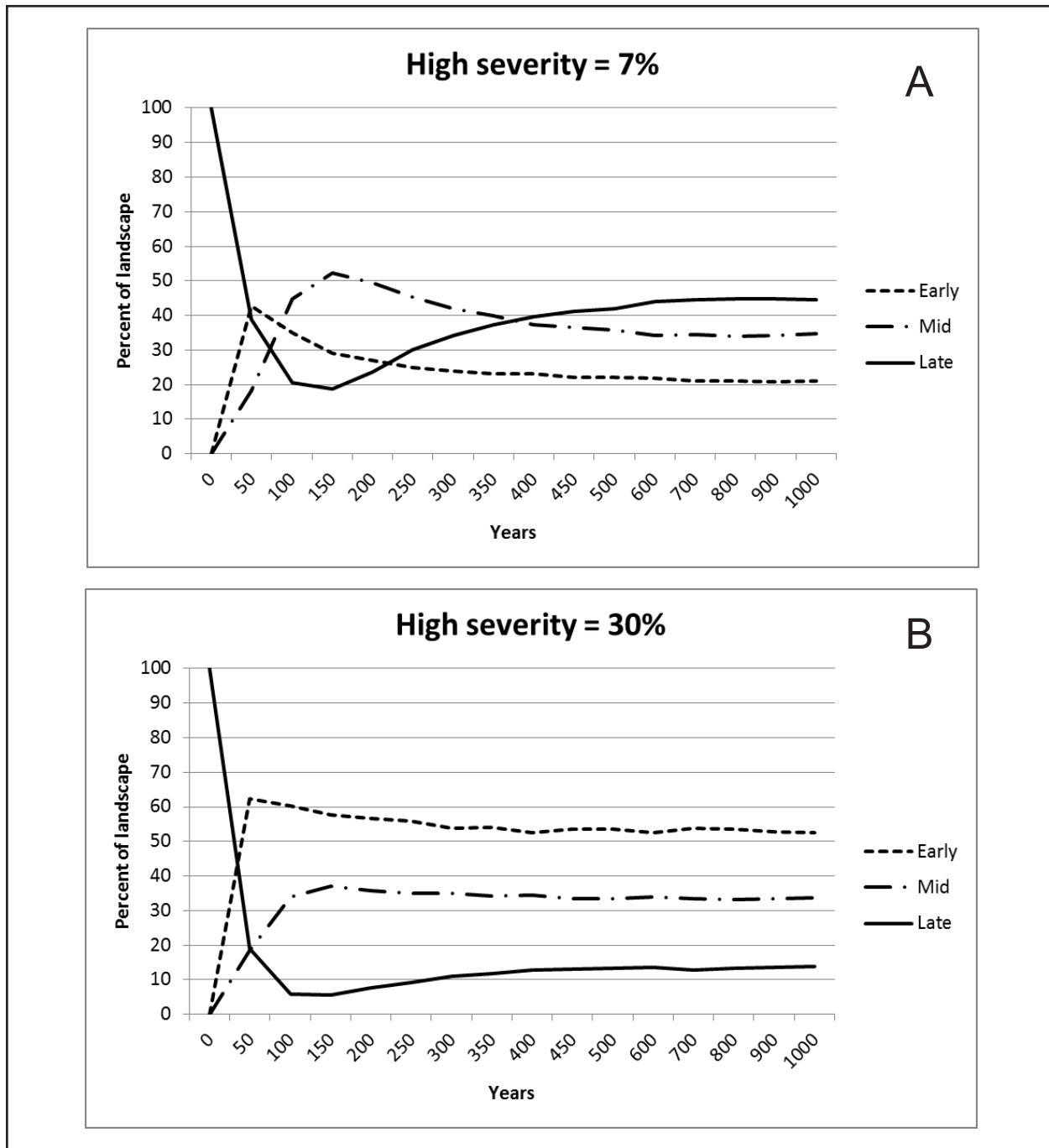


Figure 5. Model results of forest succession using Vegetation Dynamics Development Tool and the LANDFIRE biophysical setting model for Mediterranean California Dry-Mesic mixed conifer forest and woodland (0610270): A) forest conditions based upon the proportion of severities of 7:30:63 (high: moderate:low) representing pre-settlement conditions (original model parameters), and B) forest conditions using severities 30:22:48 (high:moderate:low) typical of late twentieth century (Mallek *et al.* 2013). See Table 1 for early, mid, and late definitions.

with 2.7 times more early development, and 3.5 times less late development compared to the pre-settlement model (53 %, 34 %, and 13 % for early, mid, and late states, respectively; Figure 5B). Open forest conditions (<50 % canopy cover) were more common than closed conditions (>50 % canopy cover; results for open and closed conditions not shown). In the pre-settlement model, 5.6 times more of the landscape (mid and late combined) was in the open canopy versus closed canopy condition (67 % versus 12 %, respectively). The pre-settlement model had 1.9 times more open canopy forests than did the hypothetical model. Closed canopy conditions in the two models were similar (12 % versus 13 % for the pre-settlement and hypothetical models, respectively).

Discussion

Inferences from Early Twentieth Century Maps

The 1930s VTM map appears to retain some characteristics of pre-settlement forests. Compared with the VTM, the modern CALVEG map shows a replacement of yellow pine by mixed conifer forests that corresponds to the post-suppression densification and infill by white fir and incense-cedar documented by numerous studies (Figure 2 and Table 2; e.g., Vankat and Major 1978, Beaty and Taylor 2007, North *et al.* 2007, Scholl and Taylor 2010, Taylor *et al.* 2014).

The percentage of early seral vegetation in the VTM may also provide hints as to the amount of high-severity fire that occurred prior to its creation, because montane chaparral, which is often early seral successional to conifer forests following severe fire, can persist for many decades in the absence of fire. However, chaparral patches can persist for centuries in the case of repeated fire (Wilken 1967, Risser and Fry 1988, Russell *et al.* 1998, Nagel and Taylor 2005, Collins and Stephens 2010). Therefore, it is not always possible to know

when fire originally converted forest to chaparral and, without direct evidence of fire killed trees, mere evidence of recent fire is likely not indicative of a recent conversion of forest to chaparral. Furthermore, in some cases, montane chaparral may persist due to edaphic and topographic factors, rather than repeat fire (Risser and Fry 1988).

Leiberg (1902), whose study area is entirely within the northern extent of the VTM (Figures 2 and 3), recognized that many of the chaparral fields he mapped were likely due to fires ignited by miners:

The only older burns which give any clue to the age are those which stretch in a line from northwest to southeast through the central district of the region. They are marked by the occurrence of large tracts covered with chaparral. Most of these are situated contiguous to placer camps, worked from the earliest times, and might be regarded as having been burned over by fires spreading from such camps. (Leiberg 1902: page 41)

The amount of montane chaparral in Leiberg's study area was thus likely greater than in pre-settlement forests. This hypothesis is supported by the fact that the amount of montane chaparral in the VTM within Leiberg's study area is >2.4 times than in the remainder of the VTM area (Table 2 and Figure 3), which experienced much less late-nineteenth century human disturbance.

We also found that the amount of montane chaparral in CALVEG outside Leiberg's study area is slightly greater than in the VTM (5.8 % versus 5.0 %), although such a small difference could be caused by mapping errors. Subsequent to CALVEG mapping (2000 to 2009, depending upon location), an additional 3 % (22816 ha) of conifer forests (CWHR conifer types Douglas-fir, eastside pine, Jeffrey pine, lodgepole pine, ponderosa pine, red fir, Sierran

mixed conifer, and white fir) outside Leiberg's study area have burned at high severity through 2014 on National Park Service and Forest Service managed lands in our study area. It is therefore probable that the amount of montane chaparral outside Leiberg's study area is currently greater than when the VTM was created.

The scale of the VTM (i.e., 16 ha MMU) is important when considering the amount of montane chaparral in pre-settlement forests. Under a frequent low- to moderate-severity fire regime, dry YPMC forests would have been less dense and more heterogeneous compared with modern forests, characterized by patches of trees, solitary trees, and abundant canopy gaps (Hessburg *et al.* 2005, Collins *et al.* 2011, Larson and Churchill 2012, Haggmann *et al.* 2013, Fry *et al.* 2014). High-severity patches would have followed a power law distribution with many small patches and relatively few large patches (Perry *et al.* 2011). Groupings of similarly aged trees suggest that most canopy gaps resulting from high-severity fire (but also insects, drought, or disease) in the SNEP area were <1.0 ha (Bonnicksen and Stone 1982, Beaty and Taylor 2007, Scholl and Taylor 2010, Taylor 2010, Safford and Stevens 2017). Therefore, the amount of montane chaparral in pre-settlement forests might be underestimated with a 16 ha MMU.

Inferences from Succession Modeling

Comparing the amount of montane chaparral in the VTM to the outputs of the state-and-transition simulations, there is much more similarity between the VTM and the VDDT pre-settlement model (early development vegetation = 20 % of the landscape), than the hypothetical model (early development vegetation = 53 % of the landscape; Figure 5). Considering only the YPMC CWHR types (eastside pine, Jeffrey pine, ponderosa pine, Douglas-fir, Sierran mixed conifer, and white fir), the percentage of montane chaparral in the

VTM (16 ha MMU) is 12.5 % (16.2 % for Leiberg's study area, 8.5 % outside Leiberg's study area; Table 2). We should note that there are some challenges in comparing the amount of early development state in the state-and-transition results with the VTM. First, the LANDFIRE 0610270 model that we used defines early development state to not only represent areas where trees are absent and early seral chaparral might dominate, but also areas dominated by small trees (<12.7 cm dbh). Although tree size information was collected in the vegetation plots, it was never attributed to the maps. Therefore, the VTM only exhibits vegetation type, and areas with young trees cannot be distinguished from mid or late development states. Second, since state-and-transition models are aspatial, there is no MMU.

The pre-settlement state-and-transition model resulted in about 45 % of YPMC forests in late development condition; this is at the low end of independent estimates in the literature. For example, at the beginning of the twentieth century, Greeley (1907) estimated that 40 % to 65 % of trees in uncut yellow pine and mixed conifer forests were "decadent" or "mature," referring to large trees that were no longer rapidly growing. The national parks contain the best examples of old forests in the SNEP area, although some areas were minimally impacted by logging in the late nineteenth and early twentieth centuries (Beardsley *et al.* 1999, Lutz *et al.* 2009). Franklin and Fites-Kaufman (1996) estimated that up to 55 % of mid-elevation conifer forests in the national parks within the SNEP study area were in old-growth condition (structural rating of 4 or 5) at the end of the twentieth century. Twentieth century suppression policies may have led to a higher proportion of late twentieth century forests in the national parks being in late successional or old-growth condition (which are not necessarily the same). Many forested areas within the national parks are denser compared with pre-settlement forests

because of suppression policies, but there are also fewer trees >92 cm dbh (Parsons and DeBenedetti 1979, Taylor 2000, Lutz *et al.* 2009, Scholl and Taylor 2010). What is clear, though, is that the average of 30% high severity in modern YPMC fires would have been much too high to maintain more than a small area of old forest if it were typical of pre-settlement fire regimes.

In addition, the pre-settlement state-and-transition model appears to support the assessment that a majority of YPMC forests were of an open nature, as documented by early twentieth century surveys (Collins *et al.* 2011, 2015; Stephens *et al.* 2015).

Other Evidence for Low Levels of Fire-Caused Tree Mortality

Show and Kotok (1925) reported that repeated enlargement of fire scars on individual trees (so-called “cat faces”) in the entire “California pine region” resulted in mortality of about 5% of the merchantable timber (>30 cm dbh; but overall loss of timber volume because of trees with fire scars was 14%). Show and

Kotok (1925) do not provide an estimate of timber lost due to crown fire. In an earlier report, however, Show and Kotok (1924) reported the volume of merchantable timber killed in several early twentieth century fires, including mortality from both direct heat and repeated surface fires that scarred and hollowed out tree trunks. Restricting Show and Kotok’s fires to those that occurred in the SNEP area, the area-weighted average volume of killed trees was 1562 board m ha⁻¹ (Table 3)—the equivalent of one 91 cm dbh ponderosa pine tree ha⁻¹ (conversion of merchantable volume in units of Scribner board meters to 91 cm dbh, basal area 0.66 m² ha⁻¹; McDonald and Skinner 1989: Table 1). Show and Kotok did not report average merchantable volume within each fire. However, most late nineteenth and early twentieth century inventories of unlogged forests in the Sierra Nevada show basal areas for merchantable timber mostly between about 16 m² ha⁻¹ and 50 m² ha⁻¹ (Scholl and Taylor 2010; Taylor *et al.* 2014; Stephens *et al.* 2015; B.M. Collins, USDA Forest Service, Pacific Southwest Research Station, Davis, California, USA, personal communication; E.E. Knapp,

Table 3. Fires that occurred from 1911 to 1922 in the northern and central Sierra Nevada sampled for mortality of merchantable timber (data from Show and Kotok 1924).

Fire name	National forest	Fire size (ha)	Fire scarred trees felled (board m ha ⁻¹) ^a	Direct damage from heat (board m ha ⁻¹) ^b
Bear River	Eldorado	202	181	29
Butler Meadow	Eldorado	453	375	173
Ferris Creek	Plumas	1876		2531
Ham Station	Eldorado	3839	358	414
Lassen-Walker	Lassen	89		2523
Pilot Creek	Eldorado	154	3134	188
Quincy Junction	Plumas	81		1582
Slate Mountain	Eldorado	142	153	38
White Horse	Modoc	8296	467	1198
Weighted average			455	1106

^a Includes trees that fell due to loss of structural integrity from the enlargement of fire scars created by repeated fires.

^b Includes trees that were killed due to direct heat (i.e., crown fire).

USDA Forest Service, Pacific Southwest Research Station, Redding, California, USA, personal communication), although Sudworth reported plots with basal areas of 130 m² ha⁻¹ to 215 m² ha⁻¹ (University of California, Bioscience and Natural Resources Library, Berkeley, USA, unpublished field note books of Sierra Nevada forest reserve inventory). The Sudworth plots have been the source of much discussion in the ecology literature, with the general consensus that Sudworth's plots were purposely sited in the largest stands he could find (Stephens and Elliott-Fisk 1998, Stephens 2000, Baker 2014). Whatever the case, in Sudworth's plots, Show and Kotok's reported mortality would translate to $\leq 0.5\%$ of average basal area of merchantable timber, while in the other more representative stands, Show and Kotok's measured mortality would have represented between 1% and 4% of a stand (0.66 m² ha⁻¹ divided by 50 m² ha⁻¹ and 16 m² ha⁻¹, respectively). Assuming that the later mortality rate is a conservative estimate of mortality throughout an entire fire, depending upon the spatial aggregation of the mortality of larger trees described by Show and Kotok, in modern terms it could be considered at the patch scale to be anywhere from low (i.e., one to a few trees killed within a matrix of surviving trees) to high severity (i.e., most to all trees killed in one contiguous patch) (Stephenson *et al.* 1991, Sugihara *et al.* 2006a, Perry *et al.* 2011).

A recent paper that examined early forest inventory data from the same time period as Show and Kotok's reports provides additional evidence of low amounts of conifer mortality due to fire. Stephens *et al.* (2015) examined forest survey data (0.9 ha belt transects) collected *circa* 1911 covering 11 500 ha in the southern Sierra Nevada in an area that had not been logged. Assuming that areas of chaparral or dense immature timber reported by the surveyors were indicators of high-severity fire, Stephens *et al.* found that the proportion of the total landscape that burned at high severity was 1% to 3% in mixed conifer forests and

4% to 6% in ponderosa pine forests, which is much less than what our succession modeling predicts for the proportion of early seral in pre-settlement forests. It is likely that the surveys were conducted to inventory timber resources; however, the survey data included tallies for at least some trees that were not generally included in merchantable timber surveys (<30.5 cm dbh), and similar survey data from the Stanislaus National Forest included transects that were entirely chaparral (Collins *et al.* 2015).

Conifer mortality from fires in modern analog reference sites also support the supposition that pre-settlement fires in our study area were predominately of low severity. The Sierra de San Pedro Mártir (SSPM) of northern Baja California, Mexico, is a modern reference site for drier Jeffrey pine-dominated YPMC forests in the eastern Sierra Nevada (Minnich *et al.* 2000, Stephens and Fulé 2005, Dunbar-Irwin and Safford 2016). The SSPM has never been logged, and fires have only been effectively suppressed since the 1980s (Stephens *et al.* 2003). As a result, forest structures do not yet exhibit the levels of infill documented in Sierra Nevada YPMC forests (Dunbar-Irwin and Safford 2016). A recent study shows that forest fires in the SSPM between 1984 and 2010 burned only 3% to 4% of their area at high severity, and maximum high-severity patch sizes were at least an order of magnitude smaller than those typical of contemporary fires on Forest Service managed lands in the Sierra Nevada (Miller *et al.* 2012, Rivera-Huerta *et al.* 2016).

Contrary Evidence

Three recent papers have challenged the low-to-moderate-severity paradigm for YPMC forests, and assert that such forests previously supported extensive amounts of high-severity fire similar to or greater than modern fires (Baker 2014, 2015; Odion *et al.* 2014). Each of these studies rely on estimates of early seral

vegetation or small trees to estimate high-severity fire rotation. However, the underlying assumption that tree regeneration in dry forests could only have arisen after high-severity fire is not well founded. In a critique of this assumption, Fulé *et al.* (2014) point out that tree regeneration in dry forests throughout the western US is spatially heterogeneous, often occurring in canopy gaps, and is more closely linked to periodic wet episodes or longer fire-free periods such as the twentieth century suppression era (Brown and Wu 2005, North *et al.* 2005, Scholl and Taylor 2010, Fry *et al.* 2014, Taylor *et al.* 2014). Therefore, the methods used by these studies to estimate proportions of small to large trees in pre-settlement forests led to estimates of percent area affected by high-severity fire in pre-settlement YPMC forests in the SNEP area that are too high.

Baker (2014, 2015) used late nineteenth century tree data as well as surveyor notes on vegetation cover along section lines acquired by the US General Land Office (GLO) in surveys used to establish the public land survey system (PLSS). There is debate whether the GLO section corner tree data can be used to estimate forest structure because of the small sample. Methods for pooling the data have been devised (Williams and Baker 2011). However, tree density estimates from the Williams and Baker pooling methodology are 2.1 to 5.9 times higher than estimates from several other studies based upon early twentieth century forest surveys that sampled orders of magnitude more trees per unit area, with small trees comprising most of the differences in density (Collins *et al.* 2011; Hagmann *et al.* 2013, 2014; Stephens *et al.* 2015). Recent work also suggests that errors in Williams and Baker's methods explain the nature and magnitude of their overestimated tree densities (C.R. Levine, Department of Environmental Science, Policy, and Management, University of California, Berkeley, USA, unpublished data). Small tree density estimates that are too high, coupled with Baker's unrealistic assumptions about tree

regeneration in dry forests, suggest that Baker's estimates of percent area affected by high-severity fire in late nineteenth century Sierra Nevada forests may be unreliable.

Odion *et al.* (2014) assume that stand age recorded by the Forest Service's Forest Inventory and Analysis (FIA) program represents a single stand initiation date due to high-severity fire. That assumption implies that fire is the only cause of tree mortality, and that trees older than the calculated stand age in the modern FIA plot must have survived a hypothetical high-severity fire. There are several fundamental issues with these assumptions. First, the stand age attribute is an average value derived from the observed or inferred ages of a subset of canopy trees, and often does not capture the ages of older trees in multi-aged stands that were typical of pre-settlement dry conifer forests (Scholl and Taylor 2010, Taylor 2010, USDA Forest Service FIA Program 2014, Stevens *et al.* 2016). In addition, other biological factors other than fire are important in causing tree mortality that would limit the age and number of older trees (Loehle 1988). Consequently, many trees present in the nineteenth century would have died for reasons other than fire before they were measured in a modern FIA plot. Finally, because tree regeneration in these forests is more closely linked to periodic wet episodes or longer fire free periods, none of the tree ages in an FIA plot can be linked to fire without independent evidence (Stevens *et al.* 2016). Thus, modern FIA data are not appropriate to infer rates of historic high-severity fire in dry pine and mixed conifer forests.

Baker (2014) also did not account for fundamental ecological principles that limit the range of conifer forests (i.e., actual evapotranspiration and water deficit; Stephenson 1998). Many of the PLSS sections that Baker identified as having experienced high-severity fire occur below 900 m on south-facing slopes west of Yosemite NP and below 1400 m in Sequoia and Kings Canyon NPs (Figure 6; Baker

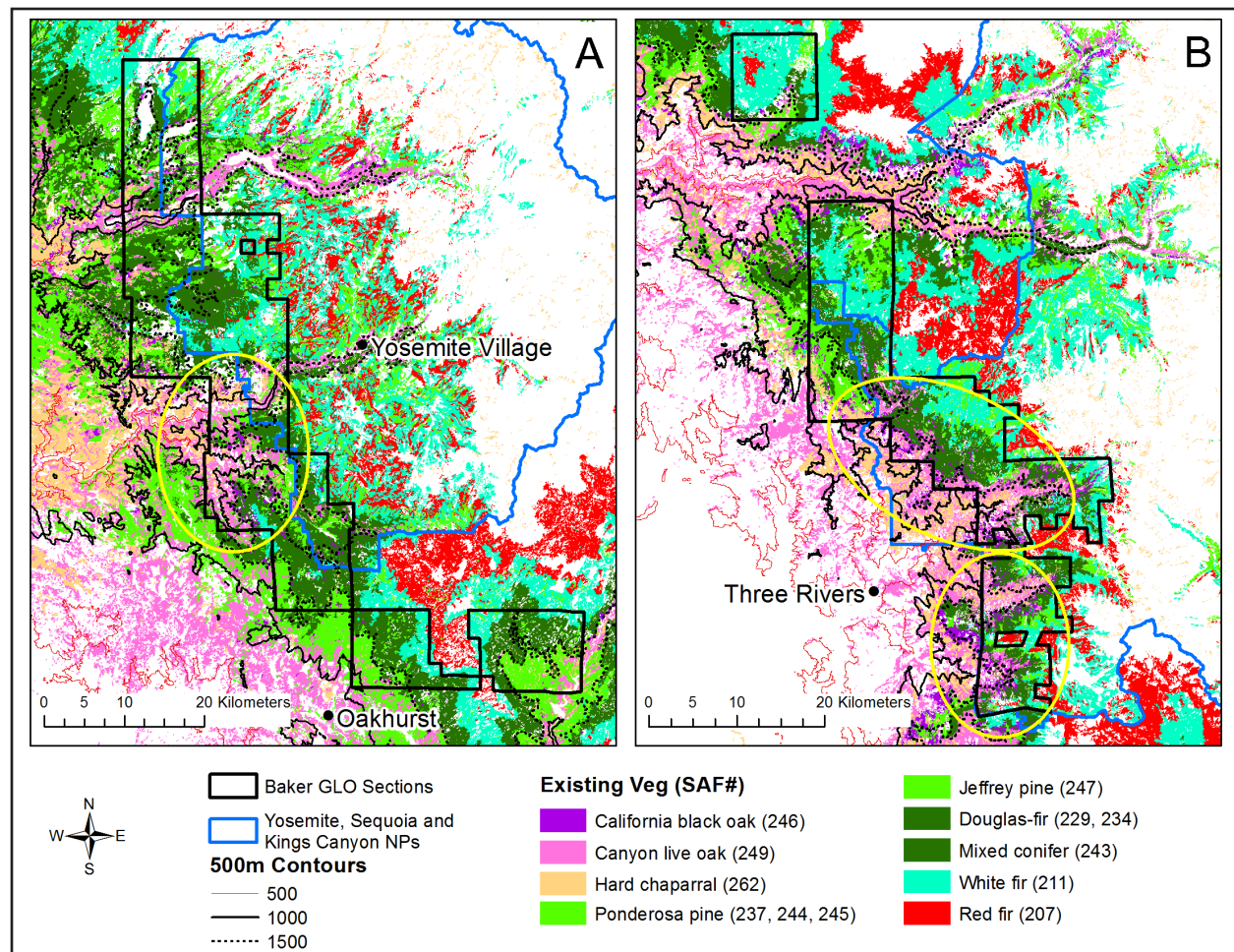


Figure 6. Existing vegetation (CALVEG circa 2000 to 2009) in which Baker (2014) analyzed GLO survey data. The following plates correspond to Figures 1b, 1c, 4b, and 4c in Baker (2014: 5,19): A) the western edge of Yosemite National Park, and B) the western edge of Sequoia and Kings Canyon National Parks. Vegetation types are labeled with Society of American Forester (SAF) types (Eyre 1980) to allow comparison to Baker (2014). Areas circled in yellow correspond to locations that Baker mapped as open or with scattered trees that he concluded were a result of severe fire. However, the circled areas are currently composed of canyon live oak or hard chaparral (SAF cover types 249 and 262 on Baker's maps, corresponding to CWHR types montane hardwood and mixed chaparral, respectively; CWHR type montane chaparral, which can be early successional, was excluded on the map), on either steep south or west facing canyon slopes, or are below the elevation where conifers (excluding foothill pine) naturally occur except in very low densities.

2014: 19), topographic settings that generally correspond to the driest extent of YPMC forests (Fitch 1900a, Vankat 1977, Fites-Kaufman *et al.* 2007). Contemporary vegetation maps (CALVEG) demonstrate that these areas are currently covered with canyon live oak or hard chaparral (Society of American Forester [SAF] cover types 249 and 262 corresponding to

CWHR montane hardwood and mixed chaparral types; circled areas in Figure 6). The CWHR mixed chaparral type is not seral to conifer forests (England 1988b). Where SAF cover type 249 corresponds with CWHR montane hardwood type in the CALVEG map, it refers to either canyon live oak or interior live oak (*Quercus wislizenii* A. DC.). Interior live

oak occurs mostly at elevations below conifer forests (Myatt 1980). In addition, although canyon live oak can be associated with varying densities of Douglas-fir or ponderosa pine, it can also occur in nearly pure stands on steep, rocky south- and west-facing canyon slopes. Where conifers do occur in these types of locations, they are not remnants of a severely burned forest, but rather they are moisture-limited isolated trees (Mallory 1980, Myatt 1980, McDonald 1988, McDonald and Tappeiner 1996). In summary, many areas identified by Baker (2014) as having experienced high-severity fire are unsuitable for the persistence of YPMC forests, and are not representative of early seral conditions.

CONCLUSIONS

Percentage of high-severity fire; fire frequency; and landscape proportions of early, mid, and late developmental forests are intricately linked. While undoubtedly there was variation due to local biophysical settings, we do not see evidence that very large fires with large proportions of high severity were typical during pre-settlement times in SNEP YPMC forests. Early twentieth century vegetation data and succession modeling corroborate previous estimates that the percentage of high-severity fire on pre-settlement YPMC forests was generally low. Succession modeling also substantiates previous estimates that around half of pre-settlement YPMC forests were in late development condition, which is fully compatible with—and indeed dependent on—the low-severity paradigm. In contrast,

our modeling demonstrated that the preponderance of large, old trees in pre-settlement YPMC forests that was described by so many early Euro-Americans would have been impossible if fires at that time burned at the levels of severity that we see in the modern Sierra Nevada. The implication is clear: if 40% to 60% of the Sierra Nevada supported old-growth or late development forests, then the average proportion of high severity per fire could not have been more than about 5% to 10% in YPMC forests.

Management objectives often call for fuels treatments that mimic pre-settlement fire rotations and fire effects to increase the resilience of dry conifer forests to current and future stressors (North *et al.* 2009, Long *et al.* 2014). However, mechanical treatments can be implemented on less than half of the productive forested lands in the Sierra Nevada national forests (North *et al.* 2015). Furthermore, restoration of fire frequency (either prescribed or wildland fire) that would mimic pre-settlement rates may not be achievable in modern times due to land ownership patterns and smoke restrictions (Quinn-Davidson and Varner 2012). Nevertheless, proactively increasing overall area burned under moderate weather conditions will moderate fire severity, decrease high-severity patch size, and decrease smoke emissions in comparison to wildfires burning under more severe weather conditions, while at the same time create and maintain heterogeneous forest structures that are important to biodiversity, ecological and hydrological function, and overall ecosystem resilience (Schweizer and Cisneros 2014).

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