



Forest Vegetation Change and Its Impacts on Soil Water Following 47 Years of Managed Wildfire

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ABSTRACT

Managed wildfire is an increasingly relevant management option to restore variability in vegetation structure within fire-suppressed montane forests in western North America. Managed wildfire often reduces tree cover and density, potentially leading to increases in soil moisture availability, water storage in soils and groundwater, and streamflow. However, the potential hydrologic impacts of managed wildfire in montane watersheds remain uncertain and are likely context dependent. Here, we characterize the response of vegetation and soil moisture to 47 years (1971–2018) of managed wildfire in Sugarloaf Creek Basin (SCB) in Sequoia-Kings Canyon National Park in the Sierra Nevada, California, USA, using repeat plot measurements, remote sensing of vegetation, and a combination of continuous in situ and episodic spatially distributed

soil moisture measurements. We find that, by comparison to a nearby watershed with higher vegetation productivity and greater fire frequency, the managed wildfire regime at SCB caused relatively little change in dominant vegetation over the 47 year period and relatively little response of soil moisture. Fire occurrence was limited to drier mixed-conifer sites; fire-caused overstory tree mortality patches were generally less than 10 ha, and fires had little effect on removing mid- and lower strata trees. Few dense meadow areas were created by fire, with most forest conversion leading to sparse meadow and shrub areas, which had similar soil moisture profiles to nearby mixed-conifer vegetation. Future fires in SCB could be managed to encourage greater tree mortality adjacent to wetlands to increase soil moisture, although the potential hydrologic benefits of the program in drier basins such as this one may be limited.

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INTRODUCTION

Many forests in California's Sierra Nevada, like other dry mixed-conifer forests of the western USA, have experienced fire exclusion since the end of the 1800s and were managed under an active policy of fire suppression throughout the twentieth century (McKelvey and others 1996). The consequences of fire exclusion for the vegetation of the Sierra Nevada are well known and include increases in forested area, increases in forest stem density and uniformity of stands, and reductions in landscape heterogeneity (Collins and others 2011; Safford and Stevens 2017). By creating large connected patches of dense fuels, fire exclusion and suppression have also set the stage for a dramatic escalation in the frequency and extent of severe fires (Westerling and Swetnam 2003; Stephens and others 2013; North and others 2015; Stephens and others 2016)—for example, five of the ten largest and most destructive fires in California (as of fall 2018) occurred after 2010 (CalFire 2018a, 2018b). The scale of fire-caused tree mortality in these and many other contemporary fires is well outside the historical range of variability in Sierra Nevada forests (Collins and others 2011; Safford and Stevens 2017). Recent large-scale stand-replacing fire effects, combined with the densification and homogenization brought about by widespread fire suppression, have negatively impacted some animal taxa, water resources, and forest resilience (Grant and others 2013; Ponisio and others 2016). Such negative impacts have motivated the adoption of a broad suite of forest management practices ranging from mechanical forest thinning to prescribed fire (Stephens and others 2016) to restore a forest structure resilient to the future fires.

An additional forest restoration strategy, managed wildfire, is drawing increased attention (North and others 2012; Boisramé and others 2017a). Managed wildfire involves allowing naturally ignited wildfires to burn unimpeded unless specific predefined criteria (for example, relating to hazard or air quality) are met and trigger intervention. In the Sierra Nevada, two wilderness areas, the Illilouette Creek and Sugarloaf Creek Basins—in Yosemite and Sequoia-Kings Canyon National Parks, respectively—have used managed wildfire for nearly 50 years. The resulting wildfire regime in these basins has near-historical fire frequencies for at least a portion of the past 50 years (Collins and Stephens 2007). In addition, the emergence of non-overlapping fire extents in these basins suggests self-limiting behavior as the fuel distribution becomes more fragmented in space (Collins and

others 2007; Collins and others 2009; Collins and others 2011; Parks and others 2015; Collins and others 2016). Although these outcomes suggest that managed wildfire has had a positive effect in restoring historical fire regimes and mitigating fire hazard, its co-benefits on other ecosystem services remain less certain.

The influence of managed wildfire on water supply, given the importance of these forests for water resources in California and the western USA more generally, is of particular interest. Although there is a well-established literature in fire hydrology (for example, Stoof and others 2012; Ebel 2013; Wine and Cadol 2016; Atchley and others 2018), studies that explore longer-term hydrologic responses (for example over decadal scales) are rare (but see Kinoshita and Hogue 2015). The sites in question here allow the investigation of not only a longer-term set of hydrologic responses to fire, but more interestingly again, the responses to a change in fire regime and the imposition of multiple disturbance events on a catchment.

In the Illilouette Creek Basin (ICB), the imposition of managed wildfire led to large (24%) decreases in forested area and the replacement of forests with new areas of shrubland, grassland, and dense meadows/wetlands (Boisramé and others 2017b). Field measurements in ICB showed that vegetation type is a strong predictor of soil moisture: for example, dense meadows indicate wet soil conditions, in comparison to the dry soils conditions associated with shrublands or sparse meadows (Boisramé and others 2018). With sufficient information relating soil moisture, vegetation cover, and other landscape predictors of soil moisture, statistical models can be trained to predict soil moisture based on mapped vegetation (Boisramé and others 2018). Such models suggest that the fire-induced changes to vegetation cover in ICB (less forest cover, but more meadows and shrublands) are associated with an overall increase in water storage and plant available water resources (Boisramé and others 2018). This finding is consistent with comparisons to similar but fire-suppressed Sierra Nevada river basins (Boisramé and others 2017a), and with mechanistic ecohydrologic modeling of ICB (Boisramé and others 2019), which suggest that soil moisture and streamflow have increased, and plant water stress decreased, in response to the changed fire regime. Model results showed that these hydrologic changes could be explained by reductions in forest cover causing a combination of reduced interception, reduced transpiration, and

deeper peak snowpacks (Boisramé and others 2019).

These results suggest a promising co-benefit for water resources associated with restoration of a near-natural fire regime in the ICB. However, it is unclear how the effects of managed wildfire will play out in other Sierra Nevada forests. ICB is a relatively wet, mid-elevation watershed containing productive forests. Basins with different climates, soils or vegetation types found at other elevations and locations in the Sierra Nevada could exhibit different responses to a changed fire regime, as could subtle differences in how a managed wildfire regime is operated. Sugarloaf Creek Basin (SCB) in Sequoia-Kings Canyon National Park offers a chance to explore the impact of managed wildfire beginning in 1973 in a slightly less productive, drier, and less-frequently burned watershed than ICB. In this study, we draw on historical (1970) and contemporary forest plot surveys, historical (1973) and contemporary aerial photography and vegetation classifications, and contemporary soil moisture and meteorological observations within SCB to address four questions:

- (1) How has forest composition and structure at the survey plot scale changed from 1970-present, and how are these changes associated with fire?
- (2) Has vegetation cover changed in the SCB from 1973-present at the landscape scale, and if so, how are these changes associated with fire? Are different vegetation cover types in the SCB associated with differences in soil moisture, and what does this imply about hydrologic response to wildfire in the SCB?, and finally
- (3) How do changes in landscape vegetation cover (2) and soil moisture (3) compare with those previously described in the Illilouette Creek Basin, a wetter and more productive basin that has burned more frequently over the same period?

METHODS

Study Site and Climate

The Sugarloaf Creek Basin (SCB) covers 125 km², spanning elevation ranges of 2000–3200 m in Sequoia and Kings Canyon National Parks. Average daily temperatures range from –10 to 31 °C, with the annual average being 14.5 °C (Global Historical Climate Network, station USR0000CSUG). Vegetation in this region varies with elevation, topography, and soil type (Stephenson 1998; Caprio and

Graber 2000). The dominant tree species found in SCB are Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus contorta*), white fir (*Abies concolor*), and red fir (*Abies magnifica*), which occur interspersed with meadows and shrublands. There is no evidence of logging in SCB. Based on fire scar reconstructions, fire was common in this area prior to 1900, with a mean fire interval of 9 years for the period 1700–1900 (Collins and Stephens 2007). Fire exclusion and suppression appear to have started in SCB shortly before 1900, resulting in an anomalously long fire-free period lasting until the early 1970's (Collins and Stephens 2007).

In 1968, the National Park Service changed its fire policy and began to use prescribed fires and managed lightning fires to meet ecological goals; previously all fires had been suppressed (van Wagtenonk 2007). Yosemite National Park (including the 150 km² ICB) is the only other place in the Sierra Nevada that has had a policy of allowing lightning-ignited wildfires to burn for as long as Kings Canyon National Park (van Wagtenonk 2007). The first notable fire in SCB under the fire use policy was the Ball Dome Fire in 1971, which burned nearly 100 ha. In total, 10 fires over 40 ha in size burned partially or completely in SCB between 1970 and 2016, the largest of which was over 4000 ha (Appendix A, Table A1). For comparison, ICB had 27 fires larger than 40 ha between 1970 and 2016 (Collins and others 2016).

We obtained fire perimeters for all SCB fires between 1952 and 2016 from a statewide database maintained by the California Department of Forestry and Fire Protection (FRAP 2017). These perimeters were corroborated with those maintained by park staff (personal communication, A. Caprio, Sequoia and Kings Canyon National Park). Because our historical imagery dates to 1973 (see below), we removed four small (<100 ha) fires that burned between 1952 and 1972 from our imagery analyses (Figure 1; Table A1). Our historical forestry plots date to 1970 (see below), but none were located within the perimeters of these four fires (Figure 1). We also removed two fires, from 2004 and 2006, that were both less than 5 ha and located on the margins of the watershed (not shown in Figure 1). Of the 12 fires included for analysis, the mean fire size was 830 ha (median 248 ha).

In addition to the increased fire frequency at ICB compared to SCB since 1970 (27 compared to 10 large fires), differences in water balance and site productivity between the basins may influence vegetation response to the reintroduction of fire. ICB and SCB have similar mean elevation (2500 m

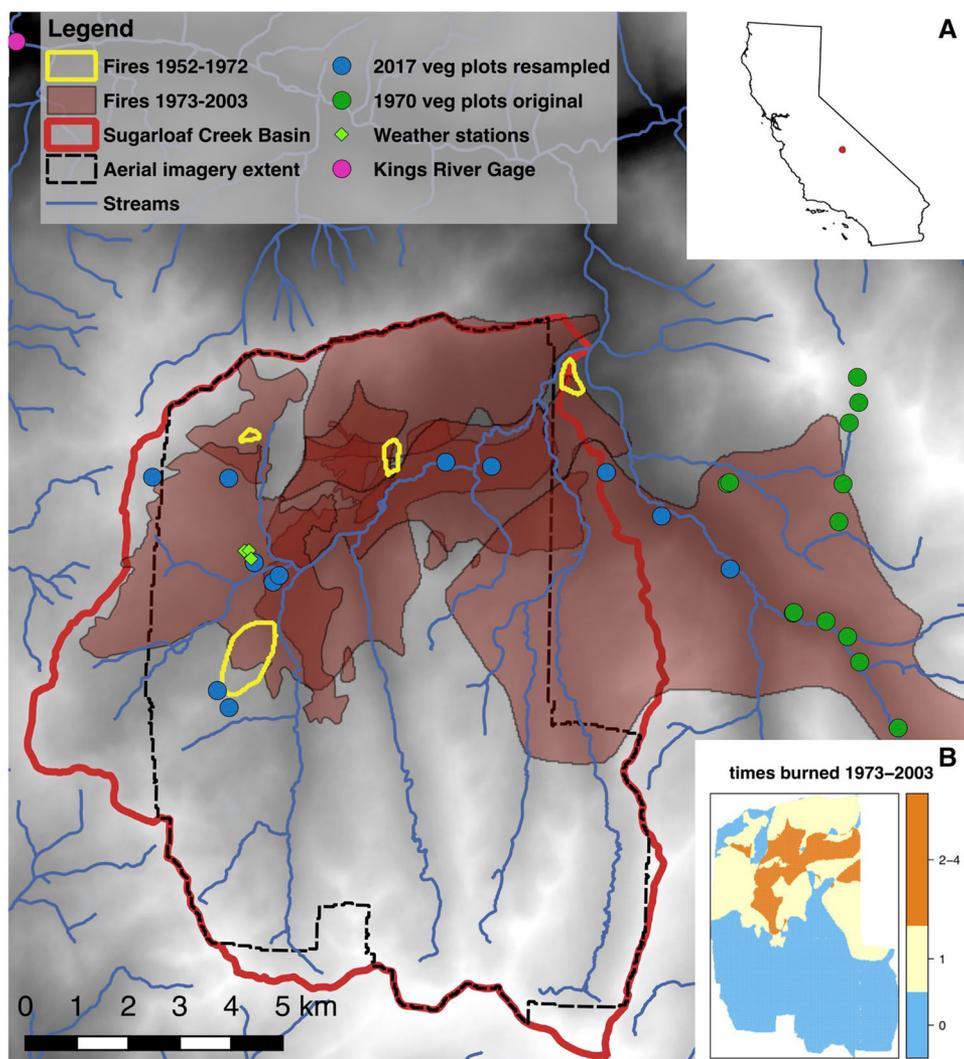


Figure 1. Sugarloaf Creek Basin (SCB) shown in red (and in panel **A**). Base layer DEM ranges from 1480 m (black) to 3375 m (white; Data source: ASTER GDEM, a product of METI and NASA). Overlapping fire perimeters since 1973 shown in transparent red. Inset (**B**) shows composite of overlapping fires from 1973 to 2003, with colors indicating number of times burned, over the extent represented by the 1973 aerial imagery. Green points in main figure indicate main vegetation (forestry) plots installed in 1970, a subset of which (blue) were re-sampled in 2017. The pink point is the approximate location of the Kings River streamflow gage near Cedar Grove; USGS gage 11212500 (exact coordinates given in Table A2) (Color figure online).

and 2700 m, respectively) and forest types (Collins and others 2016), but three lines of evidence suggest that ICB is the wetter and more productive basin. First, temporary weather stations (Appendix B) at both sites showed greater precipitation (Table 1) at ICB than SCB for the duration of our field data collection (2016–2018). Second, specific discharge (total streamflow divided by watershed area) measured downstream of ICB is greater (0.65–0.66 m/y) than that measured downstream of SCB (0.48–0.55 m/y) over a time period through the 1950’s where data from both basins were available (Table A2).

Third, these differences in water inputs are reflected in slightly higher productivity in ICB than SCB (Figure 2). To assess productivity, we used the LANDSAT-derived normalized difference vegetation index (NDVI) product during the early-mid growing season at both basins, available at <https://ndvi.ntsg.umt.edu/> (Robinson and others 2017). To minimize the effect of recent fires on productivity estimates, we used the earliest available data from 1984 and 1985, prior to the 1985 Sugarloaf Fire (Table A1), and at least 3 years after the most recent fire in either basin. We filtered out any region of either watershed that was likely granite or water

Table 1. Weather Station Data from Sugarloaf Creek Basin (SCB) and Illilouette Creek Basin (ICB)

Weather station vegetation type		Total precipitation (mm)		Cumulative shallow (12–60 cm) soil water gain (mm)		End of WY VWC [%] at 100 cm		Days saturated at 100 cm		Correlation coeff. between 12 and 100 cm VWC for Jun–Aug	
WY		2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
SCB	Wetland	680	429	473	469	34	14	155	81	0.85	0.97
ICB		1067	537	56	30	43	43	365*	365	0.88	0.54
SCB	Shrub	842	546	362	287	16	10	88	0	0.93	0.67
ICB		1137	590	940	378	10	5.6	86*	0	0.87	0.84
SCB	Forest	577	397	834	184	4.7	3.4	56	0	0.99	0.97
ICB		769	450	776	334	3.5	3.4	31*	0	0.90	0.87

*Approximated due to missing data as a result of the 2017 Empire Fire.

Gap-filled precipitation totals measured by rain gauge; cumulative shallow soil water gain was calculated from shallow soil moisture time series (Appendix B). End of water year (WY) deep soil moisture (volumetric water content [VWC]) and number of saturation days were based on the 100 cm soil moisture probe record. Pearson's correlation coefficient was calculated between daily average 12 cm and 100 cm soil moisture for months of June–August.

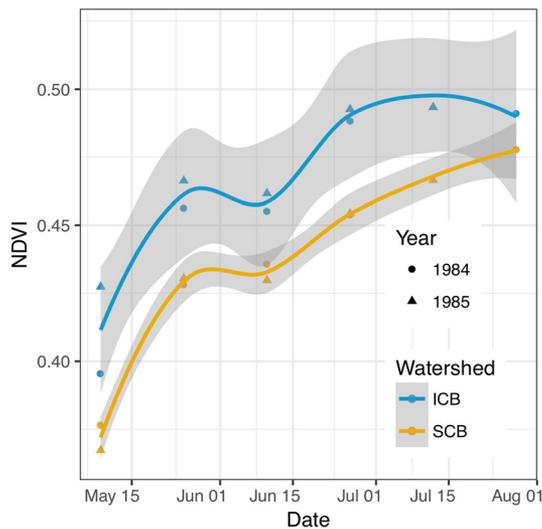


Figure 2. Normalized difference vegetation index (NDVI; averaged across a given basin for a given date), a proxy for productivity, was consistently higher in Illilouette Creek Basin (ICB; Boisramé and others 2017a) than Sugarloaf Creek Basin (SCB; this study). Curves with error bands represent loess smoothing estimates of mean NDVI across the two years.

(NDVI < 0.15) or cloud cover (filtered out during image processing), and only compared the vegetated portions of each watershed that had data for every image date.

Question 1: Forest Composition and Structural Change

In areas of SCB that did not convert to alternative vegetation patches (Question 2 below), we explored the question of how forest structure has

changed over time in response to fire by resampling a historical forest plot dataset. Forest surveys were conducted in Sugarloaf Creek Basin in July 1970 by Hammond, Jensen & Wallen Mapping and Forestry Services, Oakland CA. Surveyors measured 25 plots (Figure 1), which consisted of five 0.2 ac (0.08 ha) subplots each. Each subplot was surveyed for conifer trees (stems > 7.6 cm DBH), saplings (stems ≥ 0.6 m tall up to 7.6 cm DBH, where DBH was not recorded), and seedlings (stems < 0.6 m tall). The surveyors estimated representative tree heights and woody (shrub) ground cover within the plots. All shrubs and trees were identified to species level. Subplots were arranged along linear transects with generally 40 m spacing between them, from an anchor point and a given transect azimuth that was described in the field notes. We re-surveyed 12 of these plots in 2017 (Figure 1) following the same methods, leading to a total of 57 subplots sampled in both 1970 and 2017, which constituted our sample size for analysis.

For each subplot, we used the collection of fire perimeters from Sugarloaf Creek Basin to identify the number of times each subplot had burned since fire was reintroduced in 1973 (0, 1, or 2–4). We calculated density of all trees (> 7.6 cm DBH), medium trees (> 15.2 cm DBH), large trees (> 61 cm DBH), and very large trees (> 100 cm DBH) and calculated basal area of each of these size classes by species as well. For each size class, we compared the change in density and basal area over time, using linear mixed-effects models that assigned a random intercept to subplot ID, accounting for repeated sampling of the same plots over time by allowing a given plot to have higher or lower overall values of the response variables,

using the R package *lme4* (Bates and others 2013). We evaluated the significance of these trends using the Kenward–Rogers approximation to estimate degrees of freedom in the mixed-effects models, via the R package *pbkrtest* (Halekoh and Højsgaard 2014).

Question 2: Vegetation Cover Change

In order to assess potential impacts of vegetation change on soil moisture (Question 3 below), we mapped the change in larger vegetation patches in SCB since the first large fire in 1973. We created these maps by classifying aerial photographs into granite (exposed rock), water, sparse meadows (areas dominated by bare ground, with sparse shrub and/or herbaceous cover), dense meadows (wetlands and other areas of dense herbaceous cover), conifer forest, and shrublands, following the methods used by Boisramé and others (2017b). We obtained the earliest set of aerial photographs available for the region from Sequoia Kings Canyon National Park. These black and white photographs were dated to 1973, prior to the first large fires occurring in SCB, scanned at 600 dpi, and covered 10,120 ha (81%) of the 12,500-ha watershed (Figure 1). Contemporary cover was represented by color imagery from the 2014 National Agriculture Imagery Program and clipped to the same extent as the 1973 imagery. The 1973 images were orthorectified using ERDAS IMAGINE software, using approximately 15–20 control points per image. We used the eCognition object-oriented software package (produced by Trimble, www.ecognition.com) to classify the images into objects of similar color band values, texture, and shape (Blaschke and others 2014). Our supervised classification approach produced objects in the following categories: mixed-conifer forest, shrub, sparse meadow, dense meadow, rock, and open water. Following classification, the 1973 images (representing approximately 16.7 km² each) were mosaicked together in ArcGIS, as were the 2014 images (representing approximately 39 km² each).

During post-processing, the vector-object layers produced by eCognition were converted to raster layers in ArcGIS, with a 40-m pixel resolution, ensuring alignment of the 1973 and 2014 rasters to enable a change detection analysis. Because the rasterization process created single isolated pixels of a given class derived from polygon slivers, we smoothed the resulting raster surface using the *adjacent* function in the R library *raster* (Hijmans and van Etten 2016). We removed isolated pixels surrounded by other vegetation in the four cardinal

directions, changing the pixel in question to the most common vegetation type surrounding it.

We used the spatial layers from 1973 and 2014 to determine the direction and proportionality of vegetation change in the intervening 41 years. We then analyzed the relationship between these changes and the number of times each pixel had burned. We overlaid the fire perimeter polygons on the two vegetation raster layers to extract a “times burned” attribute for each pixel. Due to subsequent chi-squared tests not converging for analyses of pixels burned 3 times (218 ha) and 4 times (15 ha), we combined these categories into a single “2–4 times burned” category, in addition to analyses conducted for once-burned pixels, unburned pixels, and the entire mapped area. We excluded pixels classified as granite or water from this analysis, leaving four vegetation classes which could transition from one to another: shrubs, sparse meadow, mixed conifer, and dense meadow. We assessed which types of vegetation transitions were overrepresented relative to a null expectation of no difference in transition types, for the entire watershed and based on number of times burned, using a chi-squared analysis (Appendix C). As a basis for comparing the post-fire vegetation landscapes at SCB and ICB (Question 4), we assessed landscape metrics (Appendix C) to describe the heterogeneity of the landscape and spatial distribution of individual vegetation classes in SCB, in both 1973 and 2014, using FRAGSTATS (McGarigal and others 2012) and compared these to values calculated for ICB (Boisramé and others 2017b). At the landscape level, these metrics included the evenness index and the aggregation index, and at the vegetation class level, they included mean, standard deviation, and maximum of patch area, and mean patch fractal dimension.

Question 3: Soil Moisture Variability

Spatially Distributed Soil Moisture Measurements

To assess the drivers of spatial variability in shallow soil moisture, we sampled soil moisture in the field at 40 sites in 2016, 2017, and 2018, which included three sites where we installed temporary weather stations (see below). We measured soil moisture in the top 12 cm of soil using Hydrosense 2 Time-Domain Reflectometer (TDR) probes (campbellsci.com/hs2). We measured most of these sites in both early and late summer of 2016 and 2017. Twenty-nine of these sites were re-measured in June of 2018. In most sites, 25 evenly spaced measurements of soil moisture were made within a 30 m × 30 m grid, with additional measurements

made in heterogeneous sites in order to better capture variability. One-meter-spaced measurements were made across a 30 m transect in sites with obvious strong gradients in soil moisture (for example, wetland sites bordered by dry uplands).

At each site, we categorized the vegetation of the site into one of the four classes used in our imagery analysis ($n = 3$ plots for shrub only, 1 plot for sparse meadow only, 2 plots for dense meadow only, 28 plots for mixed-conifer only, 2 plots split between sparse meadow and dense meadow, and 4 plots split between mixed-conifer and dense meadow). We also quantified slope and aspect, and recorded the presence of burned snags or fire-scarred trees. Sites were georeferenced using handheld Garmin GPSMAP 62nd and 64th devices (horizontal accuracy 3–10 m). We used these geographic positions to extract additional topographic variables that could predict soil moisture (below) from raster grids created using a digital elevation model (DEM) in ArcMap. These variables include topographic position index (TPI; a continuous variable ranging from concave to convex), upslope area (that is, area contributing drainage to the plot), and topographic wetness index (TWI; $\ln[\text{upslope area}/\tan[\text{slope}]]$). To aggregate the 25–30 point moisture measurements made within a sampling site to a scale more consistent with our DEM-created maps of topographic variables, we grouped the within-site measurements for a given sampling date and vegetation cover type and calculated the mean values within each group. These aggregated means were used for all data training and validation, so there is only one measured soil moisture value for any unique combination of site, vegetation, and date.

We analyzed how soil moisture varied across SCB among sampling dates, vegetation types, and other environmental variables, using a random forest model implemented in the R package *RandomForest* (Liaw and Wiener 2002). Specifically, we created the model to predict continuous soil moisture using the following site characteristics: 2014 vegetation type, 1973 vegetation type, measurement year, day of year, elevation, slope, aspect, TPI, upslope area, TWI, year since fire, number of times burned since 1973, maximum fire severity (only available for fires after 1984, from the US Forest Service Pacific Southwest Region Fire Severity Mapping Program) (Miller and others 2009), and distance from nearest stream. This model used the same methods as Boisramé and others (2018). The drivers of soil moisture distribution vary with time since precipitation, with certain local topographic and soil texture factors being more important predictors under dry conditions compared to wet

(Grayson and others 1997; Famiglietti and others 1998). Accordingly, our method includes a variety of local (for example, vegetation cover, slope, aspect) and nonlocal (for example, distance from nearest stream, upslope area) controls, and the use of the day of year as a predictor allows the model to account for late-summer changes in dominant controls, as suggested by Grayson and others (1997).

While information on soil type may have increased this model's accuracy (Famiglietti and others 1998), we did not include soil properties since we did not have verifiable basin-wide soils data that would have allowed us to upscale the measurements to the rest of the watershed. Because random forest is a statistical model, rather than a physically based model, it does not require information about physical soil parameters in order to represent soil moisture, as long as the covariates used are correlated with soil moisture state. Statistical models such as random forest provide multiple benefits, including their ability to fit nonlinear relationships without needing to make (potentially erroneous) assumptions about the relationship between a predictor and the modeled variable (Grömping 2009). However, the model may not perform well when being used to infer conditions outside the range of observations, since there is no guarantee that the fitted relationships hold true for predictor values not included in the model fitting. Although it was not possible to capture the complete range of predictors and their combinations present throughout the watershed, we selected our measurement sites in order to cover as broad a range of conditions as possible (in terms of fire history, vegetation type, water year type, and topography) in order to make the model validation applicable to a wide range of conditions. We cross-validated the model by selecting a subset of measured sites as training data and using the resulting model to predict soil moisture at the remaining measured sites. To compare the drivers of soil moisture at SCB and ICB (Question 4), we examined the ability of a similar soil moisture model trained on ICB data (Boisramé and others 2018) to explain soil moisture variation observed at SCB.

We also used the random forest model to extrapolate our soil moisture measurements to unmeasured areas of the watershed and estimate soil moisture changes due to fire changes. We modeled soil moisture on a 40 m grid across the entire area of the watershed where vegetation was mapped. At each grid point, we used our vegetation maps, fire maps, and the DEM to extract the nee-

ded covariates to run the model. To estimate soil moisture levels in the absence of fire, we modeled soil moisture on the same 40 m grid, with the same covariates, except that we set times burned and fire severity to zero, time since fire to 100 years, and replaced 2014 vegetation cover with 1973 vegetation (because this vegetation represents the watershed's state after years of fire suppression). We then compared these two modeled soil moisture datasets—one with “unburned” conditions and one using contemporary vegetation and fire histories—in order to quantify the change in soil moisture due to fire. This technique assumes that only a negligible amount of vegetation change between 1973 and the present is due to causes other than fire, which is supported by the fact that the largest patches of changed vegetation occur in burned areas (Figure 5D). This method also assumes that our model is able to capture pre-fire conditions accurately, despite the observational data being from burned areas. Although we could not access any completely unburned areas of the watershed for measuring soil moisture, we measured sites that had not burned since 1974 and/or burned only at very low severity; we believe such sites provide reasonable proxies for unburned areas and are therefore appropriate for fitting a model that is meant to simulate both burned and unburned conditions.

Continuous Soil Moisture Measurements

In addition to low-frequency, spatially distributed moisture sampling described above, we addressed Question 3 by measuring in situ, continuous soil moisture dynamics in soils at three weather stations installed in September 2016. The three weather stations are located within 250 m of each other, in an area that was burned once since 1973, by the Williams fire in 2003 (Figure 1), with one weather station each in dense meadow, mixed conifer regeneration and shrubs, and mature mixed conifer vegetation types (see details and visuals in Appendix B). For simplicity, the dense meadow site is referred to as the “wetland,” the shrub/conifer regeneration site as the “shrub” site, and the mixed-conifer site as the “forest” site hereafter.

At these weather stations, we collected data on soil moisture, soil texture, and precipitation (Appendix B). The precipitation record includes rainfall and snowmelt, but not solid-phase snow. Therefore, we augmented our information on snowpack dynamics by recording four visual images of the stations and surrounding area per day using time-lapse cameras (Brinno TLC200), allowing us to

estimate snow depth at each station and derive equivalent water depth (Appendix B). The weather station soil moisture record is substantially complete for the period September 2016–September 2018, with no more than 1.3% of data points missing for a given weather station. However, up to 32% of the precipitation time series was missing in the 2016–2018 period, due to a combination of snowmelt runoff outside of the precipitation gauge, a frozen tipping mechanism, and/or external damage to the tipping bucket and associated wiring from wildlife and extreme weather. To gap-fill missing precipitation data, we used multiple imputation via predictive mean matching (Little 1988) on precipitation observations from the neighboring stations (Appendix B). We also calculated cumulative shallow soil moisture gain between 12 and 60 cm using depth- and time-integrated soil moisture time series (Appendix B). Cumulative soil moisture is a useful metric to gauge how much water shallow soils have received and to approximate precipitation amounts in unsaturated soils (in combination with snowmelt estimates; Appendix B) when the tipping bucket record is missing or not reliable. However, in saturated wetland sites and during periods of steady-state infiltration, cumulative water gain cannot be calculated.

The weather station soil moisture record provides important context for interpreting the spatially distributed soil moisture measurements. Specifically, it allows us to explore relationships between soil moisture at very shallow depths (the top 12 cm as measured in our spatially distributed measurements) and soil moisture throughout the top 1 m. Because soil moisture could behave idiosyncratically across the depth profile (Bales and others 2011), this comparison helped determine whether the spatially distributed measurements across the watershed are reasonable proxies for soil moisture storage and plant available water at greater soil depths. Furthermore, these stations were built and sited in a similar manner to three weather stations at ICB (Table B3) and provide an additional point of comparison between the two basins (Question 4).

RESULTS

Question 1: Forest Composition and Structural Change

Within the 10,120 ha of the SCB watershed where we classified vegetation via remote sensing imagery, 1,240 ha (12%) burned 2–4 times, 3,173 ha (31%) burned once, and 5,707 ha (57%) did not

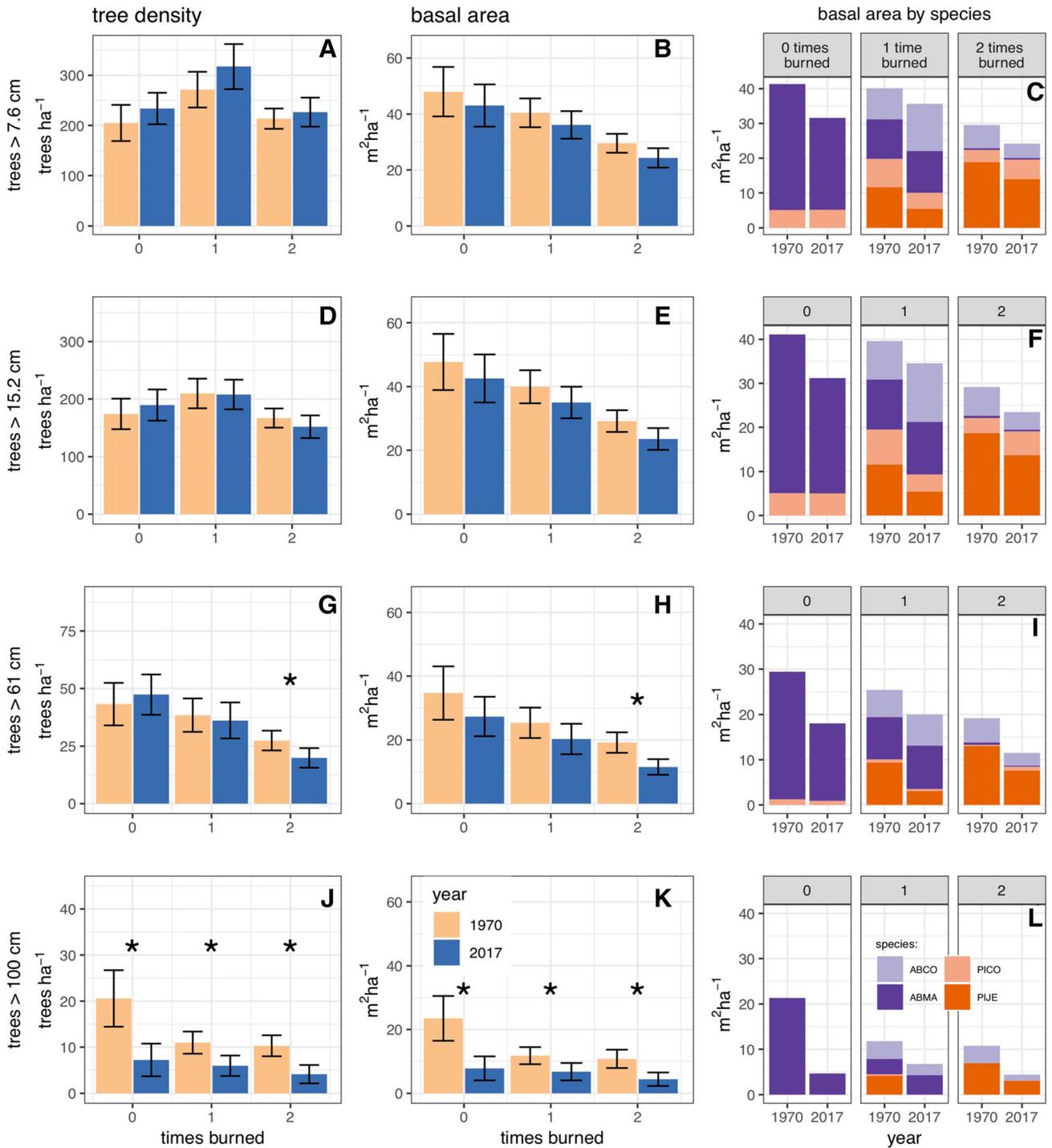


Figure 3. Change in forest structure based on forestry plots. Column 1 shows changes in density, column 2 shows changes in basal area, and column 3 shows changes in composition of the four most common species by basal area fraction (the minor presence of additional species in some plots accounts for the minor height differences between columns 2 and 3). Row 1 is for all trees greater than 7.6 cm, row 2 is for trees greater than 15.2 cm, row 3 is for trees greater than 61 cm, and row 4 is for trees greater than 100 cm. Asterisks in columns 1 and 2 indicate significant differences in the response variable between 1970 (gold) and 2017 (blue). Note the different axis scaling in panels (G) and (J) (Color figure online).

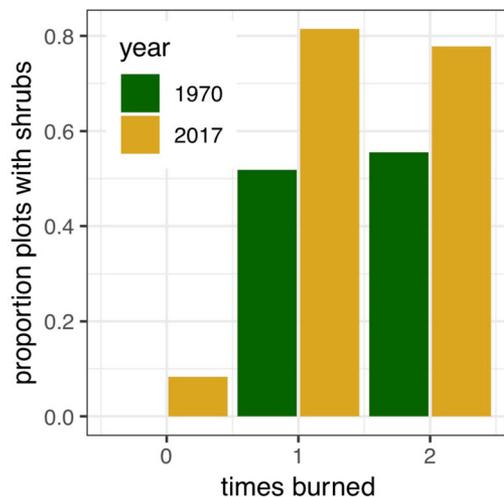


Figure 4. Change in the proportion of subplots where shrubs were detected, from 1970 to 2017, by number of times burned. These data apply to all plots across vegetation type, as in Figure 3.

burn between 1973 and 2014 (Figure 1 inset). Among our 57 forestry subplots, 18 (32%) burned 2–4 times, 27 (47%) burned once, and 12 (21%) did not burn. Increased fire occurrence did not lead to decreases in basal area or density in most size classes (Figure 3). There was a significant influence of fire frequency for large trees greater than 61 cm DBH, where density and basal area in this size class decreased between 1970 and 2017 when burned 2 or more times (Figure 3g, h). This effect of number of times burned was likely driven by trees in the 61–100 cm size class, because for very large trees above 100 cm DBH, there was a significant decrease in density and basal area regardless of fire occurrence (Figure 3J, K). Furthermore, even in plots that had burned twice, total tree density increased, possibly due to post-fire density increases in the fire-intolerant *Pinus contorta*, which increased in basal area over the 47 years (Figure 3C).

The number of times a plot burned was not independent of the forest species composition: even prior to the reintroduction of large managed wildfires in 1973, plots that would eventually burn twice were located in predominantly *Pinus jeffreyi* forest. Plots that would eventually burn once were located in mixed-conifer forest with comparable proportions of *P. jeffreyi*, *P. contorta*, *Abies magnifica*, and *A. concolor*. Finally, plots that did not burn in the 47 years were located in *A. magnifica*-dominated forest (Figure 3C). There was also a strong difference in initial abundance of shrubs in the different forest types, with shrubs being absent in 1970 from all subplots in *A. magnifica* forest that did

not burn in the subsequent 47 years, but present in about 50% of the plots that eventually burned (Figure 4). The reintroduction of even a single wildfire was sufficient to increase shrub abundance to 80% of subplots in 2017 (Figure 4).

Question 2: Vegetation Cover Change

The dominant types of vegetation transitions we observed in the watershed were generally observed similarly across all three burn classes (0, 1, and 2–4 times burned; Figure 5). In particular, transitions from shrub to sparse meadow, mixed-conifer to sparse meadow, and mixed-conifer to shrub were overrepresented compared to the null expectation of no change, both in the watershed as a whole ($\chi^2 = 236$, $df = 15$, $P < 0.001$) and in unburned, once-burned and 2–4 times burned areas ($\chi^2 = 47$, 272, and 88, respectively; all $df = 15$, all $P < 0.001$). However, transitions toward earlier-seral vegetation types, particularly shrub to sparse meadow and mixed conifer to sparse meadow, were more strongly overrepresented in the burned areas than in the unburned areas (Figure C1c-d). Dense meadows did not show a consistent response to fire but in general there was limited dense meadow area to begin with and limited expansion or contraction of this vegetation type in absolute terms (Figure C1).

The magnitude of vegetation type change in SCB was much less than in ICB over a similar period of time (Figure 6). Over roughly four decades, net cover of mixed-conifer at SCB only decreased from 83 to 82%, whereas at ICB it decreased from 81 to 62% (Figure 6). Landscape-scale indices of heterogeneity increased slightly in 2014 compared to 1973, though the changes were much less pronounced than those that occurred in the ICB over a similar time period of repeated wildfires (Appendix C). The major differences in land cover patterns for SCB were that the mean size of conifer patches decreased from 15 to 13 ha (Figure C5a), and sparse meadows experienced small increases in mean patch size (0.38 ha to 0.52 ha; Figure C5c).

Question 3: Soil Moisture Variability

There was variability in spatially distributed soil moisture measurements in SCB, both among vegetation types and to a lesser degree among site visits (Figure 7). Specifically, soil moisture in dense meadows was over 3 times higher than in the other vegetation types (Figure 7). Furthermore, soil moisture in 2017 was higher than in 2016 or in 2018 across all vegetation types (Figures 7, 9), consistent with measurements that 2017 was the

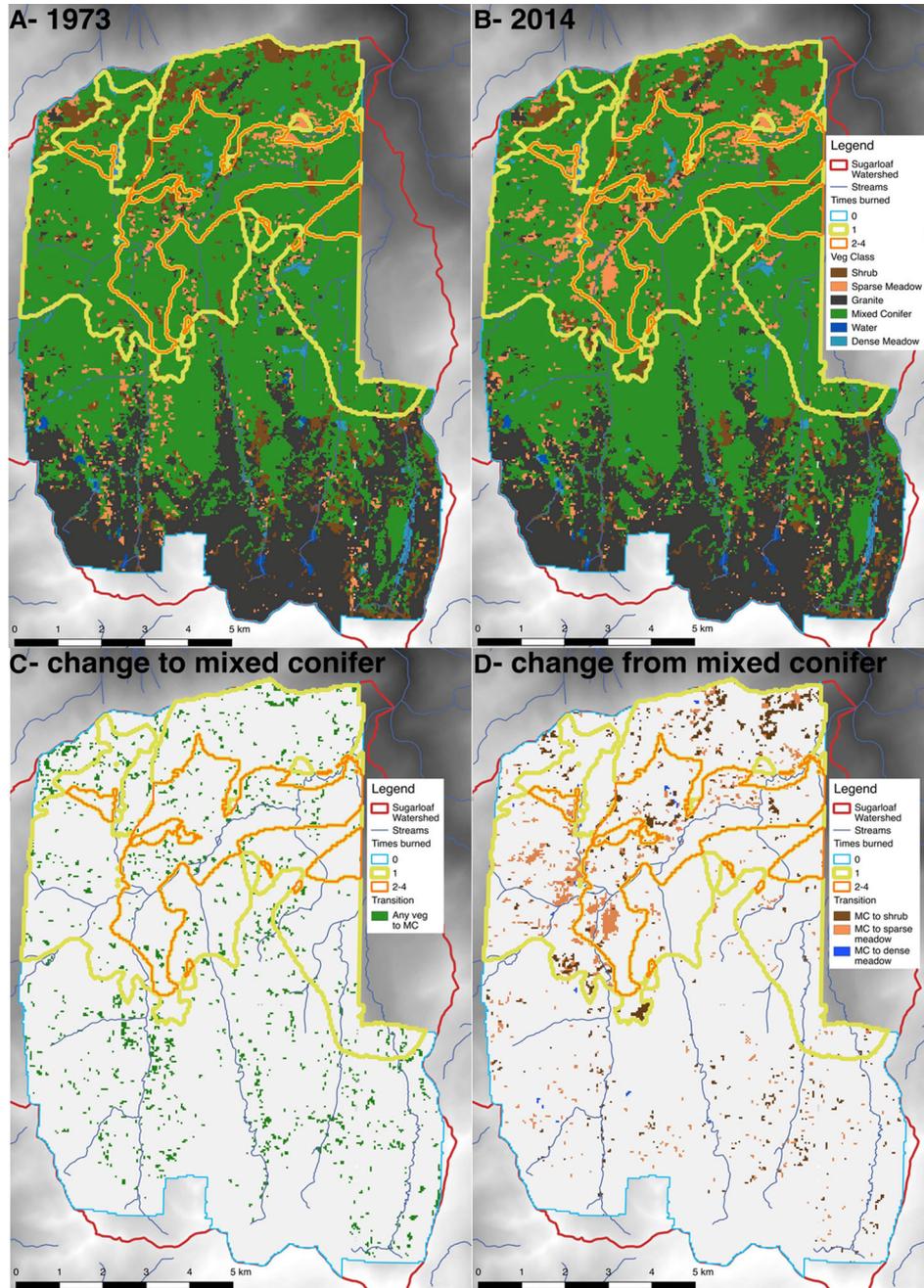


Figure 5. Comparison of classified aerial images from 1973 (**A**) and 2014 (**B**) in Sugarloaf Creek Basin. Perimeters of fires that burned between 1973 and 2014 are shown, aggregated by number of times burned. Four vegetation classes (shrub, sparse meadow, mixed conifer (MC), and dense meadow) are shown, along with granite and water. Transitions from non-forest to MC (**C**) and from MC to non-forest (**D**) are highlighted.

wettest year of the three at our study site and in the southern Sierra Nevada in general (Tables 1, B3).

A random forest model fit to the measured soil moisture (expressed as % volumetric water content; VWC) was able to predict the data with an RMSE of 3.6% VWC and a Pearson correlation coefficient of 0.98. We tested the model's ability to

extrapolate beyond training data: on average, when the model was trained on only 70% of the measured locations, it was able to predict soil moisture at the remaining 30% of locations with an RMSE of 10 and a correlation of 0.82. The relationship between soil moisture and site properties was similar for ICB and SCB, but not identical. In

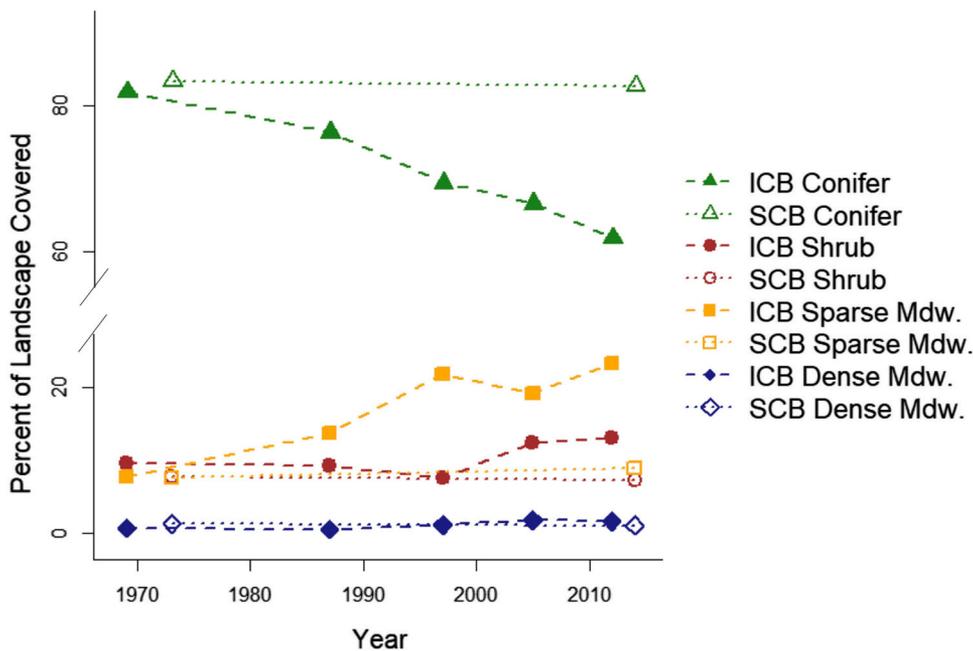


Figure 6. Percent of the total vegetated area covered by each vegetation class for both Illilouette Creek Basin (ICB) and Sugarloaf Creek Basin (SCB).

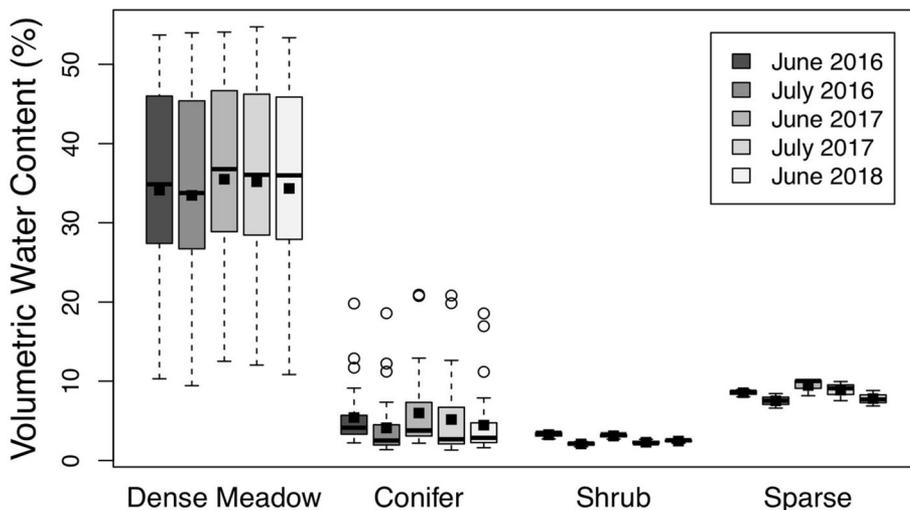


Figure 7. Distribution of modeled soil moisture (in terms of volumetric water content) for each site-date-vegetation class combination, based on the random forests model but not controlling for site-specific variation in topography and other covariates which also influence these modeled values (see Figure D3). Modeled values are binned by date (either June or July of each measurement year) as well as by vegetation class: dense meadow ($n = 9$), conifer ($n = 32$), shrub ($n = 3$), and sparse meadow ($n = 3$). Within each box, the dark horizontal bar denotes the median, while the box spans the 25th to the 75th percentile and dotted bars show the full range of the data. Circles show outliers; black squares show the mean within each bin.

both watersheds, current vegetation type was the most important predictor of soil moisture (Appendix D; Figure D1). The random forest model trained on ICB measurements fit the SCB soil moisture measurements with a correlation coeffi-

cient of 0.82, whereas the model fit to SCB data was able to predict them with a correlation of 0.98 (Figures D4, D5).

The random forest model showed small, but generally positive, changes in modeled June soil

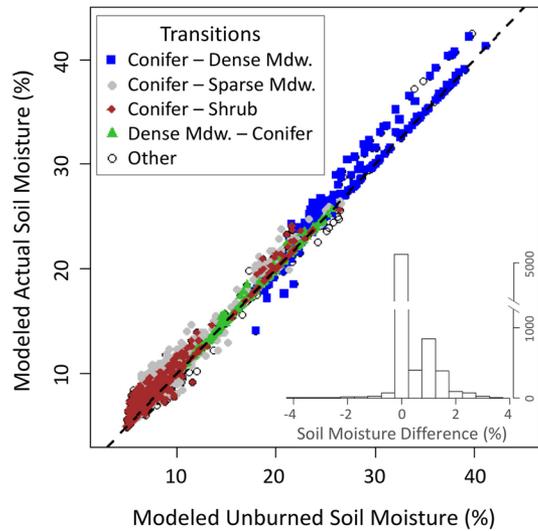


Figure 8. Modeled actual soil moisture (current vegetation cover and fire history) compared to modeled soil moisture assuming the same climatology (date set to early June) but no fire or vegetation change since 1973. The inset shows a histogram of the point-wise differences between these two sets of modeled values. Only locations where vegetation type changed between 1973 and 2014 are shown (see Figure 5). Locations that transitioned from conifer to dense meadow (mdw.) are shown as blue squares, conifer to sparse meadow as gray circles, conifer to shrub as red diamonds, and dense meadow to conifer as green triangles. Other types of transitions are rare (open black circles). Points above the dashed one-to-one line represent locations where the model predicts soil moisture is higher than it would have been without fire (positive numbers in the inset histogram) (Color figure online).

moisture as a result of fire in SCB (Figure 8). These results did not vary with year, but changes were slightly greater earlier in June compared to July or August (data not shown). The largest modeled changes in volumetric water content were less than 5 percentage points (Figure 8 inset), whereas in ICB, a similar model predicted fire-related changes of up to 30 percentage points (Figure D6). Figure 8 also suggests that all areas that transitioned from conifer to dense meadow already had relatively high soil moisture prior to fire, and areas where forests encroached on meadows were relatively dry areas of meadow.

Consistent with the data from spatially distributed soil moisture measurements (Figure 7), continuous weather station records (Figure 9; Appendix B) indicated that the wetland site was associated with the highest soil moisture among the three weather stations, followed by the shrub and forest sites, at all three soil depths measured (12,

60, and 100 cm). All sites experienced greater and more persistent soil moisture during the 2017 WY than the 2018 WY, as a result of large precipitation differences (SCB weather stations were installed in September 2016 at the end of the 2016 WY, so data were not available for that period). The forest stations tended to measure the least amount of precipitation (Table 1) and experience the earliest snowmelt (Figure B3) and had the greatest inter-annual soil moisture differences (Figure 9).

Cumulative shallow soil water gain showed idiosyncratic trends among sites and years (Table 1), although soil type and texture were generally similar between ICB and SCB for each vegetation type (Appendix B). Cumulative soil water gain reflects any detectable increase in VWC of shallow soil; however, it does not always reflect change in storage or availability of water for vegetation uptake. At SCB, cumulative soil moisture gain was greatest at the forest site in 2017 but greatest at the wetland site in 2018 (Table 1). Soil moisture gain at the forest site may be explained by rapid wetting and drying during the snowmelt period in 2017 (Figure 9), possibly due to relatively shallow snowpack (compared to the shrub and wetland sites) experiencing diurnal fluctuations in freezing and thawing. Low values of cumulative soil moisture gain may also be attributable to saturation and/or steady-state infiltration at certain sites, as such conditions preclude additional moisture gains. During the wet 2017 WY, all sites were saturated at 1-meter depth for some period of the year, yet during the drier 2018 WY, only soils at wetland stations experienced saturation. In ICB, the wetland site remained fully saturated for both 2017 and 2018 WYs, whereas in SCB, the wetland site was saturated only for a portion of each year (Table 1). In general, deeper soils contained more water and were saturated longer than shallow soils, whereas shallow soil moisture was more responsive to precipitation, though water input pulses were apparent at 60 and 100 cm depths as well (Figure 9). Very shallow (12 cm) soil moisture was positively correlated with deep (100 cm) soil moisture across sites and years (Table 1).

DISCUSSION

Fire-driven changes in dominant vegetation type (from aerial imagery analysis; Figure 5) and forest structure (from forestry plot data; Figure 3) were minimal at Sugarloaf Creek Basin (SCB), despite over 40 years of managed wildfire and ten fires greater than 40 ha over that time period in the basin. The minimal changes are a notable contrast

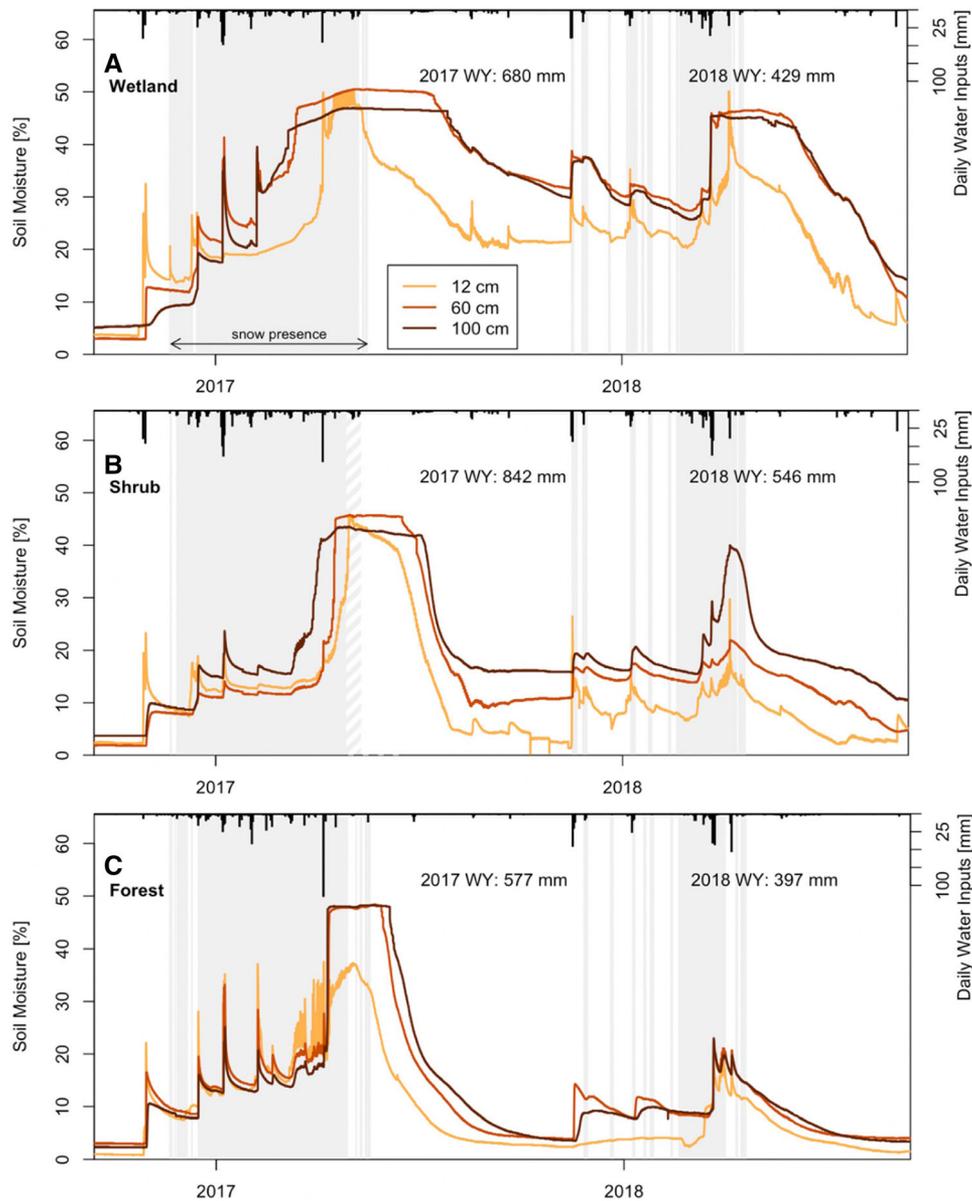


Figure 9. Volumetric water content [%] in shallow (12 cm), mid (60 cm), and deep (100 cm) soils as measured by weather stations located in dense meadow (**A**), shrub (**B**), and forest (**C**) sites. Data were measured at 10-minute intervals for 2017 and 2018 water years. Vertical bars at top of panels indicate daily water inputs in the form of rain and snow melt. Gray regions represent periods of time when snow is present around the base of the weather station (at the shrub station camera data were not available in spring 2017, shown by gray hatching). Water year (WY) summaries are also provided for total water inputs recorded at each station. Refer to Appendix B for visuals of each site.

from the nearby Illilouette Creek Basin (ICB; Figure 6), which had a similar duration of a restored seminatural fire regime yet saw much greater vegetation turnover (even within the first 20 years), heterogeneity of vegetation patches, and soil moisture response (Boisramé and others 2017a; Boisramé and others 2017b; Boisramé and others 2018). A number of potential explanations for this discrepancy exist, including differences in the fire

history of the two basins, and differences in water balance and vegetation productivity between the two basins.

Approximately 5,500 ha (44%) of the 12,500 ha SCB watershed burned at least once and approximately 1,300 ha (10%) of the watershed burned 2–4 times since 1973. Fires were more active in ICB, with 52% of the ICB burning at least once in the same period, and 25% burning 2–4 times. The

number of fires larger than 40 ha from 1973 to 2016 was also much higher in ICB ($n = 27$) than SCB ($n = 10$), and particularly in recent decades, with ICB experiencing 12 fires larger than 40 ha after 1985 (<https://frap.fire.ca.gov/mapping/gis-data/>) and SCB only experiencing 4 (Table A1). Despite a marked increase over the fire exclusion and suppression period (Mallek and others 2013), this comparison with ICB demonstrates that the amount of fire activity in SCB since 1970 may represent a relative lack of fire compared to an expected historical fire return interval (and what is possible under a managed fire regime) over this period, since both ICB and SCB had pre-suppression fire return intervals below 10 years (Collins and Stephens 2007). This low fire return interval may partially reflect recent changes in how the managed wildfire policy has been applied: only 1 ha has burned in the SCB between 2004 and 2017, with 59% of active ignitions suppressed, compared with 7,289 ha burned and only 23% of ignitions suppressed between 1969 and 2003 (Table A1; A. Caprio, personal communication).

The greater emphasis on fire suppression in recent years suggests that additional changes in vegetation cover and forest structure might have been observed had a historical fire return interval been more closely approximated. This is especially true given that the last large fires across the central and eastern portions of SCB were in 1977 and 1985. Although the 2003 fire reburned a portion of the 1985 fire, much of the area affected by the 1985 and 1977 fires has not reburned. This means there is considerable area for which the time since last fire exceeds the historical fire return interval by threefold to fourfold. In addition, the proportion of area burned at high severity (since 1984) is quite small at only 2% of burned area or 69 ha total (Table A1). For comparison, ICB had 1129 ha of area burned at high severity (13% of burned area) from 1984–2016 (B. Collins, unpublished data). Taken together, these points all demonstrate that fires in SCB had much less potential to manipulate vegetation structure and composition relative to ICB.

The predominantly low-severity fires that burned in SCB by definition caused relatively little conversion to alternative vegetation patches (Figures 3, 6), due in part to the range of acceptable fire management conditions. Two of the most recent fires in SCB, the 1997 Sugarloaf Fire and the 2003 Williams Fire, were responsible for the bulk of the larger patches of overstory tree mortality that we detected in our vegetation change analysis (Figure 5; Table A1). These two fires are also in a da-

tabase of fire weather indices that enable comparison to 475 other fires across California in similar mixed-conifer and fir forest (Stevens and others 2017). For maximum high temperature during the burn window, which was the number one climatic predictor of burn severity in this database (Stevens and others 2017), the Williams Fire was in the 9th percentile (23.4 °C) and the Sugarloaf Fire was in the 4th percentile (21.7 °C), indicating mild fire weather conditions.

Although weather conditions for many SCB fires may have been mild, it is also possible that there was reduced fuel accumulation in SCB relative to ICB in the fire-suppression period, potentially due to lower precipitation and productivity in SCB. Three lines of evidence support wetter and more productive conditions in ICB vs SCB: first, in situ weather station data (Table 1) and interpolated PRISM data (Table B3) show higher annual precipitation in ICB; second, streamflow per watershed area is greater in ICB and its encompassing watersheds (Table A2); third, remote sensing analysis revealed greater vegetation productivity in ICB compared with SCB (Figure 2), which is generally correlated with fuel accumulation (Collins and others 2016).

Climatically driven reductions in fuel accumulation rates in SCB could explain differences in alternative vegetation patch sizes post-fire (Appendix C) if tree densities were reduced and less continuous in the drier SCB (for example, Stephens and others 2018). Although similar proportions of both basins were dominated by conifers prior to the reintroduction of managed wildfire (Figure 6), our analysis did not account for potential differences in forest density. Forest densities in the more productive ICB may have increased more during fire exclusion than in SCB, which could have led to larger patches of alternative vegetation once fire was reintroduced. Besides reducing productivity, drier conditions may make the SCB less hydrologically responsive to wildfire-induced changes (Saksa and others *in press*). This is because any additional water that becomes available in a water-limited forest (for example, due to fire-caused tree mortality reducing canopy interception and competition for soil water) is likely to be taken up by the remaining water-stressed vegetation rather than contributing to increased streamflow or soil moisture. For example, Roche and others (2018) found that the Kings Watershed had less post-fire reductions in ET than the American River Watershed, which had higher precipitation and greater post-fire basal area.

Although it is not possible from this study to disentangle the relative contributions of low fire frequency and low productivity to the minimal changes observed in SCB relative to ICB, we found clear evidence of those minimal ecosystem changes from our vegetation patch analysis, our forestry plot analysis, and our soil moisture analysis in response to the restoration of managed wildfire to SCB. With respect to the vegetation patch analysis, the proportional area (Figure 6) and the maximum patch size of areas (Figure C4) converted from forest to non-forest was higher in ICB. For larger high-severity patches to develop, there needs to be a confluence of topography, weather, and fuels sufficient to cause complete tree mortality (Collins and others 2007). Relatively small patches of alternative vegetation are one of the primary goals of managed wildfire (Hessburg and others 2016), so in that respect the fires within SCB may have met some management objectives with respect to the fine-scale heterogeneity on the landscape to improve resilience to the future fires.

With respect to the forestry plot analysis, we did not observe the changes in forest structure from our re-measurement of forestry plots (Figure 3) that we would have expected under managed wildfire (Larson and others 2013). For instance, we observed a uniform decrease in large (>61 cm) and very large (>100 cm) trees, even in unburned red fir forest (Figure 3). This is consistent with long-term trends that have been observed across the western USA (van Mantgem and Stephenson 2007; van Mantgem and others 2009; Das and others 2016) and may be indicative of climate or pest/pathogen influences in addition to fire, which we would not expect to disproportionately target large fire-resistant trees in low-severity burns.

Although large tree density in the forestry plots decreased over time, we observed a slight increase in small (7.6–15.2 cm dbh) tree density regardless of number of times burned (Figure 4A). One of the objectives of managed wildfire is the removal of smaller understory trees, particularly of fire-sensitive species (North and others 2012; North and others 2015), an outcome that has been observed with managed wildfire in other wilderness areas (Larson and others 2013). However, in SCB in twice-burned plots, we saw an increase in species more easily killed by fire (for example, *Pinus contorta*) in smaller size classes (Figure 3C). The four plots that burned twice (Figure 1) were all classified as low to moderate burn severity in the second fire (the initial fire in each case pre-dated remotely sensed burn severity maps). Given the absence of recent fire in the watershed discussed above

(Table A1), the regeneration we observed in the smallest size class (Figure 3A) may have filled in since the fires of the 1980's and late 1990's even if those fires did consume much of the previous regeneration layer, highlighting the importance of repeated fires to continue to regulate fuels and the spatial heterogeneity of fire-prone forests (North and others 2012). The increase in shrubs at all burn frequencies (Figure 4) was expected, as the dominant shrub species of *Arctostaphylos* and *Ceanothus* in this system have fire-cued seed germination (Safford and Stevens 2017).

With respect to the soil moisture analysis, the lack of a strong watershed-wide signal of changing soil moisture is primarily due to (1) minimal detectable differences between forest, shrub, and dry meadow soil moisture profiles when accounting for other moisture drivers (Figure D3c), and (2) the relatively low initial abundance and minimal post-fire expansion of the dense meadow vegetation class (the vegetation type associated with the highest soil moisture; Figures 7, D3c). Both of these factors could be attributable to soil and topographic properties of the watershed as well as precipitation and productivity effects as discussed above. In contrast, within the more productive ICB (Appendix B), pronounced increases in the dense meadow vegetation type were observed following fire (Boisramé and others 2017a; Boisramé and others 2017b). In ICB, there may have been a greater encroachment of trees, particularly *Pinus contorta*, into meadows during the late nineteenth century fire exclusion period. This higher encroachment could be due to the ICB's higher productivity relative to SCB, greater consistency in soil saturation of the SCB meadows (this limiting conifer growth), or a combination of both. Alternatively, climate, topography, and soil type may be constraining meadow locations at SCB more than at ICB, as we observed little dense meadow encroachment into the margins of the existing dense meadows on the rare occasions where those meadow margins burned (Figure 3). It is possible that fire might have greater impacts on soil moisture at shorter time scales; our hydrologic data collection all took place at least a decade following the most recent fire, which could be sufficient time for ET processes (which impact soil moisture) to recover to pre-fire conditions (Roche and others 2018) and highlights the need for repeated fires to truly restore fire-adapted forests.

High correlations between shallow and deep soil moisture during summer months (Table 1) suggest that our spatially distributed soil moisture measurements can reflect conditions in deeper soils.

However, this correlation only captures relative changes over time, not absolute values. In late summer, there was a greater difference between deep and shallow soil moisture at the shrub and wetland stations than there was at the forest station (Figure 9). Therefore, it is possible that transitions from mature forest to more open vegetation cover might lead to greater increases in deeper soil moisture than would be suggested by shallow soil moisture. This could mean that the modeled surface soil moisture changes in Figure 8 may underestimate the total change in plant-available moisture. Findings from the ICB also suggested that the soil moisture impact of forest removal might be larger in deeper soils (Boisramé and others 2018). However, there is high uncertainty regarding the changes to deeper soil water storage, since we cannot determine how broadly these relationships between deep and shallow soils extent beyond the weather station locations.

Similarities in the random forest models trained on ICB and SCB moisture data show that certain variables are consistently strong predictors of soil moisture. For example, vegetation cover type and TWI were within the top 4 most important predictors of soil moisture for both ICB and SCB, with years since fire, times burned, and year of measurement being the least important predictors in both watersheds (Figure D1). However, the relatively poor ability of the ICB-trained model to predict SCB moisture values indicates that the relative importance of these factors for controlling summer soil moisture varies between the watersheds. The extent to which this variation should be attributed to physical and ecological factors in the watershed, and the extent to which it reflects features of the random forest methodology, is not clear given the information available.

CONCLUSION

Our characterization of vegetation change and the hydrologic response following the implementation of a natural fire program in SCB demonstrates the contextual nature of landscape-level fire-ecosystem interactions. Although the nearby ICB is similar to SCB in size, elevation, forest types, and time since establishment of a managed wildland fire policy, assuming similar fire-related changes in SCB would have overestimated fire-driven change in vegetation and in water availability. This discrepancy highlights the importance of the place-based field and imagery datasets that we used in our analysis here. Although the direction of change and predictors of soil moisture were similar for the two

watersheds, the magnitude of change was much lower in SCB, likely due to the interaction between watershed-level productivity and fire effects. In SCB, the lower overall productivity, the reduced fire frequency, and the lesser proportions of high severity fire effects relative to ICB led to greater stability in vegetation over time and a more muted hydrologic response to managed wildfire in SCB. More landscape-level experimentation in other watersheds, including lower elevation sites more productive than ICB, would further clarify the range of possible landscape and hydrologic responses to natural fire regimes.

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REFERENCES

- Atchley AL, Kinoshita AM, Lopez SR, Trader L, Middleton R. 2018. Simulating Surface and Subsurface Water Balance Changes Due to Burn Severity. *Vadose Zone Journal* 17: 13pp.
- Bales RC, Hopmans JW, O'Geen AT, Meadows M, Hartsough PC, Kirchner P, Hunsaker CT, Beaudette D. 2011. Soil moisture response to snowmelt and rainfall in a Sierra Nevada mixed-conifer forest. *Vadose Zone Journal* 10:786–99.
- Bates DM, Maechler M, Bolker BM, Walker S. 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5. CRAN.R-project.org/package=lme4.
- Blaschke T, Hay GJ, Kelly M, Lang S, Hofmann P, Addink E, Feitosa RQ, Van der Meer F, Van der Werff H, Van Coillie FJJop, sensing r. 2014. Geographic object-based image analysis—towards a new paradigm. 87: 180-191.
- Boisramé G, Thompson S, Collins B, Stephens S. 2017a. Managed wildfire effects on forest resilience and water in the Sierra Nevada. *Ecosystems* 20:717–32.

- Boisramé G, Thompson S, Stephens S. 2018. Hydrologic responses to restored wildfire regimes revealed by soil moisture-vegetation relationships. *Advances in Water Resources* 112:124–46.
- Boisramé GFS, Thompson SE, Kelly M, Cavalli J, Wilkin KM, Stephens SL. 2017b. Vegetation change during 40 years of repeated managed wildfires in the Sierra Nevada, California. *Forest Ecology and Management* 402:241–52.
- Boisramé GFS, Thompson SE, Tague C, Stephens SL. 2019. Restoring a natural fire regime alters the water balance of a Sierra Nevada catchment. *Water Resources Research* 55:5751–69.
- CalFire. 2018a. Top 20 largest California wildfires. http://www.fire.ca.gov/communications/downloads/fact_sheets/Top20_Acres.pdf.
- CalFire. 2018b. Top 20 most destructive California wildfires. http://www.fire.ca.gov/communications/downloads/fact_sheet/Top20_Acres.pdf.
- Caprio AC, Graber DM. 2000. Returning fire to the mountains: can we successfully restore the ecological role of pre-Euroamerican fire regimes to the Sierra Nevada? In: Cole, David N.; McCool, Stephen F.; Borrie, William T.; O'Loughlin, Jennifer, comps. 2000. Wilderness science in a time of change conference-Volume 5: Wilderness ecosystems, threats, and management; 1999 May 23–27; Missoula, MT. Proceedings RMRS-P-15-VOL-5. Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 233–241.
- Collins BM, Everett RG, Stephens SL. 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* 2: art51.
- Collins BM, Kelly M, van Wagtenonk JW, Stephens SL. 2007. Spatial patterns of large natural fires in Sierra Nevada wilderness areas. *Landscape Ecology* 22:545–57.
- Collins BM, Lydersen JM, Fry DL, Wilkin K, Moody T, Stephens SL. 2016. Variability in vegetation and surface fuels across mixed-conifer-dominated landscapes with over 40 years of natural fire. *Forest Ecology and Management* 381:74–83.
- Collins BM, Miller JD, Thode AE, Kelly M, van Wagtenonk JW, Stephens SL. 2009. Interactions among wildland fires in a long-established Sierra Nevada natural fire area. *Ecosystems* 12:114–28.
- Collins BM, Stephens SL. 2007. Managing natural wildfires in Sierra Nevada wilderness areas. *Frontiers in Ecology and the Environment* 5:523–7.
- Das AJ, Stephenson NL, Davis KP. 2016. Why do trees die? Characterizing the drivers of background tree mortality. *Ecology* 97:2616–27.
- Ebel BA. 2013. Wildfire and Aspect Effects on Hydrologic States after the 2010 Fourmile Canyon Fire. *Vadose Zone Journal* 12.
- Famiglietti JS, Rudnicki JW, Rodell M. 1998. Variability in surface moisture content along a hillslope transect: Rattlesnake Hill, Texas. *Journal of Hydrology* 210:259–81.
- FRAP. 2017. Fire and Resource Assessment Program. Fire perimeters [Database]. Sacramento, CA: California Department of Forestry and Fire Protection. Available from: http://frap.fire.ca.gov/data/frapgisdata-sw-fireperimeters_download; last accessed 13-March_2019.
- Grant GE, Tague CL, Allen CD. 2013. Watering the forest for the trees: an emerging priority for managing water in forest landscapes. *Frontiers in Ecology and the Environment* 11:314–21.
- Grayson RB, Western AW, Chiew FHS, Blöschl G. 1997. Preferred states in spatial soil moisture patterns: Local and non-local controls. *Water Resources Research* 33:2897–908.
- Grömping U. 2009. Variable Importance Assessment in Regression: Linear Regression versus Random Forest. *The American Statistician* 63:308–19.
- Halekoh U, Højsgaard S. 2014. A Kenward-Roger Approximation and Parametric Bootstrap Methods for Tests in Linear Mixed Models - The R Package pbrtest. *Journal of Statistical Software* 59:1–30.
- Hessburg PF, Spies TA, Perry DA, Skinner CN, Taylor AH, Brown PM, Stephens SL, Larson AJ, Churchill DJ, Povak NA, Singleton PH, McComb B, Zielinski WJ, Collins BM, Salter RB, Keane JJ, Franklin JF, Riegel G. 2016. Tamm Review: Management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. *Forest Ecology and Management* 366:221–50.
- Hijmans RJ, van Etten J. 2016. Raster: Geographic data analysis and modeling. R package version 2.8-4.
- Kinoshita AM, Hogue TS. 2015. Increased dry season water yield in burned watersheds in Southern California. *Environmental Research Letters* 10:014003.
- Larson AJ, Belote RT, Cansler CA, Parks SA, Dietz M. 2013. Latent resilience in ponderosa pine forest: effects of resumed frequent fire. *Ecological Applications*.
- Liaw A, Wiener MJRn. 2002. Classification and regression by random. *Forest* 2:18–22.
- Little RJA. 1988. Missing-data adjustments in large surveys. *Journal of Business & Economic Statistics* 6:287–96.
- 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.
- McGarigal K, Cushman SA, Ene EJ. 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- McKelvey KS, Skinner CN, Chang C, Erman DC, Hussari SJ, Parsons DJ, van Wagtenonk JW, Weatherspoon CP. 1996. An overview of fire in the Sierra Nevada. Status of the Sierra Nevada. Sierra Nevada Ecosystems Project: Final Report to Congress. Volume II: Assessments and scientific basis for management options. Davis, CA: University of California, Centers for Water and Wildland Resources, p 1033–1040.
- Miller JD, Knapp EE, Key CH, Skinner CN, Isbell CJ, Creasy RM, Sherlock JW. 2009. Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. *Remote Sensing of Environment* 113:645–56.
- North M, Collins BM, Stephens S. 2012. Using fire to increase the scale, benefits, and future maintenance of fuels treatments. *Journal of Forestry* 110:392–401.
- North MP, Stephens SL, Collins BM, Agee JK, Aplet G, Franklin JF, Fulé PZ. 2015. Reform forest fire management. *Science* 349:1280–1.
- Parks SA, Holsinger LM, Miller C, Nelson CR. 2015. Wildland fire as a self-regulating mechanism: the role of previous burns

- and weather in limiting fire progression. *Ecological Applications* 25:1478–92.
- Ponisio LC, Wilkin K, M'Gonigle LK, Kulhanek K, Cook L, Thorp R, Griswold T, Kremen C. 2016. Pyrodiversity begets plant–pollinator community diversity. *Global Change Biology*: n/a–n/a.
- Robinson NP, Allred BW, Jones MO, Moreno A, Kimball JS, Naugle DE, Erickson TA, Richardson AD. 2017. A Dynamic Landsat Derived Normalized Difference Vegetation Index (NDVI) Product for the Conterminous United States. *Remote Sensing* 9:863.
- Roche JW, Goulden ML, Bales RC. 2018. Estimating evapotranspiration change due to forest treatment and fire at the basin scale in the Sierra Nevada, California. *Ecohydrology* 11:e1978.
- Safford HD, Stevens JT. 2017. 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. Albany, CA: USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-GTR-256.
- Saksa PC, Bales RC, Tague CL, Battles JJ, Tobin BW, Conklin MH. in press. Fuels treatment and wildfire effects on runoff from Sierra Nevada mixed-conifer forests. *Ecohydrology*: e2151.
- Stephens SL, Agee JK, Fulé PZ, North MP, Romme WH, Swetnam TW, Turner MG. 2013. Managing forests and fire in changing climates. *Science* 342:41–2.
- Stephens SL, Collins BM, Biber E, Fulé PZ. 2016. U.S. federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere* 7: e01584–n/a.
- Stephens SL, Stevens JT, Collins BM, York RA, Lydersen JM. 2018. Historical and modern landscape forest structure in fir (Abies)-dominated mixed conifer forests in the northern Sierra Nevada, USA. *Fire Ecology* 14: art.7.
- Stephenson NL. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* 25:855–70.
- Stevens JT, Collins BM, Miller JD, North MP, Stephens SL. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. *Forest Ecology and Management* 406:28–36.
- Stoof CR, Vervoort RW, Iwema J, van den Elsen E, Ferreira AJD, Ritsema CJ. 2012. Hydrological response of a small catchment burned by experimental fire. *Hydrol. Earth Syst. Sci.* 16:267–85.
- van Mantgem PJ, Stephenson NL. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters* 10:909–16.
- van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fulé PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323:521–4.
- van Wageningen JW. 2007. The history and evolution of wild-land fire use. *Fire Ecology* 3:3–17.
- Westerling AL, Swetnam TWJE. 2003. Transactions American Geophysical Union. 2003. Interannual to decadal drought and wildfire in the western United States. *EOS, Transactions American Geophysical Union* 84:545–55.
- Wine ML, Cadol D. 2016. Hydrologic effects of large southwestern USA wildfires significantly increase regional water supply: fact or fiction? *Environmental Research Letters* 11:085006.